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2D:4D

- ▶ Digit Ratio
- ▶ John Manning

A Man of Stature

- ▶ Big Man

Abhorrence

- ▶ Disgust

Ability and Willingness of Victim to Retaliate

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Synonyms

Avenge; Penalize; Punish; Revenge; Strike back

Definition

Action taken in return for an injury or offense.

Introduction

The concept of retaliation has historically been defined from both a behavioral and functional aspect. At its core, retaliation is based upon the premise of inciting organisms to increase benefit while reducing cost to oneself (McCullough et al. 2013). If a target organism can emit the potential ideal for retaliation toward an aggressor organism (typically in the form of retaliation itself), the target organism may increase its chances of lifetime productivity and may continue to evolve due to this willingness to retaliate. In other words, by making the potential costs of harm too high for an aggressor (imminent retaliation), the target organism is more likely to survive by avoiding harm against oneself.

Definitions that have previously influenced academics in the conceptualization of retaliation have typically been defined from a functional prospective. The *Oxford English Dictionary* defines revenge as both an act and a desire. To be more specific, Govier (2002) wrote “When we seek revenge, we seek satisfaction by

attempting to harm the other [persons] as a retaliatory measure” (p. 2). Additionally, Uniacke (2000) also noted that “revenge is personal and non-instrumental: with revenge we seek to make people suffer because they have made us suffer, not because their actions or values require us to bring them down” (p. 62). Finally, scholars within the social sciences have further defined retaliation as “the intention to see the transgressor suffer” (Schumann and Ross 2010, p. 1193) along with a plethora of definitions focused upon retaliation being offered as a response to a violation and/or infliction of harm upon a person or one’s property (Govier 2002). However, for this entry, the use of McCullough et al. (2013) definition will be used. They purport retaliation to be a “deterrence system designed to change other’s incentive regarding the self.” In other words, in order to survive, *Homo sapiens* have developed cognitive adaptations specifically designed to utilize the benefits of retaliatory behavior.

Evolutionary Benefit of Retaliation

Many scholars believe retaliation evolved for three adaptive purposes. First, the possibility of retaliations’ ability to directly deter would-be aggressors. Secondly, if an aggressor chooses to harm another individual, retaliation may be a source of penalization for the transgressor’s wrongdoing. Lastly, retaliation encourages societal cooperation by discouraging aggressors from taking advantage of other individuals within their societal unit.

Benefit of Direct Deterrence

As previously noted, the first benefit of retaliatory action developed within many species is the ability for an organism to alter an aggressor’s behavior and ultimately prevent initial and/or future incidents of harm. In other words, if the costs of harming another organism become too high (greater than the benefits), then an aggressor may reconsider his/her actions and desist his/her aggressive behavior (Govier 2002).

Specifically, some scholars purport the evolution and adaptation of retaliatory behavior as

a direct means to provide additional costs for individuals who may seek to engage in harmful behavior, therefore, directly deterring a would-be transgressor from targeting persons who are willing to provide retaliatory impositions. In other words, a victim who is willing to retaliate (i.e., economically, socially, legally) against his/her aggressor is less likely to experience initial or future harm due to the high cost victimization would require from the aggressor. Therefore, the adaptive retaliate systems provide the benefit of increasing lifetime productiveness for would-be victims (Govier 2002). Through direct deterrence, academics believe that when an aggressor has made the decision to inflict harm, an individual who has a history of retaliation or is believed to be willing to retaliate is less likely to be chosen as a potential victim (Shumann and Ross 2010). In other words, a potential victim’s willingness to retaliate may change an aggressor’s incentive to inflict harm.

Empirical evidence in concert with the concept of direct deterrence lies within economic games (i.e., sequential and iterated prisoner’s games) (Axelrod 1984). For example, in sequential games, only a single round of interaction is played with options of cooperation or defection being allowed. However, the second player in the round makes his/her move only after viewing the first player’s initial selection. Research indicates that the second player is more likely to make a defective choice if the initial player begins by choosing the same. Alternatively, if the first player makes the decision to cooperate as his/her first choice, the second player is also more likely to choose the choice of cooperation (Hayashi et al. 1999). In addition, iterated prisoner’s games involving multiple rounds of play either with the same partner or with different partners also found that inmates almost always counter defection with defection (Bixenstine and Wilson 1963).

Additional experiments within social psychology have also discovered the ability for retaliatory action to directly deter a potential aggressor. In a study conducted with undergraduate males, Diamond (1977) found that participants who believed they could harm their instigator without retaliation were more likely to provide stronger punishments

(shocks) to the individual whom they believed had wronged them. However, participants who believed their actions could be avenged after inflicting harm upon the confederate were not as quick to retaliate.

Further evidence in support of the potential for direct deterrence indicates that retaliatory behavior may also be incited by others known to the victim. For instance, a domestic violence study conducted in Madrid, Spain, concluded that women with more male relatives (especially located within close proximity) were less likely to be victims of domestic violence (Figueredo 1995). These findings are believed to result from a protective and retaliatory effect against harm. In other words, even if a victim is not willing to provide retaliatory behavior by his/her own hands, knowing individuals who may be willing to retaliate against an aggressor on behalf of a potential victim still increases the costs of exploitation/harm beyond any potential benefit allotted to the transgressor.

Benefit of Penalization for Wrongdoing

Secondly, retaliation as a source of penalization for wrongdoing has also been found to be psychologically beneficial for *Homo sapiens* victims. For instance, Adams (1965) found that participants reported feelings of distress when they felt treated unfairly or wronged by another individual. Therefore, the act of retaliation may result in a reduction in an individual's distress level if the individual believes equality to the situation can be restored. In addition to retaliation among *Homo sapiens*, retaliatory action has also been found to be a form of punishment among nonhuman organisms as well (Clutton-Brock and Parker 1995). In support of this ideal, Clutton-Brock and Parker (2005) believed that victim retaliation would produce productiveness gains for the avenging organism by reducing the likelihood that the aggressor would repeat the harmful actions to the organism in the future, thus, increasing a victim's odds for survival.

Benefit of Deterring Third-Party Aggressors

In addition to the potential benefits of direct deterrence and correcting wrongful action, retaliatory

behavior may also be beneficial in the deterrence of third-party aggressors. Scholars believe the expression of aggression by an individual which signals an avenger's potential for retaliation could potentially deter potential third-party aggressors. Historically, *Homo sapiens* have lived in small bonded units without the protection of larger governing bodies; thus, a reputation for a willingness to retaliate against interpersonal harms may have been a vital component to the protection of the unit (Govier 2002). Moreover, violence in the name of honor and the use of violent retaliation has historically been well documented by researchers (McCullough 2008; McCullough et al. 2013). Therefore, the reputation of retaliatory action appears to have been evolutionarily vital to the survival of the primitive family unit.

In concert with the premise of retaliation as an adaptive feature for the promotion of reputational concerns, cognitive studies have found the mechanisms associated with retaliation to be responsive in the presence of third parties. For instance, laboratory studies have found that victims retaliate more vehemently when third parties are present, communicate with the victim that he/she is aware of the injustice, and tell the victim he/she looks powerless as a result of the aggressor's actions (Kim et al. 1998).

Conclusion

Alternative to these three potential benefits associated with retaliation is the potential costs (for both aggressor and avenger) associated with avenging behavior. While retaliation may result from the intention to encourage cooperation, instances of counter-revenge and feuding have also been noted (Kim and Smith 1993). For instance, while an avenger may view retaliation as an equalization of intent, the initial transgressor may consider the action excessive and, thus, feel the need to retaliate against the avenger (Govier 2002). This form of revenge and counter-revenge may result in a perpetuating cycle of aggressive and/or violent behavior. Since retaliatory action may result in additional costs to an organism, individuals who feel they have been wronged

may seriously weigh both the potential costs and benefits before asserting retaliatory action. Due to the potential for further harm by an aggressor who feels the need for counter-revenge, the initial avenger may choose to reject personal retaliation and pursue additional legal channels to attain justice.

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Cross-References

- ▶ [Altruism](#)
- ▶ [Altruistic Punishment](#)
- ▶ [Sex Differences in Ability to Assess Fighting Ability](#)

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Ability to Recognize Individuals

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Synonyms

[Individual recognition](#), [Individual discrimination](#), [Face recognition](#)

Definition

The ability to recognize individuals is a highly advantageous skill for social living species. Although not always clear, an important distinction in the literature is that between individual discrimination and individual recognition. Individual discrimination is the ability to differentiate one individual from all the rest, whereas individual recognition is the ability to differentiate each individual from every other individual and is the most precise form of recognition (Beecher 1989). This entry discusses the evidence for the recognition of conspecific individuals in nonhuman animals, specifically through the auditory and visual systems.

Introduction

Studying nonhumans provides important insight into the evolution of human sociocognitive skills,

such as individual recognition. As in human societies, most social species live in groups that are structured by kinship, dominance, and reproductive status (Smuts et al. 1987), making the ability to recognize others critical to navigating their social world. Animals may use olfactory, auditory, behavioral, or visual cues to recognize others. As much of the research has been conducted in the auditory domain, research on vocal recognition is first discussed briefly. Then, because most social living animals, particularly mammals (including humans), are highly reliant on vision, the majority of the text will focus on recognition within the visual domain.

Of course, there are many different types of recognition, including the recognition of one's own species, kin recognition (see entries on ► “[Kin Recognition](#)” and “[Kin Classification Systems Support Kin Recognition](#)” for more information), the recognition of familiar versus unfamiliar individuals, individual recognition, the recognition of sex, age, and so on. Individual recognition is the most precise form of recognition. Therefore, the discussion will center on individual recognition within one's own species or the ability to discriminate one particular individual from every other conspecific individual. Individual recognition underlies many sociocognitive processes, facilitates group cohesion, and is prerequisite for more complex behaviors such as reconciliation (see ► “[Reconciliation](#)”). This implies that there was strong evolutionary pressure in group-living species to individually recognize others and remember those with whom they have interacted.

This entry will focus on the nonhuman primate (NHP) literature because we ourselves are primates and, thus, the majority of research on individual recognition in animals has focused on NHPs (although see section “[Face Recognition in Non-primates](#)” for evidence in other species). Moreover, some researchers have posited that social problems may have been the most cognitively complex problems that humans may have faced in our recent evolutionary history, and this may help explain our large brain to body ratios compared to the rest of the animal kingdom (e.g., Byrne and Whiten 1988). Thus, NHPs provide us with the opportunity to study the evolutionary

function of human sociocognitive skills and visual perception within a comparative framework. Studying other NHPs allows us to determine whether a particular trait is shared with humans due to common evolutionary history (i.e., homology) or due to shared evolutionary pressures (i.e., convergence).

Auditory Recognition

A large portion of the research examining the ability to recognize individuals has been conducted in the auditory domain, primarily through playback experiments in which researchers record naturally occurring vocalizations and then play the prerecorded stimuli back to subjects in order to gauge the subjects' responses to novel situations or in order to reproduce events that may occur naturally. Playback experiments designed to help elucidate the ways in which NHPs classify each other have found evidence that NHPs recognize their infants, more distant kin, and their neighbors (e.g., Cheney and Seyfarth 1990; Rendall et al. 1996).

For instance, a study conducted on wild vervet monkeys (*Cercopithecus aethiops*) played the scream of a 2-year old juvenile in the presence of its mother and two other adult females (who had offspring of their own) while they were separated from their offspring. The mother of the juvenile responded more quickly than control mothers, looking and approaching the speaker from which the call originated, indicating that vervet monkeys recognize their infant as distinct from other infants. Furthermore, it was noted that the control females responded by looking at the infant's mother, often before the mother made any movement. The anticipatory behavior of the control females suggests that they recognized the relationship between the screaming juvenile and its mother (i.e., third party relationship; Cheney and Seyfarth 1990).

Other evidence in the auditory domain indicates that the ability to recognize individuals may go beyond immediate kin. Rendall and colleagues (1996) first found that adult female rhesus macaques (*Macaca mulatta*) responded faster and

looked longer towards the origin of matrilineal kin calls compared to non-kin, suggesting that they were able to discriminate the calls of matrilineal kin from non-kin. Following this, they implemented a habituation-dishabituation paradigm to test for individual recognition. In this paradigm, subjects typically experience a series of habituation trials during which an exemplar of the stimulus class is repeatedly presented, in this case, various calls of one matrilineal relative. Following habituation, the test stimulus of either the same or different class is presented, such as the call of a second matrilineal relative. A significant difference in response (dishabituation), such as a longer looking time, is taken as evidence that the subject judged the two types of stimuli as different. Following habituation in this study, females responded significantly more to the call from the second matrilineal relative, suggesting vocal recognition at the individual level.

There is also evidence that vocal recognition may extend beyond the boundaries of the group. For example, vervet monkeys reacted more strongly to the calls of individuals from a neighboring group when the calls originated from an inappropriate territory compared to when the calls originated from within the groups' typical territory. This implies that the monkeys had expectations about where those individuals should be (Cheney and Seyfarth 1990).

Many of the studies described above have been taken as evidence for individual vocal recognition. However, for individual recognition to take place, subjects must not only recognize a call as familiar but also perceive that it belongs to a specific individual (Beer 1970). Although it is certainly possible that individual recognition occurred in the aforementioned studies, subjects may have categorized the vocalizations at a more general level rather than identifying each of these individuals specifically. For instance, mother-offspring recognition may simply involve discrimination between one's own offspring from all others. This should be considered discrimination, rather than individual recognition. Moreover, the discrimination of one's own offspring or kin from all others may occur through signature cues such as family specific acoustic cues.

Likewise, the recognition of group mates may simply involve the discrimination of familiar versus unfamiliar vocalizations. In the case of the vervet monkeys, vocal recognition of neighbors may reflect an association between a familiar neighbor's sound and its familiar location.

Thus, while these studies present behaviors that seem to indicate individual recognition, controlled laboratory studies that manipulate the exposure to stimuli allows researchers to better evaluate the importance of particular features and how such information is organized in the brain. To date, however, the majorities of laboratory studies have focused on how animals perceive, process, and organize nonsocial information. The few experimental studies that have employed social stimuli to examine how animals acquire complex social knowledge have primarily been conducted in the visual domain (although intermodal studies are notable exceptions, e.g., Adachi and Hampton 2011).

Visual Face Recognition in Nonhuman Primates

Much of the research on visual recognition has employed two-dimensional photographs as experimental stimuli in place of real-life objects to assess human and nonhuman sociocognitive processes. The use of photographic stimuli is more reliable than presenting real objects or individuals because it allows researchers to manipulate subjects' exposure to social information, helping rule out alternative hypotheses. Moreover, the use of photographs provides controlled investigation of image qualities such as brightness, contrast, viewpoint, and so forth. A number of studies have used indirect measures, such as looking time duration or habituation-dishabituation procedures, to examine individual recognition in the visual domain; however, some have used more objective measures, requiring subjects to make a direct response in the task. Although studies that require an objective response from subjects tend to require more extensive training, these studies provide conclusive results for individual recognition, particularly the perception and recognition of faces. Faces are

a highly salient class of visual stimuli as they provide primates, both human and nonhuman, and perhaps other species as well (discussed below) with valuable social information such as the age, sex, individual identity, and the emotional state of others (for reviews see Bruce and Young 1998; Leopold and Rhodes 2010; Parr 2011). Thus, the ability to individually discriminate faces and use the information present in faces likely played an important role in primate evolution.

Neurological Evidence

Within the primate order, the majority of neurological, developmental, and behavioral research suggests a common evolutionary route for the visual recognition of faces. First, growing evidence indicates that at least some species of non-human primates possess a face processing system that shares similar neural underpinnings with humans. From a large body of behavioral and neurological data, we know that humans possess a specialized mechanism for face processing (see Tsao and Livingstone 2008, for a review). Functional magnetic resonance imaging (fMRI) studies in humans have revealed a system of face-selective areas in the inferotemporal (IT) cortex that are involved in face recognition, including (but not necessarily limited to) the fusiform face area (FFA), the occipital face area (OFA), and an area of the superior temporal sulcus (STS-FA). These areas may be specialized for different functions. For example, the FFA is thought to be involved in processing identity, whereas the OFA is involved in processing face parts and the STS-FA appears to respond selectively to emotional expression and eye gaze and therefore is thought to be involved in the processing of changeable aspects of the face (Tsao and Livingstone 2008).

Electrophysiological studies in rhesus macaques have found regions in the rhesus macaque brain similar in number and relative size to those in humans. Neurons in the STS of the temporal cortex respond to a variety of human and monkey faces, changes in facial expressions, eye gaze, and facial orientation (Tsao and Livingstone 2008). These findings suggest certain

homologies between cortical areas in the human and monkey brain suggesting a common neural mechanism for face recognition in primates. Although this may be true for at least some primate species, it is unclear whether a common face-processing system exists for all primates. That is, a basic structure from which species specializations may have evolved.

Behavioral Evidence

The behavioral evidence for a common face recognition system among primates has been mixed. For instance, it is unclear to what degree NHPs rely on second-order configuration, which refers to the relative spatial arrangement of facial features unique to each individual that are thought to provide the information necessary for individual face recognition in humans. Humans incorporate both the basic configuration of the components of a face (i.e., the eyes, which are above the nose, which are above the mouth), or first-order configuration cues, and second-order configuration cues (e.g., the relative spacing and positioning of facial features) into a single perceptual whole through a fast-acting process referred to holistic processing. This is exemplified by the inversion effect, in which humans are slower and less accurate in recognizing faces (but not objects) when they are presented in an upside-down orientation compared to an upright orientation, due to the disruption of holistic processing (Valentine 1988). Holistic processing (and the inversion effect) is often taken as evidence that face processing is different from nonface object processing in that faces are represented as a whole rather than as a combination of component parts (eyes, nose, mouth) and the relations between them.

Yet, behavioral evidence of the inversion effect in NHPs is mixed. In chimpanzees (*Pan troglodytes*), the inversion effect seems to be dependent upon expertise, such that chimpanzees demonstrate the inversion effect for human and chimpanzee faces but not capuchin faces or cars (Parr 2011; see also Tomonaga et al. 1993). However, this does not seem to be the case for monkeys (Parr 2011). Thus, it is possible that the inversion effect may reflect one facet of face processing (i.e., holistic processing) that is an adaptive

specialization of the face recognition system of apes and humans, yet further work is needed to rule out the possibility that differences in methodology contributed to inconsistent results. Comparative research on the inversion effect outside the primate order would also be helpful in elucidating the role of holistic processing in face recognition abilities.

On a more general level, behavioral research on NHPs' ability to individuate conspecific faces have provided relatively consistent results. One of the most direct ways to evaluate NHPs' ability to individuate faces is to present them with a task in which they must match the same individual across different viewpoints. This task helps rule out the possibility that subjects are relying on irrelevant perceptual features specific to each photograph, such as symmetry or lighting, to discriminate the stimuli and thus provides additional evidence that face recognition is distinct from basic visual processing. Accordingly, positive results obtained from studies employing paradigms that require direct responses from subjects are generally accepted as evidence for individual recognition (see Parr 2011, for a review). Using this type of methodology, all of the species tested thus far, including chimpanzees, orangutans (*Pongo spp.*), rhesus macaques, crested macaques (*Macaca nigra*), and capuchin monkeys (*Cebus apella*), have demonstrated the ability to discriminate conspecific faces (Micheletta et al. 2015; Parr 2011; Talbot et al. 2015, *in press*).

Previous studies typically examined this ability using unfamiliar faces; however, many of the more recent studies have included familiar facial stimuli as well. The majority of these studies have found differences in performance based on familiarity, suggesting that experience with, exposure to, and the familiarity of faces may play a critical role in influencing face recognition. In humans, changes in lighting, facial expression, or viewpoint of the facial stimuli impair the ability to recognize unfamiliar, but not familiar, faces (Bruce and Young 1998). Likewise, chimpanzees, orangutans, and capuchin monkeys all performed better when individuating familiar conspecific faces across viewpoints compared to unfamiliar

conspecific faces (Parr 2011; Talbot et al. 2015, *in press*). However, one Old World monkey, the crested macaque, discriminated familiar and unfamiliar faces equally well (Micheletta et al. 2015).

The fact that this effect has been observed in New World monkeys, but not Old World monkeys, which are more closely related to Hominoids (apes), suggests one of three possibilities. First, it may have been present in the common ancestor of Hominoids and New World primates but was subsequently selected against in Old World primates. However, this seems improbable given the presumed benefits of recognizing familiar individuals and because traits tend to be preserved in all of the descendants of a common ancestor unless there were strong selective forces working against the trait. To date, we have been unable to identify such a pressure in Old World monkeys.

A second possibility is that the familiarity effect is a convergent trait of the face-processing system, affected by selective social pressures, with species that live in larger, more complex social groups exhibiting greater nuances in face perception. However, this seems unlikely for several reasons. First, crested macaques live in large multi-male, multi-female groups of up to 100 individuals, whereas tufted capuchins groups are significantly smaller, ranging in the teens to low twenties in size. Second, orangutans, a species that only recently became a primarily solitary species, also exhibit the familiarity effect (Talbot et al. 2015), suggesting that once the effect is established, there does not seem to be sufficient selective pressure for losing it. It may be that the face recognition system evolved in the primates and is maintained despite the diversity in social group size and organization, indicating that current group size or organization is not the key feature.

A third possibility is that differences in methodology may have impacted results. The classic methodology for experiments requiring training calls for the use of novel test stimuli to be presented a limited number of times. In tests of individual recognition, therefore, each individual should only be presented once or twice in order

to evaluate any potential differences in spontaneous discriminations as a function of familiarity with those individuals, not the test stimuli themselves (Talbot et al. [in press](#); Thompson [1995](#)). However, in the NHP face recognition literature, there is a trend to adapt a loose definition of “novel,” in part due to the scarcity of high-quality photos that met criterion for testing. For example, new photos of the same individuals observed in training are often used during testing, and/or subjects are repeatedly presented with the same stimuli. Although this is a difficult standard to achieve, the novelty of both the photos and the novelty of the individuals represented in those photos is imperative for a true transfer test. Otherwise, it is impossible to rule out nonconceptual factors, such as memorization of the training stimuli, to explain subjects’ performance. Overall, current evidence indicates that despite apparent differences among species, the familiarity effect is nonetheless a widespread phenomenon observed in many species that exhibit individual recognition.

Developmental Evidence

Much evidence shows that faces are highly salient social stimuli for humans and NHPs from a very early age. Infants orient more towards face-like patterns compared to nonface-like patterns (Pascalis and Kelly [2009](#)). These “face-like patterns” can be as simple as three dots arranged in a triangular fashion, reflecting the basic arrangement of the eyes above the nose, which is above the mouth, which is referred to as first-order configuration. First-order configural cues are important for identifying faces at the categorical level, that is, discriminating faces from nonfaces. Both human and NHP infants demonstrate a preference for faces even when they have never seen a face. In a particularly telling study, infant Japanese macaques (*Macaca fuscata*) raised in an enriched, but face-deprived, environment for 6–24 months demonstrated a preference for both human and monkey faces over other complex visual stimuli, indicating an innate preference for first-order configural cues (Sugita [2008](#)).

Still, other developmental evidence corroborates the importance of familiarity and the role of

exposure on individual face recognition. In particular, evidence suggests that early exposure to faces during a critical developmental period may fine-tune cortical networks to become specialized for the prototypical face to which an individual is exposed. Following a face-deprivation period, infant Japanese macaques preferred to look at and selectively discriminated the species that it was first exposed to (either human or conspecific faces). Likewise, 6-month old human babies discriminated both human and monkey faces, but at 9 months of age, they only discriminated human faces. These results elucidate the role of experience in the development of the “species-specific effect,” which has been likened to the “other race effect” in which it is easier to recognize members of one’s own ethnic group or species, or, perhaps more accurately, to the prototypical face to which one is frequently exposed (see Pascalis and Kelly [2009](#), for a review).

There is evidence in humans and NHPs that the species-specific effect and the other-race effect can be reversed with appropriate experience. For example, a classic study found that rhesus macaques exhibited a species-specific effect in which they discriminated conspecifics, but not domestic animals, yet after several months of exposure to the domestic animals, the macaques could discriminate them as well (Humphrey [1974](#)). Korean children reared exclusively with Koreans and later adopted by Caucasian families between the ages of three and nine demonstrated the same own-race effect as Caucasians exhibit as adults, suggesting that this effect may be reversible with experience (Sangrigoli et al. [2005](#)). Moreover, children as young as 3 months old demonstrated the other-race effect, yet, short-term exposure to other-race stimuli was sufficient to cancel this effect (Sangrigoli and Schonen [2004](#)). Taken together, these studies suggest that experience with and exposure to faces greatly influences face processing both within and across species. In addition, there may be a critical period during early development during which the face processing system undergoes perceptual narrowing, but with appropriate exposure this is reversible to a certain extent.

Face Recognition in Non-Primates

Face recognition is by no means limited to the Primate order, but compared to human and NHPs, less is known about whether other animals discriminate and process faces and the underlying cognitive and neural processes by which they may do so. Although the literature on individual recognition in non-primate species is still relatively nascent, growing evidence across the animal kingdom suggests that individual recognition and face recognition, in particular, may not be as rare as once thought.

Similar to humans, sheep (*Ovis aries*) prefer conspecific faces to heterospecific faces, and familiar faces to unfamiliar faces. Using facial cues alone, sheep discriminated between different species, and, within their own species, the breed and sex of conspecifics. Sheep can learn to discriminate individual faces of adult sheep and can remember up to 50 familiar faces over a period of 2 years. However, individual discrimination is poorer on young lambs and unfamiliar individuals. Moreover, sheep rely on configural cues for the recognition of familiar faces, like humans and most NHPs. Neurological evidence suggests that primates and sheep may share similar neural pathways. The temporal cortex of the sheep brain contains cells that respond selectively to faces compared to other visual stimuli. The responsiveness of particular categories of these cells varies based on dominance (the size of horns), familiarity, breed, and potential level of threat (see Tate et al. 2006, for a review). Collectively, these studies provide strong evidence for a similar face processing system in sheep and primates, with the notable exception that particular groups of face-selective cells have specialized functions that are of social and ecological relevance to each species.

In birds, much of the evidence for visual individual recognition is tangential. For instance, rooks (*Corvus frugilegus*) are social corvids that live in large colonies and form long-term social bonds, suggesting that they have a strong possibility of recognizing group members individually (Emery et al. 2007). Yet, evidence of individual

recognition in this species is lacking. Bird and Emery (2008) presented rooks with a strongly affiliated conspecific and an unfamiliar conspecific through multiple modalities (including live, video, and static images) and found that rooks preferred to look at their affiliated conspecific over an unfamiliar conspecific when videos and live stimuli were used. From this evidence, the authors concluded that rooks recognize the individuals in the video. However, this should not be taken as evidence of individual recognition as the rooks may simply be discriminating familiar from unfamiliar individuals, a considerably less precise form of recognition. Perhaps the most convincing evidence of individual recognition in birds comes from budgerigars (*Melopsittacus undulatus*). Budgerigars discriminated conspecific faces from heterospecific faces and discriminated between conspecific faces, suggesting individual discrimination (Brown and Dooling 1992, 1993). While evidence demonstrating that multiple views of the same individual were perceived by budgerigars as the same individual would provide more conclusive for individual recognition, like the other species discussed, conspecific face recognition in budgerigars appears to be reliant on configural processing, as subjects processed faces in their normal configuration more efficiently than inverted faces or faces with scrambled features.

Most fish live in stable social groups or shoals throughout their lives and demonstrate behaviors that are indicative of social intelligence (see Bshary 2011 for a review). For instance, stickleback fish will not cooperate with individuals who have previously cheated in dangerous predator inspections, suggesting individual recognition and memory of conspecifics. Yet the means by which recognition occurs is poorly understood. Olfactory and chemical cues are likely modes of communication in an aquatic environment as water typically aids the dispersal of such cues; however, recent work suggests the importance of visual cues, particularly facial cues, in more precise forms of recognition in fishes. A recent study found that African cichlid fish (*Neolamprologus pulcher*) discriminated familiar individuals from

unfamiliar individuals using facial features (i.e., color patterns) alone (Kohda et al. 2015). Moreover, two species of damselfish (*Pomacentrus amboinensis* and *P. moluccensis*) use ultraviolet facial patterns for species discrimination and potentially for individual recognition as well (Siebeck et al. 2010). However, more research needs to be done in order to confirm that fishes individually discriminate conspecifics using these distinctive facial cues.

Some species of paper wasps, like the Northern paper wasp (*Polistes fuscatus*), exhibit highly variable facial and abdominal color patterns, which are used to individually recognize their nestmates. Sheehan and Tibbetts (2011) compared the face learning abilities of *P. fuscatus* and *P. metricus*, a closely related species that does not possess elevated phenotypic variation like *P. fuscatus* and has not been shown to individually recognize conspecifics. *P. fuscatus* more accurately and quickly discriminated pairs of normal conspecific and heterospecific faces compared to manipulated face images (composed of the same colors and patterns of normal faces) and nonface images, whereas *P. metricus* did not. This suggests that the specialization for face learning in paper wasps is not based on general pattern or shape discrimination and it is not due to species-specific variability in faces. Furthermore, morphological measurements demonstrate that *P. metricus* has more acute vision than *P. fuscatus* ruling out the possibility that differences in visual acuity may explain the results. Thus, specialized face learning in paper wasps appears to be a cognitive adaptation that likely evolved in response to social pressures as *P. fuscatus* colonies are founded by multiple queens and exhibit a linear dominance hierarchy, whereas *P. metricus* typically nest alone (Sheehan and Tibbetts 2011).

Conclusion

Many animals possess the ability to visually discriminate conspecifics. Collectively, these studies strongly suggest that a face-processing system is

not human, or even primate, specific. Current evidence suggests that individual recognition may be a cognitive adaptation that evolved convergently in response to ecological and social pressures. Some species (e.g., sheep and NHPs), currently appear to have more complex forms of recognition, which indicates that recognition may have evolved in a stepwise fashion with more general forms of recognition (e.g., species discrimination) emerging before more precise forms (e.g., individual recognition). It seems likely that certain aspects of face perception, such as the preference towards orienting towards simple face-like patterns or even particular features of the face such as the eyes as this was imperative for predator detection, may share a deeper evolutionary history, whereas, other, more specialized facets of face perception, such as the use of second-order configural cues, may have evolved more recently during primate evolution, explaining its presence in humans and apes but not consistently observed in monkeys. Further work in a variety of species that vary in terms of sociality, ecology, and evolutionary history will clarify which facets of face perception result from homologous or convergent processes.

Cross-References

- [Face and Object Recognition](#)
- [Individual Discrimination](#)
- [Kin Recognition](#)
- [Prosopagnosia \(Face Recognition\)](#)
- [Reconciliation](#)

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Abnormal Fears

► Phobias

Aborticide

► Abortion

Abortion

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Synonyms

Aborticide; Foetal death; Loss of conceptus

Definition

Early pregnancy loss can be described comprehensively as “a disturbance in pregnancy occurring before the period of fetal viability resulting in expulsion or retention of pregnancy” (Daftary and Chakrvarti 2007). The expulsion or extraction of the fetus or embryo weighing less than 500 g (20 weeks of gestation) from the uterus, spontaneous or induced, is called abortion (FIGO 1976).

Introduction

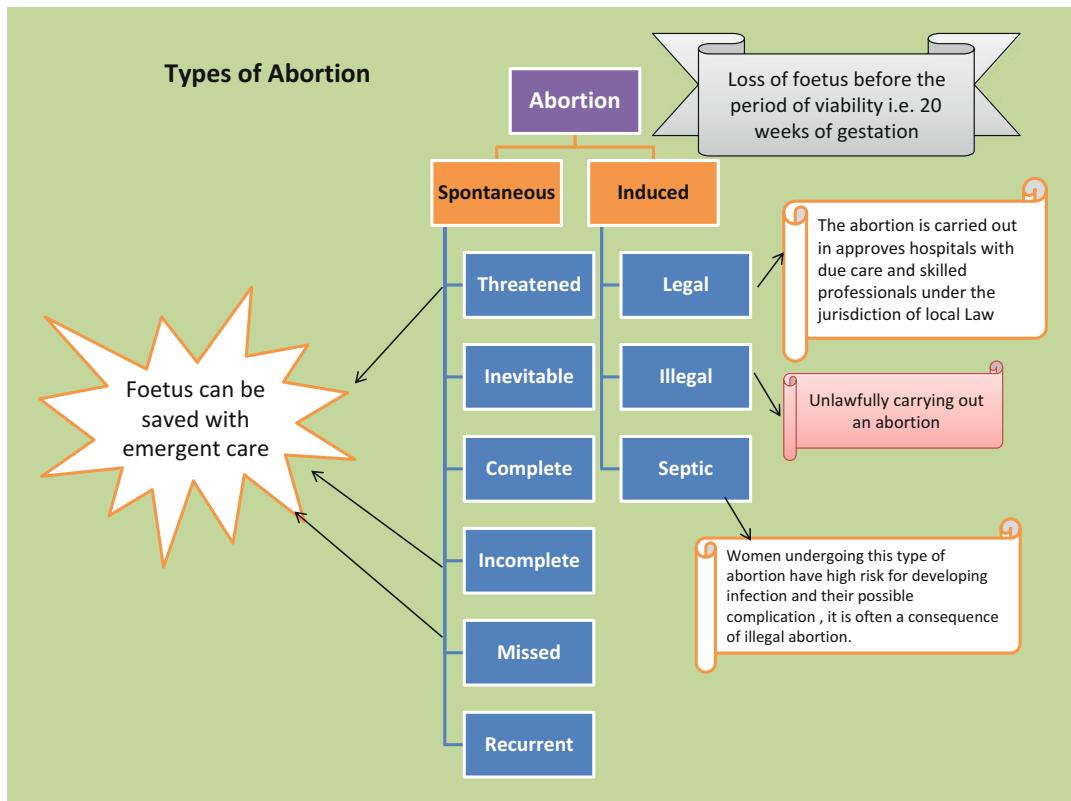
Motherhood is arguably one of the best feelings in the world. A joy for women to bring new life into the world, but pregnancy comes with its share of challenges. Abortion is one of the most dreaded outcomes of “pregnancy.” The primary manifestation of abortion is vaginal bleeding; it occurs in up to 25% of pregnancies prior to 20 weeks (Myles et al. 1993). It is a major cause of anxiety for all women, especially those who have experienced previous pregnancy loss and may be the presenting symptom of life-threatening conditions, such as ectopic pregnancy. Bleeding should always be considered as abnormal in pregnancy and investigated appropriately (Myles et al. 1993).

Incidence

There has been a significant decline in the rate of abortions compared to the 1990s in the developed

countries, but the developing countries still present with great number of abortions. The reported number of abortions are significantly less in number than the ones that occur (Sedgh et al. 2016). A recent multicentric study reported that there has been a significant decline in the number of abortions from the past millennia to the present times. Concern about the condition and quality of the services related to abortion pose a great concern throughout the world (Bearak et al. 2019). The worldwide incidence reported was 35 abortions per 1,000 (90% uncertainty interval 33–42) women within 1 year of reproductive age. Within the time period of 1990–2010, it was observed that the developing countries showed no significant decline in the number of abortions (only 2 points from 1990 to 2014 [39 (37 to 47) to 37 (34 to 46)] calculated with an uncertainty interval of 90%). It was also found that 73% of the abortions were sought out by married women, and 27% was obtained by unmarried women. In this same study, it was also reported that globally 27% of pregnancies ended up in abortions (Sedgh et al. 2016).

As of 2010–2014, an estimated 36 abortions occur each year per 1,000 women aged 15–44 in developing regions, compared with 27 in developed regions. The abortion rate declined significantly in developed regions since 1990–1994; however, no significant change occurred in developing regions (Sedgh et al. 2016). By far, the steepest decline in abortion rates occurred in Eastern Europe, where use of effective contraceptives increased dramatically; the abortion rate also declined significantly in the developing subregion of Central Asia. Both subregions are made up of former Soviet Bloc states where the availability of modern contraceptives increased sharply after political independence – exemplifying how abortion goes down when use of effective contraceptives goes up (Bearak et al. 2019). Abortions occur as frequently in the two most-restrictive categories of countries (banned outright or allowed only to save the woman’s life) as in the least-restrictive category (allowed without restriction as to reason) – 37 and 34 per 1,000 women, respectively (Sedgh et al. 2014). In much of the world, 20–24-year-old women tend to have the highest



Abortion, Fig. 1 Types of abortion

abortion rate of any age-group, and the bulk of abortions are accounted for by women in their 20s (Sedgh et al. 2016).

The World Health Organization (WHO) estimated that worldwide 210 million women become pregnant each year and that about a third of them or approximately 80 million end in miscarriage, stillbirth, or induced abortion. More than 40% of women will have miscarriage some time in their reproductive life. Approximately 20% of all pregnancies end up in miscarriages (spontaneous abortion), and about 80% of these occur in the first trimester, within 2–3 months of gestation (WHO 2018).

Types of Abortion

Threatened Abortion

A clinical entity where the choriodecidual hemorrhage (the process of abortion) has begun, but

not progressed to the stage of irreversibility. The cervix is not open, and the products of conception are not expelled (Fig. 1).

Clinical Features

The woman will present with the history of amenorrhea (no monthly bleeding) for more than 6 weeks. Currently bleeding which is fresh and scanty. Mild uterine cramps and backache (sometimes painless bleeding). Signs of early pregnancy like morning sickness, vascularization of the vagina, etc. will be present. On vaginal examination, cervix will feel soft with the os closed.

Investigations

A hemoglobin estimation of the blood to determine severity of bleeding needs to be done. A per abdominal or transvaginal ultrasonography to determine the gestational sack. A urine pregnancy test to confirm the hCG positivity. Blood test for

serum hCG may be serially done to determine any abnormality in the doubling time, which could indicate the possibilities of survival.

Treatment

The only aim in the treatment is to extend maximum support to the pregnancy in order to increase chances of survival of the pregnancy. Hospitalization and complete bed rest until bleeding stops. Hormonal supportive therapy, hematinics, laxatives, and sedatives if required. The patient is advised to continue treatment, restrict activity, and avoid lifting any heavy weight. Sexual intercourse is best avoided as long as the risk for fetal loss remains (Dutta 2004).

Inevitable Abortion

In this type of abortion, the process of abortion has begun and progressed to such an extent that expulsion of the products of conception seems inevitable.

Clinical Features

The woman will present with the history of a variable period of amenorrhea along with vaginal bleeding with passage of fresh blood and clots and pain due to uterine contractions and cervical dilation.

Signs

A clinician will observe pallor, cold, clammy extremities, tachycardia, hypotension, and on per vaginal examination it will reveal; cervix will feel soft to firm and bulky, corresponding to the period of gestation.

Investigation

A blood group and cross matching test along with several blood tests are needed to determine the condition of the woman. Ultrasonography may be needed to confirm the expulsion or residue for the products of conception.

Management

As pregnancy is unavailable, it is terminated. The method of evacuation of the uterus depends on the duration of pregnancy. General treatment includes resuscitation with intravenous fluids and

cross matched blood if required. If pregnancy is less than 12 weeks, suction and evacuation is performed. The duration of the pregnancy is more than 12 weeks, intravenous oxytocin or (uterotonic) PGF_{2α} is administered, and spontaneous expulsion is awaited (Jacob 2012).

Prophylactic immunization of tetanus toxoid, antibiotics, and intramuscular 50 µg anti-D, if the mother has an Rh-negative blood group, has to be given to prevent complications after this abortion. Ultimately the examination and histopathology of the products to ascertain any recognizable pathology.

Complete Abortion

Complete abortion can be described as a condition in which products of conception are expelled out completely from the uterus, and the uterine cavity is empty.

Clinical Features

The woman presents with the history of variable period of amenorrhea followed by lower abdominal pain, vaginal bleeding with passage of products, and followed by a decrease in the bleeding and pain. A vaginal discharge that usually subsides in a week.

The clinician may observe substantial vaginal bleeding during the course of abortion; the patient may be in a state of circulatory collapse.

Investigations

Per abdominal ultrasonography confirms that the abortion is complete, and the cavity is empty.

Management

Medical management is usually conservative. Sedatives, hematinics, tetanus toxoid, anti-D (in Rh-negative mothers), and methergine are given (Dutta 2004). Rarely, curettage may be necessary if the bleeding continues or the USG reveals products in the uterine cavity. The family and friends are asked to support the woman in recovery of physical and psychological nature.

Incomplete Abortion

In the incomplete variety, the abortion has occurred but the process is incomplete. The

cervical os is open and the products of conception are partly expelled.

Incomplete abortion can be presented by a history of amenorrhea, vaginal bleeding, continuous or recurrent passage of fleshy mass per vagina, and severe lower abdominal pain of colicky nature. Clinician may observe pallor, signs of shock, products of conception may be felt in the cervical canal or vagina an open internal Os, uterus feeling soft on examination.

Management

The patient is resuscitated if in shock with intravenous fluids and blood if required. Dilatation and curettage to empty the uterus using blunt curette under general anesthesia.

Missed Abortion

In missed abortion the fetus is dead and retained inside the uterus for a variable period of time. Woman shall present with the history of amenorrhea, with lower abdominal pain accompanied with vaginal bleeding or brownish discharge and spotting, and with subsidence of the pregnancy symptoms.

The sign and symptoms reported clinically presented by, uterine size felt smaller than the period of amenorrhea. On examination per-vaginum the cervix is felt soft with internal closed internal os open, and retrogression of breast changes.

Investigation

Urine test for pregnancy becomes negative. Ultrasonography per abdomen shows loss of gestational sack, and Doppler examination reveals absence of fetal heart sound.

Management

Patients suffering from incomplete abortion can be managed by a gynecologist by a procedure called dilatation and curettage to prevent infection. The expelled products are examined to ensure completeness. The women can also be advised to take injections of tetanus toxoid and Anti D Antibodies, in such cases (Daftary and Chakrvarti 2007).

Recurrent Abortion

Spontaneous and recurrent abortion occurring consecutively on three or more occasions is called

habitual abortion. It may be primary or secondary, if it occurs after the birth of viable babies.

Etiology

The etiological factor for recurrent abortions can be divided into two main categories; *maternal* and *fetal*. Maternal cause include systematic disorders such as syphilis, diabetes mellitus, chronic nephritis, essential hypertension, and Rh incompatibility. Hormonal problems like progesterone deficiency, polycystic ovarian disease (PCOD), and thyroid dysfunction can also be contributing factors. Structurally cervical incompetence has been a very common cause of abortions. Developmental abnormalities of uterus such as bicornuate uterus and septate uterus and for some idiopathic causes (Daftary and Chakrvarti 2007) contribute to recurrent abortions. *Fetal* causes are mainly chromosomal defects.

Investigations

The causes for recurrent abortions need to be investigated very thoroughly (Jacob 2012), and pregnancy should be planned and monitored under specialist supervision.

Management

Management of such case require a lot of interventions at various levels. Counselling of the couple to alleviate anxiety is a very essential and effective strategy. Surgical correction of uterine abnormality if possible and genetic counselling as indicated should be carried out. women who suffer from hormone deficiencies are also advised to take hormonal therapies to prevent abortion.

Induced Abortion

Induced abortion refers to the deliberate termination of pregnancy prior to fetal viability. In India, induced abortion was legalized as health welfare measure under the Medical Termination Of Pregnancy Act (MTP Act). This law permits the termination of pregnancy for selected indications.

The specified indications for induced abortion are as follows.

Criminal Abortion

Criminal abortion refers to abortions performed by quacks (untrained and unauthorized persons) often in insanitary and unhygienic conditions leading to increase morbidity and mortality as a result of complications such as traumatic injuries, infection, incomplete evacuation, and hemorrhage. In India, women used to resort to quacks to procure abortions of unwanted pregnancies resulting in loss of young lives. This prompted the government of India to adopt the MTP Law as a health welfare measure to prevent the practice of criminal abortions (Dutta 2004).

Septic Abortion

A type of abortion associated with sepsis of the products of conception. There is increased association of sepsis in illegal induced abortion because of (1) improper antiseptic measures, (2) incomplete abortion, and (3) inadvertent injury to the genital organs and adjacent organs (Payne et al. 2018).

A septic abortion can have associated bacterial infections of the following types:

Aerobic: *Escherichia coli*, *Pseudomonas*, β -hemolytic streptococci, and *Enterococcus faecalis*.

Anaerobic: Bacterides, *Clostridium*, *Neisseria gonorrhoeae*, and *Chlamydia trachomatis* are also possible pathogens.

Septic abortion is usually a dangerous condition if ignored and may lead to life-threatening complications and lead to maternal mortality.

Diagnosis

Septic abortion can be identified by the following manifestations:

History of recent termination of pregnancy (by unauthorized person).

Variable period of amenorrhea along with high fever, chills and rigors, vomiting, diarrhea and diffuse abdominal pain.

Foul smelling vaginal discharge, which is often purulent, accompanied by vaginal bleeding and history of passage of products of conception per vagina.

The woman shall present with the signs of pallor and sweating, pyrexia, tachycardia and decreased blood pressure, features of toxemia, general abdominal rigidity, guarding and/or tenderness, abdominal distension, and ileus (Jacob 2012).

Investigations

Detailed investigations case specific of blood and associated viscera must be performed.

Management

It is important to notify the police whenever a criminal abortion is suspected. Patient is admitted to the hospital. Shock is to be treated aggressively. Antibiotics and evacuation of uterus under anesthesia are usually employed. In severe cases (Udoh et al. 2016), oxygen 6–8 L/min IV crystalloids and plasma expanders are used to manage the condition conservatively.

Challenges and Issues Regarding Abortion

Abortion is often not regarded medically as “serious” and is usually not investigated further when it occurs for the first time. As a result many women do not receive an explanation of their loss (Bearak et al. 2019). There is no evidence to associate abortion with an overall increased risked of psychiatric morbidity. However, feelings of anger, grief, and guilt are common, and almost half of all women are considerably distressed at 6 weeks following abortion (Melese et al. 2017).

Women who lose pregnancies in the second trimester face the same risk of postpartum “mood disorder” as women in the normal puerperium. Grief reactions are usually more severe and may persist for up to 6 months following the loss of their pregnancy (Melese et al. 2017).

These reactions often create vulnerability toward developing psychological maladaptation

leading to predisposition of the women going through the phenomenon.

Global Efforts and Legislature About Abortion

Abortion being one of the most important areas and also a condition affecting the health status of any country, there have been global efforts to understand the extent of the issue and the legal aspects of this phenomenon (Johnson et al. 2018). A global database for abortion policies has been established. Their latest findings reported that only 32% of the countries allow abortion on the request of the women without the need for justification. About 82% of the countries allow abortion to save the life of a woman, 64% of countries have been allowing abortion on the grounds of physical and psychological health, and 51% allow abortion on the grounds of fetal condition, and 46% allow women to undergo abortion if the pregnancy is a result of rape (Johnson et al. 2018). This gives us a picture of the phenomenon globally; India has a legislation regarding the MTP Act (Medical Termination of Pregnancy), which allows women to access safe abortion services in government and private facilities since 1971 which had also been amended on various occasions resulting in increased access and low cost safe abortion services in India (Singh et al. 2018).

Conclusion

Abortion is a traumatic event in a woman's life, but it is also a nature's mechanism of preventing major genetic and other abnormalities from occurring in the offspring if it occurs naturally or an indication of other serious issues in the health of the mother and the unborn child. This chapter deals with abortion in brief; there are a lot of causes that can be related to the mother and the fetus which contribute to abortion. The effects of abortion are very varied, effecting all spheres of life of the woman as well as her family. Abortion is associated with hormonal and physiological and psychological changes. It also depletes the mother's health reserves and can also contribute

to difficulties and other aspects of her life. Abortion also has a profound social effect, which in some cultures enhances the woman's difficulties in multiple folds. There have been attempts by the governments to provide women with perks of additional medical leaves up to 6 weeks post abortion to help them build up their lost strength. This is a progressive step towards gender sensitivity. Still there are nations making abortions illegal, which is a great threat to a woman's choice of having a child. There is necessity to build up consensus worldwide to provide access to women for medical care of abortion, safe abortion services, and effective contraception post abortion to build the health and economy of women.

Cross-References

- Maternal Abandonment and Maternal-Fetal Conflict
- Miscarriage

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Absence of Events to Distinguish True Friends

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Synonyms

Events; Friends; Friendships; Reciprocal altruism

Definition

The evolutionary perspective argues that we have evolved to monitor events that would help identify true friends. These events are usually harsh or unfavorable, which are absent in our safer and more stable modern environments.

A

Introduction

Friendship confers many adaptive benefits that aid survival and reproduction (Buss 1989; Lewis et al. 2011; Tooby and DeVore 1987), especially when one successfully distinguishes true friends from fair-weather ones. However, with modern environments and tools, it is challenging to discern the different types of friends. This current entry reviews the benefits of friendship and outlines how modern context influences our evolved psychology in identifying true friends.

Benefits of Friendships

Ancestrally, friendships provided humans with benefits that aided survival (Cosmides and Tooby 1992; Lewis et al. 2011; Tooby and DeVore 1987). Being in groups allowed hunters to work together when hunting large animals (Baumeister and Leary 1995). Hunting together as a team yielded nutritious food with lower rates of deaths and injuries (Buss 2016; Tooby and DeVore 1987). They were also able to share food resources (Buss 2016; Hill and Kaplan 1988; Lewis et al. 2011), and this was especially important as food was a scarce resource in the ancestral past (Buss 2016). Having friends also provided the opportunity to form alliances, which was critical in times of conflict as their loyalty and support were vital in emerging victorious (DeScioli and Kurzban 2009). Moreover, since conflicts in hunter-gatherer societies predominantly revolved around fighting over resources, having a group of friends would not only have allowed one to win but also served to prevent conflicts (Bukowski et al. 1994; DeScioli and Kurzban 2009; Tooby and DeVore 1987). Recent

studies have also shown that having friends decreases mortality risk (Giles et al. 2005; Holt-Lunstad et al. 2010).

Apart from facilitating survival, friendships also provided mating opportunities for both men and women (Lewis et al. 2011). Opposite-sex friendships can potentially develop into romantic relationships, especially since people seek the same attributes in opposite-sex friends as they would in a mate (Buss and Schmitt 1993; Lewis et al. 2011). Developing friendships with individuals of the same sex also conferred mating benefits. Men tend to befriend other men who are more resourceful as this desirable trait of resourcefulness – that women have evolved to prefer in men – would be “transferred” to themselves, thus boosting their success in mating (Lewis et al. 2011; Vigil 2007). Likewise, with the evolved preference of men for physical attractiveness, women gravitate toward befriending other physically attractive women in order to reap the benefits of being around higher-quality men (Buss 1989).

From an evolutionary perspective, human psychology and behavior are products of evolved psychological mechanisms – adaptations that have developed over time as a result of successfully solving recurrent survival and reproduction problems. With the survival and reproductive benefits humans have enjoyed by having friends, natural selection would have favored mechanisms that motivated us to seek and develop friendships.

Events and the Identification of True Friends

According to the theory of reciprocal altruism, altruistic tendencies toward friends develop when benefits are reciprocated (Cosmides and Tooby 1992; Trivers 1971). However, not all friends provide benefits or reciprocate in times of need. As a hunter-gatherer, if one mistakes a fair-weather friend for a true friend, they would face costly outcomes that would threaten their survival (less so in reproduction) (Tooby and Cosmides 1996). For instance, when a hunter-gatherer is cornered by predators or enemies,

fair-weather friends were not likely to offer their aid in order to ensure their own survival. This would have resulted in a lower chance of survival for that attacked individual. Hence, we have developed mechanisms that allowed us to deal with the adaptive problem of friendship mimicry, specifically to monitor clarifying events that would allow us to distinguish our true friends from fair-weather ones (Tooby and Cosmides 1996).

Unfavorable events provide humans with the opportunity to assess the extent of a friend’s engagement in an individual’s physical and social welfare, in other words, allowing one to gauge the genuineness of the friendship (Tooby and Cosmides 1996). Help rendered during harsh times, particularly when a cost may be incurred, was especially meaningful as such help is likely to be critical for survival and reproduction.

In ancestral times, hunting was conducted in large groups as success rates were low and was too risky to do be done alone (Tooby and DeVore 1987). This allowed men to come together to share hunting-related skills (Lewis et al. 2011) and build alliances (DeScioli and Kurzban 2009), which were opportunities to foster friendship. More importantly, it allowed men to identify those who would offer help when it became dangerous.

Women spent a significant amount of time on childcare and gathering plant food (Lewis et al. 2011; Silverman et al. 2007). These activities provided an opportunity for helping and tending to offspring, and, consequently, friendships develop over the emotional closeness that grew during these activities (Ackerman et al. 2007; Lewis et al. 2011). Such deep engagements, as coined by Tooby and Cosmides (1996), promoted genuine friendships.

The Absence of Events in the Modern Environment

Modern environments, which are safer and more stable than those from ancestral times, lack such clarifying events that allowed humans to assess the genuineness of friendships. The absence of

those opportunities that allowed humans to foster deep mutual dependence leaves people with low confidence of their social bonds, consequently leading to more people to feeling lonely despite having social contacts (Tooby and Cosmides 1996). Moreover, advances in technology are transforming the way friendships are formed, especially with social media.

Social Media

With social media, one makes friends easily – it can be as straightforward as sending a friend request (Mahmood and Desmedt 2012). Mahmood and Desmedt (2012) created a fake Facebook account, and across 285 days, 62% of their friend requests were accepted by strangers, and the account received 6.67 times more requests from strangers in latter 185 days. People can also be “unfriended” on social media and not be notified of it (Sibona and Walczak 2011). In the event of unhappiness, usually expressed via a social media post, “help” from “friends” on these platforms is usually sent in the form of virtual hugs or likes. Hence, as much as social media facilitates connection with like-minded people, there is a significant lack of cues we have evolved to monitor in this platform to assess the genuineness of friendship. The presence of novel cues in social media, such as virtual hugs, only serves to hijack our assessment of true friends as our brains and mechanisms have not evolved to process such novelties (Li et al. 2018).

Cosmopolitan Societies

Friendship is similar to kinship (Ackerman et al. 2007). Hence, apart from clarifying events, friendship can develop when kinship indicators, such as familiarity and similarity, manifest through behaviors, such as mutual grooming and dressing, are present (Park and Ackerman 2011). However, in modern cosmopolitan societies, it is common for multiethnic individuals to live together (Kanazawa and Li 2015). This, again, is a novel phenomenon as humans lived in ethnically homogenous groups in ancestral times (Oppenheimer 2004). As kinship indicators allowed one to identify friends (Christakis and Fowler 2014), the differences that exist among

multiethnic individuals in a cosmopolitan society would mean that one will have a harder time doing so. Moreover, any individual who looked, spoke, and behaved differently would not have been from one's group ancestrally. Our brains process people of different ethnicity to be potential threats – similar to ancestral environments (Kanazawa and Li 2015). Therefore, friendship forged within the context of the modern cosmopolitan society may not be as strong as the ones that were forged among humans in the ancestral times.

Conclusion

Friendship is a significant aspect in the lives of humans over the course of evolutionary history. Having facilitated the chances of survival and reproduction, we have evolved several mechanisms that allowed us to seek and develop friendship. However, not all friends are engaged in ensuring our physical and social welfare; fair-weather friends behave similarly to true friends when circumstances are good but are less likely to extend their help in times of need, leaving us vulnerable to threats. Therefore, we have evolved to monitor behaviors in clarifying events to deal with the adaptive problem of discriminating true friends from fair-weather friends. Ancestrally, these events are harsh in nature, and having friends who helped, especially when it could involve some cost to the individual, was especially meaningful.

However, our modern environment lacks the events that once provided humans with the opportunities to foster deep engagements and social bonds. Additionally, with the recent advancement in technology and globalization, it is becoming increasingly difficult to identify true friends despite the expanded opportunities to meet like-minded others through social media or the multiethnic cosmopolitan society we live in. Further research using the evolutionary approach of the *mismatch theory* (Li et al. 2018) and the *savanna-IQ hypothesis* (Kanazawa 2009) should be done to investigate novel cues in the modern context that would allow us to tease apart true friends from fair-weather ones.

Cross-References

- Fair-Weather Friends Versus True Friends
- Friendship and Modern Life
- Opposite-Sex Friend
- Same-Sex Friend

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Absence Prior to Puberty

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Synonyms

[Age of menarche](#); [Father absence](#); [Reproductive maturation](#)

Definition

How absentee parents during early life shape developmental trajectories (i.e., reproductive timing)

Introduction

A large body of research has shown associations between features of childhood family environment and aspects of well-being in adolescence and adulthood (Belsky et al. 1991; Brumbach et al. 2009; Chang and Lu 2018; Mendle et al. 2009; Rickard et al. 2014; Simpson et al. 2012). One such widely replicated finding is that girls who grow up in father-absent households reach reproductive maturity (usually indexed as age at menarche) at younger ages than girls who reside with their fathers (Belsky et al. 1991; Ellis and Essex 2007; Gaydosh et al. 2018; Mendle et al. 2009; Tither and Ellis 2008). Earlier female reproductive maturation, in turn, has been implicated in a number of downstream health consequences such as higher risk for developing cardiovascular disease (Prentice and Viner 2013), reproductive cancers (Gong et al. 2013), and negative psychosocial outcomes (e.g., sexual delinquency, anxious, and depressive symptomatology) (Belsky et al. 1991; Mendle et al. 2019). Thus, the causes of variation in the pacing of female reproductive maturation are noteworthy from a public health perspective. Evolutionary social scientists have tested hypotheses, deduced from an

adaptationist approach, accounting for observed patterns in this variation. Recently, the very existence of a consistent causal link between father absence and early menarche has become controversial in light of concerns about methods, analytical procedures, and the range of human populations sampled in this research (see Sear et al. 2019; Sohn 2017). In this article, we review the history of research on effects of parental absence (usually, but not exclusively, father absence) on reproductive development. We also describe critiques of this work and avenues for future research.

Life History Theory

Life history theory (LHT; MacArthur and Wilson 2001; Pianka 1970) concerns trade-offs faced by organisms with respect to energy allocation. The three most general trade-offs are somatic effort (growth plus maintenance) versus reproductive effort, mating versus parenting effort (the two subtypes of reproductive effort), and quality versus quantity of offspring (Stearns 1989, 1992). A slower LH strategy prioritizes somatic effort over reproductive effort, parenting effort over mating effort, and offspring quality over offspring quantity. A faster LH strategy prioritizes the opposite energy allocations. Rates of extrinsic mortality are thought to be the principal driver of LH variation, with higher rates selecting for a faster LH. As a framework for studying human individual differences, LHT generates hypotheses about the covariation of developmental, physiological, psychological, and social traits, as well as hypotheses about their causal antecedents (Del Giudice et al. 2015). For example, increased impulsivity and decreased prosocial motivation are expected to co-vary as psychological components of a faster LH strategy. Early age at menarche (a form of prioritizing reproductive effort over somatic effort) has long been hypothesized as fast LH indicator (Rushton 1985). However, given the multi-decade duration of the human female reproductive lifespan, interindividual differences of a few years in age at menarche contribute only modestly to overall LH trajectory (Del Giudice 2018).

Psychosocial Acceleration Theory

Independently of research programs applying LHT to human individual differences, Draper and Harpending (1982) developed a model of the facultative calibration of reproductive strategies by the environmental cue provided by father presence or absence. They argued that father absence reliably signals to a child that in his or her social setting, short-term mating relationships, entailing little paternal investment, are both normative and adaptive. Belsky, Steinberg, and Draper (1991) built on this work by situating father absence as just one component of a broader construct, early childhood affective experience within the family, that was hypothesized to channel psychosocial development and reproductive strategies (e.g., preference for short-term vs. long-term mating relationships) in adaptive directions. *Psychosocial acceleration theory* was the name given to the causal link between harsh early environment and earlier maturation. Chisholm et al. (1993) explicitly integrated LHT with psychosocial acceleration theory, arguing that affective features of early environments serve as reliable cues of local death rates. Thus, father absence and other contributors to harsh early affective environments (e.g., rejecting, insensitive parenting) set children toward a faster LH trajectory. The foregoing brief intellectual history highlights the independent origins of psychosocial acceleration theory and the LHT-informed study of human individual differences and their eventual integration (Belsky 2012; Belsky et al. 2015; Black et al. 2017; Chang and Lu 2018; Chisholm et al. 1993; Del Giudice and Belsky 2011; Ellis et al. 2009, 2012; Ellis and Essex 2007; Richardson et al. 2018; Rickard et al. 2014).

Reviewing and synthesizing available behavioral and endocrinological evidence, Ellis (2004) concluded that father absence accelerates girls' pubertal development, whereas greater parent-child warmth and parental marital quality delay it. Contrary to the competing energetics theory of pubertal timing, earlier menarche is not associated with greater lifetime reproductive success. Since 2015, researchers have debated the roles of *biometric* and *psychometric* LH indicators in

hypothesis building and testing (Baldini 2015; Copping et al. 2017; Del Giudice 2019; Figueiredo et al. 2015; Nettle and Frankenhus 2020; Sear 2020; Zietsch and Sidari 2019). A subset of these debates concerns the uncertain associations between age at menarche (a purely biometric LH indicator) and age at sexual debut (which is partly a function of psychological traits). For example, Richardson et al. (2018) found evidence to suggest that temporary father departure in an otherwise intact family predicted earlier age of menarche, and earlier age at menarche predicted earlier sexual debut, but there was no direct causal path between temporary father departure and age at sexual debut.

Criticisms and Debates in Literatures

In recent years, the universality of the relationship between father absence and onset of reproductive maturation has been questioned. Here we highlight three sources of controversy: demonstrating causality from cross-sectional data, representativeness of the human populations sampled, and possible genetic confounds (Barbaro et al. 2017; McLanahan et al. 2013; Sear et al. 2019; Sohn 2017).

Cross-Sectional Data and Causality

A major weakness of the use of cross-sectional correlational data to test the effects of father absence on reproductive maturation is that it cannot establish causal relationships (McLanahan et al. 2013). Across households, father absence likely has multiple causes and multiple effects, making it very difficult to estimate its direct effect on early menarche. Longitudinal studies, incorporating controls for potential confounds, have confirmed hypothesized effects on reproductive maturation of father absence and in one case mother absence (see below) (Chang and Lu 2018; Gaydosh et al. 2018; Mendle et al. 2009, 2019). These types of studies allow stronger causal inferences and can track long-term persistent effects of parental absence during early

childhood. Longitudinal data also provide some flexibility with regard to various types of statistical techniques for making causal inferences, for example, lagged-dependent variable models, growth curve models, and multilevel modeling (see review McLanahan et al. 2013).

Notably, Chang and Lu (2018) used a longitudinal study design to investigate the effects of parental absence on rural Chinese “left-behind” children (defined as those who experienced the absence of both parents for more than 6 months repeatedly for 3 or more years). Structural equation modeling revealed two dimensions of environmental harshness, extrinsic risk (on which parental absence loaded), and resource scarcity. Among a number of effects of these predictors on developmental, cognitive, and behavioral outcomes was the association between parental absence with accelerated sexual maturation and psychometric indicators of faster LH strategy. A key point is that parental absence was not stratified by parents’ sex. The effects of mother absence on daughters’ reproductive timing remain unclear, possibly due to small sample size (Sear et al. 2019).

It is important to note that while efforts have been made to increase the ability to determine causality with the use of longitudinal data and advanced statistical techniques, these methods are not without limitations. Researchers should carefully consider their use in designing studies, in light of the specific research questions and the available resources (see McLanahan et al. 2013).

Populations

Most early research into the associations between father absence and age of menarche was conducted in populations characterized, to use Henrich, Heine, and Norenzayan’s (2010) coinage, as WEIRD (Western, educated, industrialized, rich, and democratic). In small-scale societies with little market integration, findings often failed to reveal associations between father absence and age of menarche (Sear et al. 2019; Sohn 2017). Thus, the psychosocial acceleration hypothesis might apply only to a limited range of

human populations, and indeed it may be least applicable to societies most similar to those in which most of the natural selection shaping human developmental programs occurred. In general, girls growing up in WEIRD societies experience greater food security and access to medical care and fewer demands for physical labor, than girls growing up in non-WEIRD societies (Henrich et al. 2010; Sear et al. 2019). Furthermore, family and social structures generally differ between WEIRD and non-WEIRD societies. In the former, the prevalence of nuclear families and low fertility means that fathers provide a large proportion of the investment received by each child, so a father’s departure typically represents a substantial reduction in parental investment received. In the extended families commonly found in non-WEIRD societies, other adult kin, and sometimes older siblings, can provide compensatory investment following a father’s departure (Ellis 2004; Sear et al. 2019). Rather than father absence per se hastening female pubertal development, it seems that father absence, in some sociocultural contexts, serves as a cue of local mortality risk (Chang and Lu 2018; Ellis 2004). Additional cross-cultural research, and statistical techniques like growth curve models, multilevel modeling, and natural experiments, for systematically comparing predictive models of reproductive maturation across populations, will paint a more nuanced picture of the effects of father absence and other cues on the development of LH trajectories (McLanahan et al. 2013; Sear et al. 2019; Sohn 2017).

Genetic Confounds

Statistical associations between father absence and earlier menarche do not necessarily demonstrate that the former causes the latter. An alternative explanatory model posits that both traits are heritable and are genetically correlated. *Genetic correlation* occurs when the genetic variation that affects one trait correlates with the genetic variation that affects a second trait (Plomin et al. 2013). To the extent that LH strategy comprises a functionally integrated, partly heritable, cluster of

physiological and behavioral traits (Figueredo et al. 2004), men who are more likely to leave their mates and children will also be more likely to transmit to their daughters, genes that predispose them toward earlier menarche. Even small genetic correlations could confound the phenotypic correlation between the two traits (Barbaro et al. 2017). Several empirical study design types afford the opportunity to disentangle the effects of genes from the effects of early life stress on reproductive maturation (Barbaro et al. 2017; Barnes et al. 2014; Ellis 2004; Gaydosh et al. 2018; Mendle et al. 2019; Tither and Ellis 2008).

Classic twin studies partition phenotypic variation into the proportions due to (1) genetic variation, (2) effects of the non-shared or idiosyncratic environment (which includes measurement error), and (3) effects of the environment shared by the twins (Plomin et al. 2013; Tither and Ellis 2008). Effects of harsh early environments on reproductive timing are expected to manifest as shared environmental effects on age at menarche, but these are not found (Barbaro et al. 2017). However, Tither and Ellis (2008) controlled for genetic effects by comparing non-twin sister pairs whose genetic father left the household when the older sister was about 12, while the younger sister was about 5. As would be expected from psychosocial acceleration theory, the younger sisters experienced earlier menarche than the older sisters, and they also experienced earlier menarche than younger sisters in a control sample of families in which the father did not leave the household.

Finally, genome-wide association studies (GWAS) allow researchers to identify potential candidate genes that might be tied to father absence and earlier age of menarche. For instance, the *LIN28B* gene, which plays a central role in female development, and its SNP variants were identified as potentially impacting female reproductive timing (see Perry et al. 2009; Zhu et al. 2011). Other findings support a gene \times environment interaction between *LIN28B* and father absence on female sexual maturation age, although finer-grain methodologies for accounting for genetic variation is needed (see Schlomer and Cho 2017). The importance

of gene \times environment interactions stems from the aforementioned concerns related to genetic contributions resulting in spurious relationships. Gene \times environment interactions essentially demonstrate individual variation as a function of differing genotypes responding to differing environments. For instance, environmental risk factors for certain diseases are passed down from parents to offspring which may play a larger role than heritability of the actual disease. The result is variation in how the disease phenotype manifests. Interestingly, a recent study used polygenic scores, derived from GWAS data to test for genetic confounds. No evidence of genetic confounds in the associations between women's polygenic score for accelerated menarche and father absence were found. Women's polygenic scores for earlier age at first birth were, however, associated with father absence, providing preliminary support for potential genetic contributions for that relationship (Gaydosh et al. 2018).

Conclusion

In WEIRD societies, the association between father absence and early menarche is among the most robust findings in the social sciences (Ellis et al. 2009; Mendle et al. 2009; Richardson et al. 2018; Tither and Ellis 2008). These findings represent a test of the application of LHT to human individual differences. However, a number of important questions remain unresolved. Father absence and early menarche are not consistently associated in the small-scale societies that more closely resemble ancestral human environments (Sear et al. 2019; Sohn 2017). Additional research is needed to specify how sociocultural contexts influence the environmental cues by which the timing of reproductive maturation is calibrated. For example, mother absence, which for obvious reasons is much rarer than father absence, might also affect the timing of reproductive maturation (Chang and Lu 2018). Finally, the relative effects of harsh early environments and genetic predispositions on reproductive maturation remain an open question (Barbaro et al. 2017; Gaydosh et al. 2018; Schlomer and Cho 2017).

Cross-References

- Bruce J. Ellis
- Cultural Universals
- Development
- Early Childhood and Adolescence
- Environmental Unpredictability
- Father Absence
- Harsh Environments
- Jay Belsky
- Life History Theory
- Parental Investment and Parenting
- Paternal Care
- Paternal Investment
- Predictors of Sexual Debut
- Puberty in Girls
- Reproductive Timing

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Absolutism

- ▶ Objectivity

Absorption

- ▶ Assimilation

Abstinence

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Synonyms

Pregnancy prevention; Sobriety

Definition

The practice of restraining from a particular behavior.

Introduction

Abstinence is a broad term that can cover many different behaviors that one may wish to avoid indulging. Although this term can be used in several contexts, abstinence in regards to sexual intercourse will be the focus. Largely used as a personal strategy to avoid pregnancy and sexually transmitted diseases (STDs), it is often associated with the avoidance of vaginal intercourse but can also include the avoidance of *all* sexual activity. Individuals will often have varying definitions of what is considered to be abstinence, but they ultimately have the same goal in mind.

A

Abstinence in Sex Education

The topics discussed in sex education is a controversial issue. Assuming that the sex education provided in schools is a driving force behind sexual lifestyles, the information that is taught within these courses should be scrutinized. Guidelines for this information are not universally distributed throughout the United States. Depending on where an individual lives in the country, the course may have an abstinence-only focus which stresses the effectiveness of abstinence either by comparing it to other birth control methods or by exclusively discussing abstinence as a birth control strategy.

According to the Centers for Disease Control and Prevention (CDC 2016), the USA has one of the highest rates of teen pregnancy among developed countries. Due to this high rate, many studies have been conducted in order to evaluate how effective the different strategies are for teaching sex education, specifically abstinence-only education. Carr and Packham (2016) recently evaluated the different outcomes of teen pregnancy and STD presence in states in which sex education courses stress abstinence. It was found that there were no differences in teen pregnancy rates or STD rates regardless of what was taught in the courses (Carr and Packham 2016). This recent study replicated what has been found in earlier studies. Abstinence-only education does not reduce the prevalence of teen pregnancy or STDs compared

to a more comprehensive course that discusses various different forms of birth control including abortion. In fact, it has been shown that individuals who participate in comprehensive sex education courses have a lower likelihood of teen pregnancy (Kohler et al. 2008).

The evidence of previous research concludes that abstinence-only education is ineffective in decreasing teen pregnancy rates and STD rates, but the causes are not quite as clear. One of the main arguments for why sex education should be more comprehensive is because of the instinctual nature of sexual intercourse. Especially during adolescence, the presence of the sexual drive will lead many to participate in sexual activities, regardless of what sexual education they have been exposed to. In order for adolescents to be better equipped to make informed decisions concerning their sexual behaviors, a comprehensive education that covers various birth control methods will provide more of a benefit than an education focused on abstinence.

Conclusion

Abstinence is a personal lifestyle choice that gives the individual a strategy that will not lead to pregnancy. Despite it being the most effective birth control method, when it is taught as the sole form of birth control in sex education, it may actually lead to riskier sexual behaviors as compared to having a more comprehensive course.

Cross-References

- ▶ [Contraception](#)
- ▶ [Sex Education in Schools](#)
- ▶ [Sexual Intercourse](#)

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Abstract Concept Formation

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Synonyms

[Abstraction](#); [Conceptual representation](#)

Definition

Concepts are formed when an organism is capable of representing a mental construct that subsumes multiple related exemplars. Exemplars may be related by virtue of shared physical features, functions, traits, capacities, relationships, or other unifying characteristics. Abstract concepts are representations of conceptual categories containing exemplars that are not strictly tied to observable features of the stimuli and that typically subsume several more concrete categories. Forming such concepts requires inference or generalization from observed features to the construct that ties exemplars together.

Introduction

The idea of abstraction is somewhat nebulous, and evidence for such in nonhuman minds is somewhat elusive. It has been suggested that most animals are not capable of abstraction by both historic (Locke 1690/1975) and more recent figures (Mackintosh 2000), and even those that believe some animals capable of some degree of abstraction have placed limits on their capacities, stipulating that they may not be capable of

reasoning about certain types of relations (Penn et al. 2008) or unobservables (Vonk and Povinelli 2006). Part of the difficulty in providing evidence for abstraction in nonhumans stems from the challenge in defining what it means to be abstract in the first place; conventional definitions focus on the idea that abstract concepts require generalization beyond strictly observable features to include constructs for unobservables such as traits, functions, and causal forces.

As such, an abstract concept can encompass qualities that are associated by virtue of underlying causal forces, thematic representations, or relations between items. Vonk and Povinelli (2006) focused on the notion of unobservables to represent a class of objects that are strictly hypothetical and cannot take on physical form: constructs such as thoughts, memories, ideas, beliefs and physical forces, such as gravity. The numerical concept of zero, or the absence of something, can also be considered abstract, as can the idea of sameness or difference, which pertains to the relationship between objects. Abstraction is required when the relationship between exemplars within an overarching category must be *inferred* based on observable qualities rather than derived directly from them. That is, having a concept of sameness goes beyond matching something orange to something else orange based on perceived perceptual similarity to abstracting the general relation “same” that could potentially be generalized to two green items or two items of the same shape or material.

Experimental Methods to Study Abstraction

The human capacity for language allows for representational content to be communicated. Humans have words for constructs that cannot be visualized, such as thoughts, physical forces, and language itself. Nonhumans do not have the luxury of communicating their thoughts in symbolic form, and therefore the content of their minds must be inferred through categorization tasks, such as matching-to-sample (MTS) and two alternative forced choice tests (2AFC),

where they are required to match a comparison stimulus to a sample based on a perceived relation (similarity as in traditional identity MTS or conceptual MTS tasks, or difference, as in oddity MTS tasks), or to choose members among pairs of items that belong to the same conceptualized category (2AFC tasks). Nonhumans are quite skilled at perceiving perceptual similarity and categorizing items that share qualities such as shape or color (Vonk 2003), but there is less evidence for their ability to categorize on the basis of more abstract qualities, such as social relationships (Vonk 2002; Vonk and Johnson-Ulrich 2014). One area in which many nonhumans excel is numerosity, which has been suggested to comprise a lower level of abstraction that might serve as a foundation for higher level symbolic thinking, which in turn may give rise to language and analogizing (Coolidge and Overmann 2012).

Researchers have presented stimuli at various levels of abstraction with categories ranging from concrete to more abstract. Concrete categories include exemplars that may look very much alike, such as bears versus humans, whereas abstract categories are broad and contain many diverse exemplars, such as “animal,” which contains insects, reptiles, fish, birds, and various mammals. Both great apes and American black bears have been shown to form categories at each level of abstraction tested, when presented with natural categories, but it has proven difficult to determine which features these animals use to perform the tasks successfully (Vonk and Galvan 2014). The possibility remains that animals are relying on perceptual features, such as particular color, luminosity, and contrast patterns to control responding in these tasks, rather than generating an overarching category such as “animal.”

Perhaps the most abstract concept assessed in nonhumans is the capacity to represent mental states, in particular the mental states of others. This capacity is known as theory of mind (ToM) and has been widely studied in both human children and nonhuman species. Although evidence for ToM in nonhumans has been hotly contested (Penn and Povinelli 2007), researchers have begun to converge on the idea that at least some species, such as great apes, may have an

understanding of some mental states, such as seeing and intentions. Evidence for understanding of knowledge states and beliefs is more equivocal. It has yet to be demonstrated that any nonhuman species represents the range and breadth of abstract concepts that can be communicated by humans through the use of symbolic systems, most notably language.

Conclusion

The extent to which nonhumans represent concepts for things that are abstractions of real objects remains uncertain as researchers struggle to make progress with experimental paradigms that will allow for a careful dissection of processes linked to observable features and those that depend upon an internal representation of an overarching conceptual category subsuming such features (Vonk and Povinelli 2006).

Cross-References

- [Concept Formation](#)
- [Concept Formation](#)
- [Learning](#)
- [Non-Human Primates](#)
- [Same-Different Categorization](#)
- [Theory of Mind](#)
- [Unobservability Hypothesis, The \(Vonk and Povinelli, 2006\)](#)

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Abstraction

- [Abstract Concept Formation](#)

Abuse

- [Physical Aggression](#)

Abusers: Husbands, Boyfriends, and Former Sexual Partners

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Synonyms

[Intimate partner violence](#); Men’s aggression against women.

Definition

Abusers are those individuals who use strategies of intimidation, threat, isolation, and physical and sexual aggression against a victim. There are different forms of abuse, which can be broadly categorized into physical, sexual, and emotional abuse. When the victims are women, the abuser is often someone close to the victim, especially male partners and male ex-partners.

Introduction

Aggression in the context of a relationship, also called intimate partner violence (IPV), has been documented across several cultures (see Archer 2006), having detrimental impacts on the victims' health, such as physical injuries, poorer cognitive functioning, and psychological problems (Lawrence et al. 2012) and on the relationship, predicting relationship dissatisfaction (Hammett et al. 2017). While Archer (2000) found in a meta-analysis that among young American couples, women are slightly more likely to use physical aggression than men, men are more likely to cause an injury in their partners, such that women represent 62% of injured partners. In the United States (US), 33% of female murder victims are killed by their partners against 3% of male murder (Fox and Zawitz 2007b). In fact, data collected worldwide demonstrated that 30% of women reported to have experienced intimate partner violence at some point in their lives, while 38.6% of female murders are committed by intimate partners (Devries et al. 2013). Such statistics demonstrate that women's current or former partners are often their abusers, and despite much research looking for potential explanations from different perspectives, predicting and preventing intimate partner violence remains a challenge.

Ultimate explanations of male aggression against women have traditionally highlighted social and cultural aspects as the driving factors behind this phenomenon. For example, a feminist perspective emphasizes the role of a patriarchal

system, marked by male dominance, in male abuse against women (Johnson 2011). More comprehensive approaches have considered a combination of several factors such as individual, interpersonal, and family factors; neighborhood and community; and policy, systems, and society (Beyer et al. 2015). In this entry, however, I will consider an evolutionary perspective, exploring the idea that male intimate partner aggression has evolved because it served survival goals, therefore reflecting male reproductive striving. Before discussing why men are particularly aggressive toward their partner or former partners, I will first discuss why men have a tendency to be more physically aggressive than women. For the purposes of this entry, the terms partner aggression and partner abuse will be used to describe any episode of physical, sexual, or emotional abuse practiced by a current or former partner.

Human Aggression: Why Are Men More Physically Aggressive than Women?

In our evolutionary past, when resources that were necessary for survival, such as food, shelter, and mates, were in short supply in the environment, to secure such resources, individuals needed to engage in competition with others, which usually required physical aggression. Whilst the winner of the contest would take home the prize, the loser would end up seriously wounded or dead (Campbell 2015). Although both men and women need resources, and therefore both would benefit from competition, the costs associated with engaging in competition vary across sexes. Overall, while men are more prone to engage in contests, women are generally more cautious and avoid physically aggressive competition.

To understand the nature of these differences, we need to take a closer look at the roles of men and women in reproduction. While men's direct contribution to reproduction is limited to copulation, women carry a disproportionate reproductive burden (Fathalla 2015). Women are responsible for the intrauterine care of fetuses and embryos

during a 9-month pregnancy, which is among primates the longest duration of gestation. On top of this, women are also responsible for postnatal parental care, particularly breastfeeding that may last several years. Whilst men increase their reproductive success by dominating other male competitors to secure access to females for copulation and other resources, women do best by avoiding direct conflict and staying alive to protect their offspring (Campbell 2015). This helps to explain why, overall, men are usually more aggressive and more willing to take risks than women are. This also offers an idea of how women became more vulnerable to partner aggression, but it is not the whole picture. Furthermore, this does not explain why men can be particularly aggressive toward their own partners.

How Did Women Become More Vulnerable to Partner Aggression?

One of the main assumptions of Trivers' (1972) parental investment theory is that the sex that invests more heavily in reproduction will be more selective in choosing a partner. This means that men would benefit from mating with basically any fertile woman, whereas women would be more selective and pick a mate with the best possible genes, or a mate that is willing to provide women with resources such as protection and parental care (Puts 2016; Trivers 1972). As such, women become a valuable limiting resource for men because men's opportunities to reproduce are constrained by women's willingness to mate with them (Daly and Wilson 1988). This creates a clear conflict of interest and if there were no consequences, the use of physical force would allow men to secure access to as many partners as possible and as a result, give them higher chances to reproduce and pass on their genes, as it happens among other primates (Baniel, Cowlishaw, and Huchard 2017). Although sexual coercion among humans is not rare (Jeffrey and Barata 2017), explaining men's aggression against their female partners is not that straightforward and other factors also need to be considered.

From an evolutionary perspective, Smuts (1992) argues that male aggression against women may have become relevant in the context of exclusive mating relationships, reflecting men's reproductive striving. Long-term committed relationships are the preferred human mating strategy that evolved to ensure people's reproductive success (Maner and Miller 2010) by solving adaptive problems such as investment in offspring, acquiring resources, and maintaining female fecundity (Conroy-Beam et al. 2015). Sex-specific benefits for women would include greater access to resources and gaining protection, whereas for men the main benefits would be increasing probability of paternity and access to better mates (Buss 2003). Smuts (1992) hypothesizes that, in our evolutionary past, women became more vulnerable to aggression from their own partners because other men would be less likely to interfere and risk jeopardizing male-male alliances. Although this explanation is only speculative, it helps to understand how women may have become more vulnerable to intimate partner aggression; however, it does not explain what motivates men to hurt their own partners.

Why Do Men Hurt Women They "Love"?

Although exclusive romantic relationships have provided several benefits for both sexes and solved adaptive problems, such arrangements also have created extra adaptive problems. Once a high-fitness partner has been secured, individuals face potential threats, such as the threat of mate poachers, to the relationship that may lead to infidelity or to relationship dissolution, which would imply the loss of all the benefits brought about by an exclusive relationship (Conroy-Beam et al. 2015). Infidelity represents a great threat to relationships, representing one of the main reasons for divorce (Fincham and May 2017). Whilst it may be disturbing for both sexes, men find it particularly costly, because infidelity may result in investment of men's resources in other men's offspring, and damage to their reputation (Shackelford et al. 2015). In fact, men's jealousy over women's infidelity is one of the main driving

forces behind lethal and nonlethal male aggression against their partners (Stieglitz, Gurven, Kaplan and Winking 2012). This is consistent with the hypothesis that romantic jealousy is an evolved adaptation designed to preserve a relationship, avoid infidelity by the partner, and therefore, retain access to the partner's relevant resources (Daly et al. 1982). Cues of a partner's infidelity activate jealousy emotions that, in turn, will put in motion strategies to deal with such a threat (Bendixen et al. 2015).

Strategies designed to solve the adaptive problem of partner potential infidelity and prevent relationship dissolution are regarded as mate retention strategies (Buss 1988). Buss (1988) identified several mate retention tactics directed either to the partner (intersexual tactics), which is our focus in this chapter, or to a potential rival (intrasexual tactics). Tactics directed to the partner can be both positive, which means that they operate by providing benefits to the partners such as love and care, and negative, in which case they operate by inflicting costs on the mate. The cost-inflicting tactics within the set of intersexual strategies are: (1) *direct guarding*, involving vigilance, concealment of mate, and monopolization of mate's time; (2) *negative inducements*, which describe behaviors such as infidelity threat, punishment of mate threat to commit infidelity, and emotional manipulation; and (3) *public signs of possession* that reflect verbal and physical possession signals. Such behaviors reflect one's attempts to restrict and regulate partner's sexual autonomy and are hypothesized to be an adaptive solution for the problem of intrasexual competition for mates because ancestral men who used such strategies were more reproductively successful since they were better at avoiding threats from rivals and at preventing partner's infidelity.

Such categories describe different forms of controlling women's sexuality by using force or its threat to increase the chances that a female will mate with the aggressor or to decrease the chances that a female will mate with a rival. Therefore, male abuse against their female partners is an attempt at deterring the partner from engaging in infidelity, which could result in paternity uncertainty and mistakenly allocating resources to a

rival's offspring. In fact, Shackelford et al. (2015) across several studies demonstrated that male mate retention tactics, particularly direct guarding and negative inducements, predict male aggression and abuse in general, providing further evidence for the hypothesis that male aggression toward their female partners reflects a male reproductive strategy.

In some extreme cases, abuse may take the form of rape. Evolutionary psychologists have hypothesized that men sexually violate their partners in circumstances of increased risk of sperm competition, which is the competition of a different male's sperm to fertilize a female's egg (McKibbin et al. 2013). This would happen particularly when a man suspects or finds out that his partner has been sexually unfaithful, in which case she risks being impregnated by a rival. In such cases, men may force themselves on their partners to engage in sperm competition and avoid investing in offspring that is not their own. A study testing this hypothesis directly demonstrated that men who suspected of a partner's infidelity were more likely to perform sexually coercive behaviors, such as rape (Goetz and Shackelford 2006). This supports the hypothesis that men have evolved psychological mechanisms that will motivate them to commit partner rape in the prospect of sperm competition as a response to partner infidelity.

Despite, or as a consequence of, a male's efforts to retain a mate, the partner may end the relationship, which may also motivate male aggression against women. Partner defection causes not only the loss of their resources but can also negatively affect the formation of new relationships. For example, it has been documented that the discovery that someone was rejected by their former partner negatively affects people's desire for dating them (Stanik et al. 2010). As such, because relationship dissolution results both in the loss of the former partner's resources and problems to have access to a new partner, the rejected man may make use of a series of strategies either to prevent the partner from dating again or to regain access to the partner or both. Over the course of our evolutionary history, women have suffered male abuse because of

sexual rejection. Strategies may include threats, stalking, and violence, which may reflect a desperate tactic and last attempt to reacquire the partner, reflecting a mate retention strategy (Buss and Duntley 2014).

Is There a Typical Abuser Profile?

Male aggression against women in general functions as a controlling tool over women's behaviors because of the high costs to women of physical injury inflicted by men. However, most men do not abuse their partners or make use of extreme measures of coercion such as physical aggression. This suggests that, on a proximal level, there are variables that influence the usage and/or intensity of male partner abuse, such as the own attributes of the abuser. Studies have focused particularly in identifying any common characteristics in abusers to elaborate a male abuse profile. However, despite some typologies available in the literature (e.g., Holtzworth-Munroe and Stuart 1994), studies have failed to provide systematic evidence regarding the psychological characteristics of abusers (Dobash et al. 2009). Recent research profiling male abusers comparing generally extra-family violent men and generalist batterers showed that these two groups do not significantly differ in their individual, family, and community characteristics, suggesting that aggression toward a partner shares a common ethiology with general aggression (Juarros-Basterretxea et al. 2018). Gondolf (2002) compared intimate partner abusers to men from the general population, but did not find substantial differences regarding psychological problems, although a small proportion of men in the first group are described as having serious psychological problems. As pointed out by Dobash et al. (Dobash et al. 2009), such mixed evidence suggests that male abusers are not actually mentally disturbed, but that they are just ordinary men, which makes it harder to predict and prevent such problems.

However, despite the apparent absence of an abuser's typical profile, men's attributes seem to influence the usage and intensity of aggression toward their partners as studies have shown

differences between abusers and non-abusers. Such differences appear to confirm the evolutionary view of male aggression as an instrument of male domination over women. For example, partner male abusers, in comparison to non-abusers, report lower self-esteem, which is associated with jealousy, greater justification of male dominance, and use of aggression for conflict resolution (Diaz-Aguado and Martinez 2015). Men's possessiveness, jealousy, and sense of entitlement are also characteristics that contribute to partner abuse, particularly to extreme cases that end in murder (Daly and Wilson 1988). Analyzing those men who make use of extreme forms of violence, neuropsychological studies analyzing male batterers have demonstrated that this group presents low performance of tests on executive functioning, verbal skills, and vocabulary (Bueso-Izquierdo, Hart, Hidalgo-Ruzzante, Kropp, & Pérez-García 2015), suggesting that these men may use violence as their form of communication in the relationship. On top of that, male batterers also have thinner brain areas related to emotion processing such as prefrontal and limbic brain areas, in comparison to other criminals, suggesting that they have poorer emotion regulation (Verdejo-Román et al. 2018). Such characteristics seem to describe a dominant and possessive male profile that find violence as a way of solving conflicts, particularly in the context of a relationships. This is consistent with the evolutionary hypotheses describing men's abusive behaviors as a way of retaining a partner and ultimately enhancing their reproductive success.

Conclusion

The evolutionary theory can tell us a lot about why men are usually more physically aggressive than women, and why they quite often direct their aggressive behavior toward their partner. In this entry, I have reviewed some evidence supporting the evolutionary view that male aggression toward their partners may be a reproductive strategy. Essentially, physical, psychological, or sexual abuse performed by men in the context of a romantic relationship are extreme, and sometimes

desperate, strategies to prevent their partners from engaging in infidelity or ending the relationship. I demonstrated this by reviewing current literature on male mate retention strategy and jealousy, demonstrating that abusive men are more jealous and possessive. In turn, jealousy predicts the usage of mate retention tactics that reflect men's efforts to retain a valuable partner and consequently ensure access to the partner's resources. Such strategies may include different types of abuse, going as far as physical aggression. Therefore, the different forms of abuse perpetrated by men against their partners are part of male reproductive strategies, reflecting men's attempt at dominating women. I discussed how male partner abusers tend to be more jealous, justify male dominance, and have poorer emotion regulation, which contributes to the usage of more extreme forms of abuse, such as physical aggression.

It is important to consider here, however, as argued by Smuts (1992) that adopting an evolutionary view of spouse abuse is not an attempt to justify intimate partner aggression or to explain the relations between the sexes using deterministic assumptions. The aim of this entry was simply to discuss the idea that male partner abuse happens because men found aggression to be a powerful tool to dominate women and enhance their reproductive success. This does not mean, however, that men are inherently aggressive, and women are inherently submissive. Male partner abuse is not inevitable, and as discussed earlier in this chapter, most men do not use measures of control over their partners, but that there are certain male attributes and circumstances that may trigger such behaviors. Additionally, despite the temporary "advantages" that the use of aggression apparently brings for men, there are a number of costs that – not rarely – outweigh its benefits.

Cross-References

- ▶ [Aggression for Sexual Access](#)
- ▶ [Contexts for Men's Aggression Against Women](#)
- ▶ [Intimate Partner Violence](#)
- ▶ [Violence to Control Women's Sexuality](#)

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Access to Alloparents

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Synonyms

[Allocare](#); [Allomother](#); [Babysitting](#); [Childcare](#); [Cooperative breeders](#)

Definition

An alloparent is any individual who is not the biological parent, who helps to raise the child by providing direct or indirect investments. Alloparents may include kin members such as

grandparents, siblings, aunts and uncles, as well as nonkin such as friends, neighbors, and professional caregivers.

Introduction

Several prominent scientists studying human behavior from an evolutionary perspective have proposed that humans are cooperative breeders. Cooperative breeding is loosely defined as a breeding system where mothers require help from other individuals for successful childrearing (Hrdy 2005).

This proposal stems from the observation that human neonates are incredibly helpless compared to other primates, only able to carry out basic functions. Human prematurity at birth is coupled with a slow development and maturation period throughout childhood and adolescence. Consequently, children require high levels of care over a prolonged period of time to successfully reach adulthood. Such intensive caregiving is a near-impossible task for mothers to complete on their own – especially given the fact that, at least in natural fertility populations, mothers tend to have multiple dependent offspring.

It has been argued that these factors have led to the coevolution of facultative parental investment (i.e., fathering) as well as “alloparenting” (i.e., nonparental childrearing support) (Hrdy 2005). Indeed, alloparenting is arguably a cross-cultural universal, though who helps and how they help varies within and between populations.

Alloparenting can be conceptualized in different ways depending on the type of investments and its effects on parenting. Further, the general relationships between alloparental investments and parental investments may vary from population to population. Evolutionary theory predicts that the relationship between alloparental and parental investments will influence pair-bond stability.

Cross-Cultural Examples of Alloparenting

Starting with forager populations, hunter-gatherers generally have a wide network of

allomothers who provide care and share food with infants and children. For example, in both the Hadza of Tanzania and the !Kung of Botswana, weaned toddlers who are too heavy to be carried are left in camp while their parents go on foraging and hunting trips. These toddlers stay in camp with other children, teenagers, and a few adults who provide informal care (Hewlett and Lamb 2005). In the Efe of the Democratic Republic of Congo, infants were found to have an average of 15 caregivers at 4 months old (Hewlett and Lamb 2005), and in the Aka of the Central African Republic, infants were found to have an average of 21 caregivers (Meehan 2009). While mothers are generally the main caregivers across all these populations, childrearing among foragers is largely a collective venture whereby children have access to numerous alloparents.

With agriculture, the childrearing system tends to focus more strongly on maternal care. Nonetheless, the necessity of “help for mothers” is often acknowledged as women face trade-offs between agricultural labor and childcare. For example, in some sub-Saharan agriculturalists such as the Giryama of Kenya and Fulani of Burkina Faso, women who are responsible for food cultivation and childrearing collaborate with each other to share food-processing tasks and child care. In the Gussi of Western Kenya, the job of assisting mothers with childcare is often given to older daughters (LeVine et al. 1996).

In developed populations with stronger nuclear family norms, childcare is generally treated as the responsibility of the mother. Nonetheless, kin and nonkin allomothers universally contribute to childrearing. In addition to fathers, grandmothers have been found to be particularly important alloparents who provide childcare and influence parenting behaviour. When alloparenting by kin is less common, state provision of formal childcare takes prominence, such as the “collectivist” approaches to childcare seen in Nordic countries (Emmott 2015).

Categories of Alloparental Investment

Alloparents who provide help with childrearing, in essence, are providing investments into child

quality (i.e., improving their fitness and future reproductive success). Across 37 high-fertility, high mortality populations, the presence of alloparental kin has been associated with greater child survival, though who matters for children seems to vary between populations.

Alloparental investments can be categorized and differentiated as: (1) direct versus indirect investments, (2) caregiving versus provisioning, and (3) substitutive versus additive investments.

First, direct alloparental investments are *any investments made by the alloparent straight to the child*, for example, by providing direct childcare, playing, or teaching. Indirect alloparental investments are *investments made by the alloparent to the child via a mediator*, for example, when an allomother provides monetary support to the mother who uses that money to feed the child. Second, these alloparental investments may also be described as caregiving and provisioning. By default, caregiving is a direct investment made straight to the child. Provisioning, on the other hand, involves a transfer of resources either directly to the child or indirectly via a mediator. Finally, allomaternal investments may either be substitutive or additive, depending on the impact it has on parental investments. As the terms suggest, substitutive investments *replace parental investments*, allowing parents to direct their freed-up energy, time, and resources into other domains of behavior. In contrast, additive investments are additional investments children receive *without impacting parental investment levels*.

Studies suggest that alloparental investments through direct care and provisioning often substitute maternal investments in high-fertility populations, encouraging mothers to divert their time to and effort into other activities. In the Karo Batak farmers of Indonesia, help from matrilineal alloparents was associated with greater childcare and lower levels of farm work by the mother, while help from patrilineal alloparents was associated with lower levels of childcare and greater levels of farm work by the mother (Kushnick 2012). Similarly, in the Aka foragers, direct caregiving by allomothers was associated with lower levels of maternal care and higher levels of foraging (Meehan 2009).

Across developed populations, direct grandparental caregiving has been associated with reduced maternal childcare and greater labor force participation, suggesting a substitutive relationship between direct alloparental care and maternal investments. However, this is not a universal relationship found across countries (Assave et al. 2012). Further, indirect alloparental investments through financial help have been found not to correlate with maternal investment activities (Emmott 2015), suggesting provisioning for children in developed populations may be an additive rather than a substitutive investment.

Alloparents and Pair-Bond Stability

Assuming that pair-bonds function as a reproductive contract, evolutionary theory predicts that pair-bond stability is influenced by the trade-off in the “loss” of other mating partners (i.e., future reproduction/mating effort), against inclusive fitness benefits of a cooperative pair-bond (i.e., current reproduction/parenting effort). Given the facultative nature of paternal investments, a key determinant of this trade-off is the impact of fathers on child quality. If successful childrearing is dependent on paternal investments, this should serve as an incentive to maintain cooperative pair-bonds. In contrast, if mothers can successfully rear children without help from fathers, the costs of maintaining a relationship may outweigh the benefits. Indeed, studies have suggested that divorce across developed populations is more likely when women are financially independent.

Alloparent availability may impact pair-bond stability by influencing the necessity of paternal investments for successful childrearing. If alloparental investments can effectively substitute paternal investments, the costs of pair-bond dissolution on child fitness are reduced. This may lower the incentive for mothers and fathers to maintain their pair-bonds, as well as increase the incentive for parents to seek alternative mates. While research in this area is sparse, studies have found evidence of increased alloparental investments followed by father absence (Bentley and Mace 2009). An examination of the Standard

Cross-Cultural Sample has found that populations with higher rates of allomaternal childcare are associated with higher rates of divorce (Quinlan and Quinlan 2007).

Conclusion

Alloparenting is a fundamental aspect of the human childrearing system, with examples of alloparenting seen across societies. Childrearing support from a range of helpers can directly and indirectly influence child quality, which in turn may influence parental behavior. It is important to remember that the trade-offs mentioned above exist among a myriad of other costs and benefits surrounding parental/alloparental investments and pair-bonding. One must also not forget the importance of cultural norms and rules which may encourage or restrict behavior. Nonetheless, if alloparental investments are effectively able to substitute paternal investments, evolutionary theory predicts that it would facilitate pair-bond dissolution.

Cross-References

- ▶ Kin Selection
- ▶ Life History Theory
- ▶ Women's Long-Term Strategies
- ▶ Parental Investment Theory
- ▶ Women's Long-Term Strategies

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Access to Resources

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Synonyms

Resource availability

Definition

Opportunity to acquire food, shelter, mates, and other necessities for survival and reproductive success.

Introduction

Natural selection is a straightforward process: Variation exists among individuals, and some of

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this variation is heritable. Some heritable attributes allow individuals to better cope with survival pressures such as predation or climactic changes and to enjoy greater success when competing for resources or mates. These individuals will leave more copies of their genes in the gene pool than individuals with less successful traits. The genetic contribution of an individual to the next generation's gene pool (relative to the average for that population) is referred to as fitness.

From an evolutionary standpoint, therefore, the fundamental problem that an organism must solve is maximizing reproductive success which in turn reduces to maximizing access to fertile mates and resources.

An individual's access to mates and resources depends on several factors. The spatial arrangement of resources in habitats influences the distribution of individuals within the habitat and their ability to acquire resources. The space between individuals is generally greater in habitats in which resources are uniformly or randomly distributed. Many environments are characterized by "patchy" resources; the density of resources (such as forage plants and water) varies spatially (clumped resources) or temporally (e.g., abundant during the rainy season and sparse during the dry season). When resources are distributed this way, individuals tend to "clump" together around them. These "clumps" typically are more than simple aggregates. Instead, they frequently constitute social groups that are characterized by kinship and rank relationships that greatly influence access to available resources.

Sociality refers to the degree to which individuals in an animal population tend to associate and interact with each other in social groups. Social living yields a reduction in predator pressure by improved detection or repulsion of enemies, improved foraging and hunting efficiency, improved defense of limited resources against intruders, improved access to potential mates, and improved care of offspring through communal feeding and protection. But there are also costs associated with sociality, including increased competition within the group for fertile mates and resources.

Kinship and Access to Resources

A key characteristic of social species is an inclination to behave more altruistically toward kin than toward unrelated individuals. Individuals are more likely to share resources with genetic kin, alloparent their offspring, and come to their defense during agonistic encounters. This is referred to as kin selection.

Status and Access to Resources

In most species, particular individuals have priority of access to resources in competitive situations. These individuals are referred to as high status, those who have lower priority of access are called low status, and the social structure of the groups is called a status (or dominance) hierarchy. Because of this differential access to resources, higher-status individuals are less likely to die of predation or starvation and more likely to leave living offspring (Clutton-Brock 1988). Among species in which status is unstable, the level of reproductive success achieved by any individual is directly related to the length of time during which that individual is high ranking (Altmann et al. 1996). Accordingly, there is a direct relationship between status and *inclusive fitness*, (reproductive success of individuals and their closely related kin).

Among humans, status hierarchies are apparent in the social groups of children as young as 3 years of age (Smith 1988). Human societies frequently take the form of status hierarchies, such as caste systems, feudalism, and modern socioeconomic stratification. Socioeconomic status has been reliably and repeatedly linked to several health indices, and these correlations cannot be explained simply in terms of differential access to health care, smoking, or other objective factors (Adler et al. 1993). Put simply, status is directly tied to an individual's ability to survive, to reproduce, and to take care of oneself, one's offspring, and one's kin.

Investigations of social interactions in a variety of species (including humans) suggest that status hierarchies are supported by a collection of

specific *cognitive* skills and that those who achieve high status are those who are particularly adept at them. These skills include (a) being adept at learning the implicit rules that constrain behavior in one's social group and monitoring compliance with them, (b) forecasting and influencing the behavior of others, and (c) forming powerful alliances based on reciprocal obligations (reciprocal altruism) (Cummins 2005). High-ranking individuals monitor the behavior of subordinates in order to protect their privileged access to resources. Subordinates engage in deceptive behavior that improves their access to resources. For example, they conceal objects or behaviors from others by hiding them from view, acting quietly so as not to attract attention, avoiding looking at a desirable object themselves, or distracting attention away from the desired object or forbidden behaviors. Subordinates also garner a larger share of resources by forming alliances with forbidden individuals through surreptitious food sharing or grooming, alliances that can be called upon during contests of rank.

Sex Differences in Access to Resources

There is a significant initial difference between potential reproductive success of males and female mammals. The ceiling for reproduction is much higher for males than females because sperm are plentiful and continually replenish, while eggs decline in number during a female's lifetime. Females also necessarily invest more energy in reproduction than do males (e.g., pregnancy and lactation) and are typically more involved in the care of very young offspring.

Female reproduction, therefore, is limited primarily by access to resources. Once a pregnancy has occurred, females cannot increase their reproductive success by engaging in further matings. Because of the greater cost to females in producing young, they increase their lifelong reproductive success by investing in their offspring to ensure their survival.

In contrast, males can increase their reproductive success by maximizing the number of fertile

females with whom they mate. If the number of males in a population is approximately equal to that of females, then there exists enormous pressure for competition among males for access to fertile females, and there will exist greater variability in male reproductive success: For every male who gains reproductive access to a disproportionate share of females, other males lose opportunities to reproduce. For this reason, male reproduction is limited primarily by access to fertile mates.

These differential reproductive pressures manifest as different mating strategies (or implicit biases) for men and women (Schmitt et al. 2003). Men seek mating opportunities with as many fertile females as possible, while females are choosy, preferring fertile mates with ample resources. Men tend to seek and acquire resources as markers of success, which in turn provides access to a wider pool of potential mates. In contrast, women primarily seek resources to support and maintain themselves and their children (World Bank Development Report 2012). Income considerations are secondary to family issues, and women will delay childbearing in order to acquire resources.

These sex differences are not obligate human traits but are instead facultative traits – they are deployed or modified to suit current environmental exigencies. For example, in polygynous societies that restrict the avenues women may pursue to obtain resources, women typically prefer to be one of many co-wives of a prosperous man than the only wife of a poor one (Betzig 1986). But when men do not constitute reliable avenues to greater resources relative to what women themselves can acquire directly, female mating strategies shift. Kasser and Sharma (1999) analyzed mate preference data across 37 cultures and found that females strongly prefer resource-acquisition characteristics in mates when their cultures limit their reproductive freedom and their educational opportunities. Zentner and Mitura (2012) examined the desirability of mate attributes among nearly 12,000 individuals across 31 nations and found that sex differences in mate preferences declined proportionally to increases in nations' gender parity.

Conclusion

An individual's access to resources depends not simply on the availability of resources in the environment but also upon the individual's place within the social group. Individuals are more likely to share resources with kin than non-kin. They are also more likely to share resources with non-related individuals if those individuals have shared resources with them in the past (reciprocal altruism). In competitive situations, some individuals achieve priority of access to resources, and are referred to as high-status or high-ranking individuals. Lower-ranking individuals improve access to resources by forming alliances with high-ranking individuals. In some species, lower-ranking individuals also increase their access to resources by engaging in deception.

Cross-References

- ▶ [Competition for Resources Desired by Females](#)
- ▶ [Cooperative Alliances](#)
- ▶ [Dominance and Health](#)
- ▶ [Dominance in Humans](#)
- ▶ [Female Mate Choice](#)
- ▶ [Higher Status in Group](#)
- ▶ [In Nonhuman Primates](#)
- ▶ [Kin Selection](#)
- ▶ [Mate Selection Strategy](#)
- ▶ [Mate Value](#)
- ▶ [Nonhuman Primates](#)
- ▶ [Primate Dominance Hierarchies](#)
- ▶ [Reciprocal Altruism](#)
- ▶ [Reproductive Strategy](#)
- ▶ [Resource Competition](#)
- ▶ [Resource Defense](#)
- ▶ [Sex Differences](#)
- ▶ [Sexual Contact and Sexual Disgust](#)
- ▶ [Sexual Strategies Theory](#)
- ▶ [Social Status and Economic Resources](#)
- ▶ [Social Dominance and Sexual Access](#)
- ▶ [Status and Dominance Hierarchies](#)
- ▶ [Status and Redistribution of Resources](#)
- ▶ [Status and Reproductive Success](#)

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Accuracy of Self-Knowledge

- ▶ [Accuracy of Self-View](#)

Accuracy of Self-Perception

- ▶ [Accuracy of Self-View](#)

Accuracy of Self-View

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Synonyms

Accuracy of self-knowledge; Accuracy of self-perception; Self-awareness; Self-insight

Definition

Accuracy of self-view refers to having accurate (or realistic) perceptions and making accurate evaluations about oneself (e.g., one's traits, abilities, attitudes, and so on); it is usually operationalized as the extent to which the individual's estimates of themselves agree with independent estimates obtained from knowledgeable others, observations of behavior, and implicit assessment.

Introduction

The notion that accurate self-view is important has a long history dating back to the Greek dictum to “know thyself,” originally engraved on the Temple of Apollo at Delphi. In theory, accurate self-knowledge enables one to establish realistic expectations of oneself and is essential for self-regulation and self-development. Indeed, accurate perception of self and reality is considered to be a prerequisite of mental health and psychosocial adjustment (e.g., American Psychiatric Association 2013). Yet, many findings highlight obstacles to accurate self-perception and suggest that most people are rather poor at self-assessment (e.g., Brown and Dutton 1995).

Perspectives on Accuracy of Self-View in the Psychological Literature

Over 100 years ago, Freud noted that the conscious mind is simply the tip of the iceberg. Thoughts, memories, and desires that are unacceptable to the rational and conscious self are held below the surface of conscious awareness, although they continue to exert a great influence on behavior. Their full expression is prevented by the unconscious deployment of defense mechanisms, some of which are more primitive (e.g., reaction formation) and other more mature (e.g., sublimation; Freud 1936). Although the defense processes in themselves are not pathological phenomena, they often turn out to be detrimental. Simply put, the cost of self-deception is psychopathology. And so, the aim of psychoanalysis is making the unconscious conscious, which requires subjecting an automatic and unconscious regulation to conscious thinking (Freud 1904). Insight and the attainment of accurate self-knowledge are seen as primary curative factors also in humanistic psychotherapy (Rogers 1951).

Many theorists share Freud's skepticism about how well people can know themselves. In fact, the contention that information is processed unconsciously is now a basic assumption of cognitive science. The so-called cognitive unconscious is not the consequence of defenses against self-threatening perceptions, but reflects the architecture of the mind. Numerous dual-process theories posit the existence of two interactive modes of information processing and, hence, two ways of knowing oneself, one conscious (rational, analytic, controlled, explicit), and the other unconscious (experiential, intuitive, automatic, implicit; Wilson 2009). As postulated by Epstein's (2003) cognitive-experiential self-theory, people's self-views are best understood in terms of their implicit self-theories. These automatically constructed theories address the four basic needs: to maximize pleasure and minimize pain, to maintain relatedness with others, to maintain the stability and coherence of one's

conceptual system (i.e., self-verification), and to enhance self-esteem (i.e., self-enhancement). People's implicit self-schemas cannot be accessed directly and may or may not be accurately reflected in their explicit self-evaluations. Previous studies on the relationship between implicit and explicit attitudes and self-esteem have shown that they are weakly to moderately correlated (e.g., Greenwald and Farnham 2000). Also, there is neurological evidence of divided consciousness, with the left and right hemispheres processing information differently and encoding different kinds of knowledge (Krebs et al. 1988).

The idea that people pursue accurate self-knowledge is a key assumption of social comparison theory (Festinger 1954) and self-assessment theory (Trope 1979). Other social-cognitive approaches posit that there are various motives affecting the way people expect, process, and react to the self-relevant information. According to Sedikides and Skowronski (2000), these are valuation motives (i.e., self-enhancement and self-protection), learning motives (i.e., self-assessment and self-improvement), and homeostatic motives (i.e., self-verification). Of these motives, only self-assessment prompts people to seek out accurate and objective self-relevant information, and it may operate independently, coincide, or conflict with other motives. Which of these self-motives governs one's reaction to feedback depends on individual differences and situational influence (e.g., task or attribute ambiguity). Nonetheless, several studies have found defensive motives (i.e., esteem- and consistency-related) to be more powerful determinants of the self-evaluation process than accuracy concerns (e.g., Sedikides 1993). The self-serving attributional bias and the illusion of control are examples of the phenomena that reflect self-enhancement biases in self-perception (e.g., Krebs et al. 1988).

In order to integrate the various models of self-perception, and to capture the role of basic motivational, cognitive, and affective processes in the self-perception process, Robins and John (1997) offered four metaphors of the self-perceiver. In some ways people are scientists, motivated by self-assessment and dispassionately searching for truth. In some respects they act like consistency seekers, driven by self-verification, and in some

they behave like egoists, motivated toward self-enhancement, and like politicians, concerned with popularity. These metaphors are not personality types, but serve as lenses through which self-perception accuracy and deviations from accuracy can be analyzed and interpreted.

As noted by Funder (2003), the avoidance of judgment error and the achievement of accuracy should not be treated as the same things. His realistic accuracy model suggests that accuracy is a function of the relevance, availability, detection, and utilization of behavioral cues. In other words, the accurate judgment of personality is possible provided that one emits relevant behavior, notices, and interprets it correctly. The model implicates that to know oneself better, one should first and foremost seek out contexts that encourage one's self-expression (Funder 2003).

Evolutionary Account of Accuracy of Self-View

The evolutionary adaptive utility of an accurate self-view appears to include enhancing functioning of the individual within the group as well as facilitating functioning of the group as a whole. For example, accurate self-knowledge allows individuals to engage in environments that match their skills and abilities – if an individual discovers that they are good at child-watching, exercising this skill to its fullest extent would likely benefit them and the group. Also, accurate self-knowledge enables individuals to find their positions in the social hierarchy, hence reducing conflict with conspecifics (Sedikides and Skowronski 2000). If an accurate self-view is adaptive, why would an inaccurate one be tolerated by the selection process?

Some theorists suggest that self-deception make individuals better able to deceive others (e.g., von Hippel and Trivers 2011). Because humans inadvertently reveal their deceptive intent through verbal and nonverbal clues, those who are taken in by their own lies make their deception harder to detect. Also, self-deception benefits deceivers by reducing the cognitive load associated with deceiving and by reducing retribution if their lies are exposed. It should be noted that,

by helping to better deceive others, self-deceptive beliefs serve both short-term strategies of cheating and long-term strategies that depend on maintaining reciprocity relationships (Nesse 1990).

Others argue for a pragmatist view of knowledge and suggest that biases in self-conception function as pragmatic shortcuts for self-understanding that, all in all, give rise to functional conclusions and behaviors that enhance an individual's fitness (e.g., Krebs et al. 1988). Beliefs that make one feel good, secure, and in control are adaptive, regardless of whether or not they are accurate in an ultimate sense, because they enhance one's health, chances for success, and social attractiveness and, thereby, also the likelihood of survival. Moreover, false beliefs tend to validate themselves – a phenomenon known as the self-fulfilling or behavioral confirmation effect (e.g., Snyder 1984). There is, however, a limit to self-deception. Since, from an evolutionary perspective, the benefits of group living exceed the costs, the adaptive value of false self-beliefs will depend upon the support they receive from others.

Measurement of Accuracy of Self-View

Because of a lack of absolute measures of a person's attitudes, traits, abilities, and so on, there is no way to know the person's true personality, and so it is difficult to evaluate whether one's self-view is accurate. The most commonly used methods for the assessment of accurate self-knowledge rely on comparison of self-reports of personality with: (1) ratings of personality provided by knowledgeable others, (2) observed behavior in relevant situations, and (3) implicit personality measures. None of these sources provides objective criteria against which self-perceptions can be compared, but rather reflects different definitions of accuracy. Thus, the so-called criterion problem remains.

Robins and John (1997) proposed a framework that identifies six conceptually based categories of accuracy criteria: operational/reality (i.e., whether individuals' self-perceptions correspond to direct operational criteria), social consensus (i.e., whether individuals' self-perceptions match

up with how others see them), functional/pragmatic (i.e., whether individuals' self-perceptions serve adaptation), normative models (i.e., whether individuals' self-perceptions align with the prescriptions of the normative model), information processing (i.e., whether individuals' self-perceptions result from the use of valid cues), and internal consistency (i.e., whether individuals' self-perceptions are consistent with their other self-beliefs or across social roles). As recommended by these authors, accuracy researchers should use multiple criteria to examine accuracy and should always state explicitly which ones they have chosen and why (Robins and John 1997).

Conclusion

Accuracy of self-view is an area of some debate within the psychology literature, and the question of whether people's self-views reflect what they are truly like will likely remain open to further discussion. Despite this, there seems to be a consensus among authors that parts of self-related knowledge are difficult to access consciously (e.g., information that is self-threatening and/or was acquired in early childhood). It is also recognized that both accurate and biased self-perceptions have an adaptive value, although the distorted ones are more likely to prove costly in the long run.

Cross-References

- [Self-Concept](#)
- [Self-Deception](#)
- [Self-Reports](#)

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Acheulean

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Synonyms

[Hand axe](#); [Cleaver](#); [Core tool](#)

Definition

A term used to classify a class of stone tools that all share a distinct oval/pear shape.

Introduction

The Acheulean class of stone tools is believed to have evolved from the Oldowan stone tools as far back as 1.76 million years ago. It has many qualities that make it different from the previous generation of stone tools, which include shape, and potential use. Furthermore, it is important to note that the Acheulean class of tools “were the dominant technology for the vast majority of human history” (Tattersall 2012).

The Acheulean Class of Tools and Their Importance

Approximately 1.76 million years ago, early humans ceased to use the Oldowan class of stone tools and adapted the Acheulean class of tools. This set of tools all share a similar shape, that of an oval or pear. An important difference between this class of tools and the older Oldowan tools is the supplementation of using some form of hammer made of bone, or wood to better refine the forefront of the tool. Another difference is that these tools are often symmetrical, and they have a sharp edge on both sides. There are many types of tools associated with the class of Acheulean including cordate, pointed, ovate, flicron, and several others. It is important to note that not all Acheulean class tools were

constructed from the same materials. The materials that were used to construct these tools were sourced from the type of local stones. Therefore, there is a large variability in materials used for the construction of Acheulean tools. For example, “in Western Europe, the most common type of stone used for constructing Acheulean tools is flint. In Africa, rocks such as basalt and mudstone were common” (Paddayya 1976). Furthermore, “In all cases the toolmakers worked their hand-axes close to the source of their raw materials, suggesting that the Acheulean was a set of skills passed between individual groups” (Gamble 1999). The actual manufacturing process of these tools often began with roughing out the teardrop shape of the tool with a harder rock. Afterwards, the edges of the tool would be sharpened by removing flakes of stone. This process would continue until the tool was considered satisfactory by the toolmaker. The Acheulean class of tools appear to be multipurpose in nature, and their uses would include hacking branches from trees, cutting apart hunted prey, or even removing hides from prey. Acheulean toolmakers may have held some form of social power, as knowing these skills would certainly give someone a large amount of respect and admiration within early social circles.

Conclusion

The Acheulean class of tools was an incredibly important piece of human development. Being the most used set of tools in human history, it is possible to further examine them to gain insight into not only early life, but perhaps early society as well.

Cross-References

- ▶ Human Tool Making
- ▶ Stone Hammers

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Acoustic Competition

- ▶ Vocal Competition

Acquaintance Rape

- ▶ Rape and Dating

Acquisition

- ▶ Encoding and Sleep

Act Nomination Method

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Synonyms

Acts; Behavioral manifestations of adaptations;
Behaviors

Definition

The act nomination method is a means by which evolutionary scientists can identify the behavioral manifestations of psychological adaptations.

Introduction

All adaptations, decision rules, cognitive procedures, personality traits, and mating strategies must be manifested in actual behavior, broadly conceived. The act nomination procedure is simply one method for identifying those behavioral manifestations (Buss and Craik 1983).

Early research using this method identified manifestations of personality traits such dominance, submissiveness, aggression, and cooperation. During the first phase of a study, participants would be asked: “Think of the most dominant individual you know or have observed. In the spaces below, list 10 acts this person has performed that reflect or exemplify their dominance.” The instructions typically had participants nominate dominant acts that a man might perform and separately nominate dominant acts that a woman might perform.

This procedure would typically yield 100 or more distinct acts, presumably covering the sample space of dominant actions. Examples include:

*He controlled the outcome of a committee meeting without the others being aware of it;
She demanded a backrub;
He insisted that others do menial chores rather than doing them himself;
She settled a dispute among members of the group.*

A key benefit of the act nomination method is sampling from the entire domain of act manifestations. This method can be viewed as a “bottom-up” method of identifying important behavioral phenomena that can supplement the “top-down” or theoretically driven identification of relevant actions.

A second step in the research program involves identifying which acts are most central to the category of dominance or most prototypical of the concept of dominance. The third step involves assessing people on reported performance of the relevant acts. Performance can be identified through self-reports, observer reports such as intimate partners, or videotapes of interactions that are subsequently coded for the relevant acts.

This set of act frequency methods sometimes yields findings unanticipated by extant theoretical frameworks. In the case of dominance, for example, studies found that dominant men were more likely to perform “egoistic” or self-serving dominant acts, such as getting others to perform menial chores, sitting at the head of the table, or insisting that the group go to the dominant person’s favorite restaurant (Buss 1981). Dominant women, in contrast, were more likely to perform “communal” dominant acts, such as settling disputes within the group or taking charge of the committee meeting, although dominant members of both sexes tended to perform both sorts of dominant acts.

The field of personality psychology has largely ignored the behavioral side of traits and motives. It has sometimes linked personality traits to important life outcomes, such as predicting scholastic achievement and future income (conscientiousness), divorce probability (impulsivity), and conflict within romantic relationships (emotional instability). The field has largely failed, however, to identify the behavioral manifestations of the traits that bring about these important life outcomes.

Identifying the Behavioral Output of Psychological Adaptations

Since the early explorations of act manifestations of personality traits, the act nomination methods have been more vigorously applied to phenomena closely linked with evolutionary psychology. These include acts of mate attraction (Buss 1988a), acts of mate retention (Buss 1988b), acts of mate poaching (Schmitt and Buss 2001), intersexual and intrasexual deception (Tooke and Camire 1991), status hierarchy negotiation (Kyle-Heku and Buss 1996; Lund et al. 2007), and many others. These explorations furnished research instruments that can be used by empirical scientists. And they have yielded important empirical discoveries previously undiscovered in evolutionary science. Examples include identifying different acts and tactics used by women and men to attract short-term versus long-term mates (Schmitt and Buss 1996), sex differences in

predictors of the effort allocated to mate retention, with men devoting more effort to guarding young attractive mates and women more effort to guarding mates higher in status and financial resources (Buss and Shackelford 1997).

Looking to the future, the act nomination method can be applied to domains that have yet been examined, but that must have behavioral manifestations. As one example, Cosmides and Tooby (1992) have identified a “cheater detection” adaptation in social exchange; people are selectively attentive to people who take benefits without reciprocating by paying costs. A key next question is: What do people do when they discover a cheater in social exchange? Do they walk away, ostracize, physically abuse, or inflict reputational damage? A more comprehensive understanding of cheater detection and other social exchange adaptations will require the identification and study of their behavioral manifestations of these adaptations – an agenda that can be facilitated by act nomination and act frequency methods.

Beyond cheater detection and social exchange, the agenda for identifying behavioral manifestations should be a core part of the exploration of all psychological adaptations. These include adaptations for kin detection, kin altruism, sibling rivalry, and kin favoritism; mate ejection; coalitional formation and maintenance adaptations; the behavioral immune system; evolved emotions such as envy, pride, and disgust; and many others.

Conclusion

In sum, the act nomination and act frequency methods have several forms of utility for evolutionary scientists. First, they can identify a range of behavioral manifestations in a “bottom-up” manner that provide an important complement to “top-down” or theoretically driven procedures. Second, they furnish research methods that can be used to make novel empirical discoveries, such as gender differences in the ways in which seemingly similar adaptations are instantiated in everyday actions. Third, they help with an indispensable agenda for adaptationist

researchers – identifying the actual behavioral output of psychological adaptations that has rendered them visible to natural and sexual selection.

Cross-References

- ▶ Adaptation
- ▶ Personality
- ▶ Mating

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Action

- ▶ Selectionist Models: Implications for Behavior

Action Regret

- ▶ Sexual Regret

Active Bait Fishing

- ▶ Bait Fishing

Activist

- ▶ Peter Kropotkin

Acts

- ▶ Act Nomination Method

Act-Utilitarianism

- ▶ Utilitarianism

Ad Exposure

- ▶ People's Responses to Personal Ads

Ad Hominem

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Synonyms

Tu Quoque, argumentum ad hominem, character attack

Definition

Ad hominem is an informal fallacy whereby an interlocutor, often on the losing side of a debate or argument, resorts to character-based attacks directed at their opponent without any reference to the content or substance of her argument.

Introduction

Making arguments and convincing others of a proposal is an essential part of human social and political life. Without engaging in arguments and the proposing of solutions, human beings would either be constantly warring with one another (why worry about convincing others when force works just as well) or forced to develop a wide range of skills. Both of these tasks, arguably, are considerably more time consuming than convincing others through well-developed and well-articulated arguments. But arguments are not always perfect, nor are we always in a position to adequately assess them. In such circumstances, arguers and assessors often employ extra-argumentative tactics to appear convincing. One such tactic is the ad hominem attack.

Traditionally, ad hominem attacks or the ad hominem fallacy take two forms: (1) Abusive and (2) Circumstantial (Johnson 2009; Putnam 2010). The circumstantial ad hominem, or tu quoque, is often employed when the principles a person advocates in her argument are inconsistent with her past actions. In colloquial terms, this is the classic “practice what your preach” objection (Johnson 2009; Putnam 2010). Abusive ad hominem attacks, on the other hand, involve a “direct attack on the arguer’s character” (Johnson 2009; Putnam 2010). That is, instead appealing to inconsistency between principles promoted and actions taken, abusive ad hominem attacks are less sophisticated by going after a person’s character traits without appeal to logical or behavioral consistency. For example, someone might charge the arguer with having poor aesthetic taste simply based on their political or otherwise irrelevant character trait.

Are Ad Hominem Attacks Ever Reasonable?

Given the description above, it is difficult to see the argumentative worth of employing any sort of ad hominem attack. To do so, one risks being labeled an unreasonable and irrational interlocutor. Recently, however, much work has been spent challenging the traditional position that ad hominem attacks are irrelevant in evaluating an argument. In *Reconsidering the Ad Hominem*, Christopher Johnson argues that abusive ad hominem attacks, in certain limited circumstances, can be quite useful and acceptable. There are three such instances. First, and in light of our epistemic and cognitive limitations, ad hominem attacks can be reasonable when we are not positive of the arguer's premises. In this instance the evaluator is telling the arguer: "While I am not sure of your premises, you have the reputation of being a swindler and cheat. Thus, one can give very little weight to the belief you are now telling the truth." The second scenario involves challenging an arguer's interests or background so as to cast doubt on her ability to assess certainty. Depending on the arguer's background or motives, their interpretation of facts and her demand for certainty may be said to be too low or too high (2009). Third, and in some ways similar to the second scenario, one might appeal to ideological differences and background for drawing concerns of the arguer's claims. Here, we might think of the classic scenario where a progressive politician critiques the policy recommendations of a conservative politician based purely on their ideological differences (as opposed to whether the policy recommendations fail to improve lives or solve a developing problem) (Johnson 2009).

Ad Hominem Attacks and Decision-Making

Contrary to traditional economic theory, behavioral economics posits that *homo economicus* fails both descriptively and pragmatically (Jolls et al. 1998). Setting aside some of the controversial insights of the behavioral economic program, one thing that is

of interest to us here is the insight that human beings often employ heuristics when information costs are high. In other words, human beings have what is called bounded rationality. According to Gigerenzer and Gaissmaier (2011), a heuristic is "a strategy that ignores part of the information, with the goal of making decisions more quickly, frugally, and/or accurately than more complex methods." Arguably, the employment of the ad hominem meets some, if not all, of these elements. In fact, the first scenario described above applies to Jolls et al.'s notion of bounded rationality. Decision-makers such as policymakers are under austere time constraints and may find it difficult to read and digest policy options proposed by their opponents. Thus, it appears reasonable, under the conditions, that they resort to abusive ad hominem attacks quite often.

Given these insights, it might be further argued that employing ad hominem attacks during an argument might contribute to our cognitive efficiency. As rational decision-makers, we are not always equipped with the most up to date and relevant information for all situations where a decision or judgment is required. As such, it is not only more convenient, but also necessary to employ heuristics or cognitive shortcuts that might allow us to make the best decision possible given these cognitive and intellectual restraints. Here, ad hominem attacks can be quite useful. Assessing, let alone winning, an argument does not always come easy. The average arguer will find it difficult to remember or recall all the relevant facts necessary to properly assess or produce an argument. As such, employing ad hominem attacks can be quite useful (Van Eemeren et al. 2000; Yap 2013).

Conclusion

In light of these insights, it would appear that ad hominem attacks are not to be dismissed as intellectually lazy and suspect. To the contrary, they can often prove to be significant resources in light of our cognitive and epistemic limitations. Further, one might also argue that employment of such tactics is not always methodologically or morally dubious. This is not to say that there is no

instance in which an ad hominem attack can be deemed unreasonable. But it is important for communities to determine under which conditions such attacks are excusable and/or reasonable and when they are merely cheap rhetorical tactics.

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Ádám Miklósi

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Synonyms

[Professor](#); [Researcher](#)

Definition

Ádám Miklósi (Ph.D., D.Sc.) is a professor and researcher at Eötvös Loránd University (Hungary) where he is the Director of the Family Dog Project and the Head of the Department of Ethology.

Introduction

Dr. Ádám Miklósi has been studying dog-human relationship from an ethological perspective for

nearly two decades and, along with his colleagues, has have revealed a number of interesting findings and insights when investigating parallels between the behavior of people and dogs (“Ádám Miklósi” [n.d.-a](#)). His most recent research focuses on communication and social learning, but he is also interested in canine emotional expression and in the genetic underpinnings of dog behavior (“Ádám Miklósi” [n.d.-a](#)). Moreover, because dog behavior provides the opportunity to theorize and design social robots that are inspired partly by the behavior of the family dog, Miklósi has worked on formulating the direction of a new research area: “etho-robotics” (“Ádám Miklósi” [n.d.-a](#)). He has authored more than 270 publications on dogs, animal cognition, animal science, animal behavior, behavioral biology, ethology, human-robot interaction, behavioral science, behavioral ecology, and primatology (“Ádám Miklósi” [n.d.-b](#)).

Projects and Research

Miklósi was born September 25, 1962, in Budapest. He received his Ph.D. in 1995 in biology and his Doctor of Science in 2005 (“Ádám Miklósi” [n.d.-a](#)). He has also received multiple awards for his work, including the Frank A. Beach Comparative Psychology Award (The best paper of the year in the Journal of Comparative Psychology) in 2003, the Distinguished Scholar Award in 2010 from the International Association of Human-Animal Interaction Organisation, the ELTE Faculty of Natural Sciences prize for coaching science students in 2011, and the Pál Juhász-Nagy prize for Talent Management in 2011 (“Ádám Miklósi” [n.d.-a](#)).

The Family Dog Project

The Family Dog Project is the largest canine research group in the world. It was founded in 1994 and is comprised of researchers from three different European institutions: Eötvös Loránd University, Department of Ethology and the Hungarian Academy of Sciences, Comparative Behavioral Research Group and the Comparative Ethology Research Group. The Family Dog

Project was founded in 1994 to study the dog-human relationship, and it has since published over 100 papers in peer-reviewed journals on behavioral and cognitive aspects of dog-human relationships. Along with publications, they also engage in public outreach through free online seminars and video abstracts describing various research and conclusions drawn by researchers with the Family Dog Project.

Researchers with the Family Dog Project hypothesize that dogs evolved to survive alongside humans, and they aim to understand the contributions of both humans and dogs to the dog-human relationship. This means they study not only the mental abilities of dogs but also any human or dog behavior that is related to the dog-human bond. Thus, the Family Dog Project has not only revealed important insights in dogs but also in us, people (“Family Dog” n.d.).

The Family Dog Project hosts a comprehensive website (<https://familydogproject.elte.hu/>) where dog owners can sign up to participate in research with their dogs. Citizens living near Budapest, Hungary, are welcomed to join in live participation at the universities, while dog owners from farther away are invited to fill out online surveys.

Book Publication

Dr. Miklósi is the author of *Dog Behaviour, Evolution and Cognition*. The second, fully updated edition was published by Oxford University Press in 2014. The book advertises itself

This is the first book to collate and synthesize the recent burgeoning primary research literature on dog behaviour, evolution, and cognition. The author presents a new ecological approach to the understanding of dog behaviour, demonstrating how dogs can be the subject of rigorous and productive scientific study without the need to confine them to a laboratory environment. Dog Behaviour, Evolution, and Cognition starts with an overview of the conceptual and methodological issues associated with the study of the dog, followed by a brief description of their role in human society—almost a third of human families share their daily life with the dog! An evolutionary perspective is then introduced with a summary of current research into the process of domestication. The central part of the book is devoted to issues

relating to the cognitive aspects of behaviour which have received particular attention in recent years from both psychologists and ethologists. The book’s final chapters introduce the reader to many novel approaches to dog behaviour, set in the context of behavioural development and genetics. Directions for future research are highlighted throughout the text which also incorporates links to human and primate research by drawing on homologies and analogies in both evolution and behaviour. The book will therefore be of relevance and use to anyone with an interest in behavioural ecology including graduate students of animal behaviour and cognition, as well as a more general audience of dog enthusiasts, biologists, psychologists and sociologists. (Miklósi 2014)

Summary of Research

Dr. Miklósi’s main research focus is on dog behavior and cognition, but his interests are much broader. For dogs, he has been involved in numerous studies on dog-human interactions. One of his most cited papers is the article “Comparative social cognition: what can dogs teach us?”. In this article, Dr. Miklósi and his coauthors take the position that dogs, via domestication, are adapted for living with humans and have marked changes in their social interactions with humans based on this evolution (Miklósi et al. 2004). In addition, Dr. Miklósi is interested in the evolution of dogs; thus, he has conducted significant research comparing dogs and wolves in their abilities to understand human communication cues. One of his most cited articles demonstrates a large difference between dogs and wolves in their communication with humans: dogs look at human faces and wolves don’t (Miklósi et al. 2003). This may reflect how dogs have evolved to live alongside humans. One communication cue of particular interest to many researchers right now is the ability to understand human pointing gestures. Dr. Miklósi has studied the ability of many other species (aside from dogs and wolves) to follow humans points. He wrote a review article about the pointing abilities in many species, specifically discussing the influence of domestication and ape competitive sociability (Miklósi and Soproni 2006). Dr. Miklósi has more recently branched out of the comparative fields and into robotics. Dr. Miklósi has

started studying how humans interact with robots and electronic devices, for example, in human interactions with robot-dog behavior (Miklósi and Gácsi 2012).

Conclusion

Dr. Miklósi is a leader in the field of comparative cognition and ethology, specializing in dog-human social interactions. He is particularly interested in the role of domestication in the evolution of dog behavior and the dog-human relationship. Dr. Miklósi performs many roles in this field: he is a prolific author of scientific research and is leader of the largest dog research group in the world, but he has also engaged in significant public outreach about dog cognition with the publication of his book, *Dog Behaviour, Evolution and Cognition*, as well as the free online seminars available via the Family Dog Project's website.

Cross-References

► Canines

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Adaptation

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Synonyms

[Adaptationism](#)

Definition

An adaptation (in the evolutionary sense) is a feature/trait that serves a particular function in an organism's environment and improves that organism's ability to survive (i.e., its fitness).

Introduction

Although the word adaptation is used in a number of different ways and its definition debated, most biological researchers agree that adaptations offer organisms higher fitness in their environments, thus enabling the organism to survive and reproduce (Kitano 2002). Adaptations arise as a result of evolutionary changes in the genetic constitution of a population of organisms (Zeigler 2014). Thus, an evolutionary adaptation may be considered as both a “process” impacting and organisms’ morphology, as well as a “feature” of the organism itself (Bock 1980).

Individual adaptations also referred to as adaptive traits/features are thus particular traits of the organism which enable species survival (O’Brien and Holland 1992). These adaptive traits are inherited by offspring from their parents and arise through processes such as genetic mutations, interactions between these genetic components

and the environment, or copying or *recombination* errors in the genetic material (Boyd and Silk 2009). For an adaptation to persist in a given population, it must increase the reproductive success of the population. However, changes in the population or environment may also result in adaptations becoming *vestigial* (i.e., *useless*) (Zeigler 2014). Adaptations may be observed at multiple levels of biological organization, all the way from the individual or organism to that of the population or species (Krimbas 2004).

Factors Important in Considering Adaptations

While the concept of an adaptation is intimately linked to that of the environment (i.e., how well suited is the feature to the demands of the environment), it is important to note that identifying the force of selection responsible for the adaptation is also an essential consideration (Bock 1980). To demonstrate that an adaptation has occurred, one would ideally need evidence indicating that natural selection is responsible in driving any underlying genetic changes associated with the feature. Given the difficulties with measuring natural selection (e.g., Morrissey and Hadfield 2012), the approach in comparative studies has been to infer that adaptive evolution has occurred based on our investigations of mean phenotypic change and the assumption that natural selection exerts a powerful influence on all organisms (Endler 1986). At a population level, adaptative traits tend to increase in frequency due to the reproductive advantage conferred on members carrying these traits (Tooby and DeVore 1987). This makes an adaptation a reliable and identifiable characteristic of a species (Krasnow and Truwax 2017). A further important feature of an adaptation is that an adaptation is not considered the optimum solution (i.e., the best or most favorable solution) to a given environment (Brock 1980) but is in fact a response to an ancestral problem, manifested in decedents of the species (Boyd and Silk 2009). This has led to debate on the role of adaptation in the evolutionary process.

While an organism might possess an adaptation, it will also possess several other features which arose as byproducts of the evolutionary process and were not the targets of selection

(Gould and Lewontin 1979). Adaptations may also be constrained by other features as is seen with developmental constraints which prevent the occurrence of mutations that have a deleterious effect on the organism. An example of a developmental constraint is the near universal occurrence of seven cervical vertebrae in all mammals due to pleiotropic effects linked to increased cancer risk (Galis 2002). Many attributes of organisms arose as evolutionary byproducts and are thus not amenable to an adaptive explanation (Gould and Lewontin 1979).

Examples of Adaptations

Adaptations can be grouped into a number of different categories depending on the level of comparison. For instance, comparative anatomists might be interested in structural adaptations which are physical changes to the structure of an organism. An example of a structural adaptation is the development of wings for flight or evolutionary changes in the pelvis to support bipedal locomotion. Other scientists might be interested in evolutionary changes to the behavior of an organism known as behavioral adaptations. An example of a behavioral adaptation includes the emergence of sociality in a species (e.g., pack hunting behavior or communication).

While adaptations are often considered solutions, which emerged in the more distant evolutionary past, some adaptations are more recent. For example, there is evidence of selection resulting in changes to human diet and providing pastoral communities with the ability to digest lactose (Tishkoff et al. 2007). Similarly, there is strong evidence of selection resulting in structural changes to human blood, and thus conferring carriers of this trait with resistance to the malaria parasite (Allison 1954).

Conclusion

While adaptions are difficult to identify and test, the concept of an adaptation remains central to understanding the evolutionary process and in helping us to reconstruct the evolutionary history of all species, including our own.

Cross-References

- ▶ [Adapted Mind, The](#)
- ▶ [Adaptationist Program, The](#)
- ▶ [Adoption Preferences](#)
- ▶ [Biological Function](#)
- ▶ [Boredom as an Adaptation](#)
- ▶ [Evolution](#)
- ▶ [Evolutionary Medicine](#)
- ▶ [Evolution of Intelligence](#)
- ▶ [Evolution of Teaching](#)
- ▶ [Evolution of the Brain, The](#)
- ▶ [Forms of Adoption](#)
- ▶ [Function of Adoption](#)
- ▶ [Human Enculturation](#)
- ▶ [Natural Selection](#)

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Adaptation and Natural Selection

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Definition

In his book, *Adaptation and Natural Selection*, George Williams (1966) discusses what is meant by the term “adaptation” and what can be done to further the study of that phenomenon. Throughout the course of the book, he provides an overview of past research on the subject and challenges misconceptions, such as group selection, which he believes to be misguided attempts at understanding adaptation.

Introduction

George Williams’ 1966 book, *Adaptation and Natural Selection*, seeks to define what is meant by researchers discussing the adaptation of species and clarify differences in understanding of the term and the process it describes. The main purpose of adaptation, as Williams understands it, is to promote the survival of the individual and that individual’s ability to reproduce in order to preserve their genes. Through the process of evolution, adaptations that are useful for the survival of the individual are retained and passed on to future generations. Contrary to the beliefs of some other scientists at the time, however, Williams asserts that such adaptations do not necessarily make for a more complex organism with more complex DNA; rather, adaptations are substituted in, not added to, an ever-increasing cumulative DNA.

Adaptation, he argues, does not necessarily progress the species to a more complex one, but a more fit one.

Another key concept outlined by Williams is the difference between the passing on of genotypes and phenotypes. This distinction proves important in his discussion of the presence or lack thereof of group selection. He argues that while an individual's environment can affect the phenotypic expression of their genes, that environment is not necessarily influencing which genotypes will be passed to the next generation. This is because while the environment can cause variation in the expression of phenotypes, that expression is not what is passed on. Though several organisms might express a genotype differently, they all possess the same genotype, and in the end, it is that genotype that is passed to the next generation. The fact that it is the genotype, and not the phenotype, that is passed through generations provides a foundation for Williams' criticism of the idea of group selection.

To distinguish between individual and group level selection, Williams refers to organic and biotic adaptation, respectively. An adaptation that produces modifications to the individual that aids in its survival and reproduction is referred to as organic adaptation, which leads to the evolution of the species. In contrast, a biotic adaptation is an adaptation that promotes group survival and cannot be explained by organic evolution. He argues that while biotic adaptation might occur, it is difficult to find an instance where what appears to be biotic, or group, evolution is actually the cumulative result of individual adaptations. Whereas it might seem like a group has adapted together, the truth in most situations is that the group is composed of adapted individuals, and this individual adaptation is what contributed to the survival of the group.

Conclusion

Williams concludes that in order to be truly useful to the study of organisms and their evolution, the term "adaptation" needs to be clearly defined and the field of study related to the adaptive traits of

organisms similarly narrowed down. Previous researchers, he argues, have applied the term too liberally, labeling traits that do not have a true directed purpose as adaptations when they are not. Rather, a true adaptive trait should be defined as one that serves a tangible function produced through natural selection and could not have happened by chance, citing the development of the eye as one such adaptation; it is obvious that the eyes of organisms have an expressed purpose, which has been honed over time through selection processes and is not a chance development that happens to benefit the organism. Once this more narrow view of what an adaptation is accepted, then a new field of study – which he tentatively refers to as teleonomy – will be able to emerge and dive deeper into what constitutes an adaptation and how they function.

Cross-References

- ▶ [George Williams](#)
- ▶ [George Williams on Group Selection](#)

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Adaptation Failure

- ▶ [Maladaptations](#)

Adaptation for Single Births

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Synonyms

[Gestation](#); [One offspring](#); [Pregnancy](#)

Definition

The propensity for primates, including humans, to have only one fetus at a time.

Introduction

Mammalian infants are born at either of two stages: altricial or precocial. Altricial infants are those that are born immature and helpless, e.g., rodents. Precocial infants are born able to move about soon after birth, e.g., deer. Animals that are born precocial, like primates, are K-selected, meaning that they give birth to a smaller number of offspring at a time (MacArthur and Wilson 1967; Martin 1983; Pianka 1970). Humans are part of a group of primates known as “higher primates” which typically give birth to single offspring at a time (Martin 2007). Having fewer offspring at a time allows the fetus to have a larger body size at birth and be more developed at birth in order to increase the chance of survival (Martin 2013). The adaptation for having a single fetus at a time may be a result of the ancestral morphology, or shape, of the uterus.

Uterine Morphology

During pregnancy, a fetus develops and grows in the uterus. Placental mammals have a uterus which has two chambers, or spaces, allowing for multiple fetuses to gestate, or grow, at a time (Martin 2013). Women are one of the few mammalian exceptions that have a uterine morphology where the uterus only has a single chamber (Martin 2013). The single-chambered uterus develops early in-utero from the fusion of reproductive tracts (Martin 2013). Today, a low percentage of women (0.033%) are born with a two-chambered uterus (Martin 2013). Although these women can still have viable pregnancies, their babies are typically born premature and via medical interventions, such as cesarean section (Martin 2013).

The adaptation for humans to have single births may be a result of the overall space

provided in the uterus to support developing fetuses. Primates are born at a more developed, or precocial, stage and thus are typically born at a relatively larger body size compared to altricial mammals. A fetus that is larger therefore affords less space in the uterus to support multiple fetuses to develop (Hamlett and Wislocki 1934). With fewer fetuses in the uterus at a time, a fetus can have a longer gestation, or pregnancy, period. A lengthened gestation period provides extra time for the fetus to grow in body size. Gestation length in precocial species is almost three times longer than that of altricial species (Martin 2007). This trend extends within precocial species, such as the primates. Relative to maternal body size, apes have longer gestation lengths than monkeys. Humans, as apes, have a gestation period of, on average, 40 weeks, whereas some monkeys have gestation periods of less than half that amount of time.

Another way to view how the gestation period influences the number of offspring is to consider the amount of energy it takes to gestate and grow a fetus. Increased gestation lengths in humans and the other apes increase the energetic burden placed upon the mother through the prolonged nutrient supply to the fetus. The timing of birth is now thought to be due to when the maternal metabolic limit is reached, and the mother can no longer support the fetus’s caloric needs (Dunsworth et al. 2012). In single birth, this metabolic limit is reached at 40 weeks and then birth occurs (Dunsworth et al. 2012). In multiple births, however, the mother’s metabolism must support more than one fetus, increasing her metabolic demands throughout the gestation. This decreases the length of gestation, as the Mother’s metabolic limit will be exceeded sooner rather than when the Mother is only providing for one fetus. Women who have twins have an average gestation length of 37 weeks, three weeks earlier than what is seen in an average singleton birth (Martin 2013). An infant born this early also affects the birth weight, coinciding with the standard threshold for premature infants (Martin 2013).

Decreased time in utero decreases the birth weight of the infant. The average birth weight of a single human infant is 7.5 pounds whereas in twins, the average birth weight decreases to, on

average, 5.25 pounds (Martin 2013). Premature births and lower birth weights are associated with greater health risks such as coronary heart disease and hypertension (Trevathan 2010). Additionally, premature infants require more direct care from the Mother in order to survive than those infants born fully developed. In premedicinal times and throughout our evolutionary history, this would have caused excess strain and burden on the Mother and may have resulted in a higher infant mortality.

Evolutionarily, primates are adapted to giving birth to one infant at a time because it is beneficial for their reproductive success. The metabolic limit for fetal growth is determined by the mother (Dunsworth et al. 2012), and having a single offspring allows for a longer gestation period and a healthier infant. A single fetus can grow larger and more developed in utero without conceding space to multiple fetuses.

Conclusion

Humans typically give birth to one offspring at a time due to the morphology of the human uterus only supporting one embryo at a time. The single-chambered uterus evolved early in primate evolution and allows the fetus to be born more developed, as well as larger in body size. These adaptations ensured a better chance at survival in the evolutionary environment in which we, as primates, evolved, as well as in today's modern world.

Cross-References

- ▶ [Fertility](#)
- ▶ [Narrowing Birth Canal](#)
- ▶ [Reproductive Strategy](#)

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Adaptationism

- ▶ [Adaptation](#)
- ▶ [Adaptationist Program, The](#)

Adaptationist Framework

- ▶ [Adaptationist Program, The](#)

Adaptationist Perspective

- ▶ [Evolutionary Social Psychology](#)

Adaptationist Program, The

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Synonyms

[Adaptationism](#); [Adaptationist framework](#)

Definition

An approach to testing theories about species-typical traits that focusses on the fit between an organism's traits and relevant features of that species' ancestral ecology.

Introduction

How do birds know when to fly south? How do they find their way? How do people learn to speak and read? When are they generous? When are they cruel?

When studying these and other questions about the nature of naturally selected organisms, one can gain a distinct advantage by considering the ecology in which the organism's ancestors evolved and what problems they faced. The adaptationist program offers a framework and approach for testing theories about naturally selected organisms.

The Adaptationist Framework

An adaptationist does not assume or purport that all (or even most) features of organisms are *adaptations*. An organism, or the “nature” of a species (e.g., “human nature”), can be dissected into an infinite number of features (e.g., having two arms, possessing a right hand, having an odd number of fingers on that hand, the relative gravity between those fingers, the configuration of those fingers that enables grasping, and so on). Not all features have specific adaptive value. The basic commitment of the adaptationist theoretical orientation is that – out of this impossibly large set – it is useful to think of a particular feature as being one of three kinds of things: adaptations, by-products, or noise (Tooby and Cosmides 1992).

Adaptations are those features that are themselves a solution to an ancestral adaptive problem. These features have an inheritable basis that increased in frequency in the population over evolutionary time *because* the individuals exhibiting these features had a reliable reproductive advantage over others (Tooby and DeVore 1987). Because of this causal relationship, the design of adaptations can be understood in part

by the fit between the form of the adaptation and the function of solving its adaptive problem. Adaptations, therefore, are reliable characteristics of a species: they tend to be common or universal in the species – reliably developing at some point in the life span – given the necessary environmental input.

While adaptations are those features that solved an adaptive problem over evolutionary history, the phenotype created by this ancestral selection will have many features that did not themselves solve any adaptive problem. Rather, they are by-products of the adaptation. By-products are reliable characteristics of a species, like adaptations, but by-products were not the target of selection that drove their own existence and instead were merely carried along with the feature under selection (the adaptation).

For example, the blood of humans and most vertebrates has the features “can bind and transport oxygen” and “appears red when oxygenated.” The former feature is an adaptation, as binding and transporting oxygen through the body solves a crucial adaptive problem. The latter is probably not an adaptation, as turning red when oxygenated solved no known adaptive problem. Instead, we can best explain the reliable presence of the “appears red when oxygenated” feature as a by-product of the fact that blood cells evolved to use the iron in hemoglobin to solve the “bind and transport oxygen” adaptive problem and the physical properties of the way iron and oxygen bond.

Features that are neither adaptations nor by-products are noise. Noise refers to features that are not reliable characteristics of a species. In the blood example, a noise feature would be whether you have an odd or even number of blood cells; you might have one or have the other, but it is random and not a reliable feature of our species.

The Adaptationist Approach

The adaptationist program provides an approach for testing theories about species-typical traits. Because of the fit between features of an adaptation and relevant features of the ancestral ecology (like the fit between features of a lock and a key), a theory that a trait is an adaptation for

solving a particular adaptive problem necessarily entails predictions about the features the trait should and should not have (Williams 1966). In contrast, a theory that a trait is a by-product of another adaptation makes different kinds of predictions about the features the trait should have (e.g., they should not be particularly well designed for solving the by-product function). That is, a primary form of evidence for testing adaptationist theories is *design evidence*: evidence that features of the trait are specialized and coordinated in such a way to solve a particular adaptive problem efficiently and economically over the range of ancestral conditions. The justification for this appeal to design evidence is that – in the absence of natural selection for features that solve a particular adaptive problem – it is exceedingly unlikely that a collection of random mutations will fixate in the genome together by neutral drift. This is a probabilistic inference similar to the inference made in hypothesis testing that the data are exceedingly unlikely if a null hypothesis is correct. Here, the implicit null model is that there was no specific selection for solving the adaptive problem in question. Following up on the blood example, consider a theory that blood involves an adaptation for appearing red when oxygenating as a signal of vitality to others. This theory predicts there should be design features enabling broadcast of the signal (perhaps arteries close to the body surface, transparent skin, obscured veins, etc.). This theory’s predictions fail, especially in contrast to the competing theory that blood evolved for oxygen transport (predicting features like a vascular system to distribute oxygenated blood, architected interaction with the respiratory system for gas exchange, etc.), and that redness is a by-product. Plausible theories about particular adaptations or by-products must make specific predictions that can be tested in this way.

Critiques of the Adaptationist Program

The adaptationist program has been widely influential and is the foundation of work in evolutionary biology and evolutionary psychology. It has also been criticized within the academic

community and the popular press, often on the basis of what has been termed “Panglossianism” and “just so storytelling” (Gould and Lewontin 1979). The Panglossian critique (named for the endlessly optimistic Dr. Pangloss) argues that work in the adaptationist program assumes that all traits are adaptations, seeing function where none meaningfully exists. By this definition, adaptationism fails if any features of any organism are not adaptations. However, as illustrated above, the adaptationist program explicitly opposes the view that all traits are adaptations; in fact, many if not most of the features of organisms are properly construed as by-products on the adaptationist account.

The “just so storytelling” critique argues that adaptationist theories make no testable predictions and are merely an exercise in telling stories that things are “just so.” However, as illustrated above, adaptationist theories – that is, theories that a trait is an adaptation for solving a particular adaptive problem, or a by-product of a trait that is an adaptation for solving a particular adaptive problem – are explicitly testable theories because they make predictions about the designs the trait should possess. In fact, the foundational premise of the adaptationist toolkit is that adaptationist theories are uniquely generative of predictions about the features of organisms; no other class of theory can predict in advance previously unknown features of organisms.

Cross-References

- [Adaptation and Natural Selection](#)
- [Adapted Mind, The](#)
- [Founders of Evolutionary Psychology](#)
- [George Williams](#)
- [Leda Cosmides and John Tooby \(Founders of Evolutionary Psychology\)](#)

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Adaptations

► Evolution of Adaptations

Adaptations for Navigating Social Hierarchies

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Synonyms

Behavioral and mental traits for navigating social hierarchies; Strategies for navigating social rank hierarchies

Definition

Adaptations for navigating social hierarchies are the evolved behavioral traits, cognitive and social skills, and emotions (reflected in human brain structure) that facilitate social hierarchies. They are manifested in hierarchical social categorization, dominance, prestige, or leadership motive systems for attaining and maintaining high social rank and verbal and nonverbal symbols signaling status.

Introduction

A hierarchical organization of social relations is ubiquitous in the animal kingdom (including

among humans). This is a starting point for considering the issue of adaptations for navigating social hierarchies in human society. Based on that, the representatives of the humanities and social science analyze the common evolutionary mechanisms of the origin of such adaptations, namely, evolved behavioral and mental traits (strong associates with brain system), that have contributed to the survival of our ancestors. These continue to determine the psychology and social behavior of contemporary humans.

The entry considers the most elaborated now evolved adaptations for navigating social hierarchies, such as an ability in humans to categorize and recognize others' roles in social hierarchies, motive systems (dominance, prestige, leadership) that stimulate the attainment and maintenance of high social rank, and verbal and nonverbal symbols signaling social status.

Hierarchical Social Categorization

Social categorization implies classification of people (as well as objects) according to different criteria that result in classifying them as different social groups (e.g., gender, race). One of the basic criteria for such differentiation is their position on the hierarchical ladder (according to perceived power, amount of different resources, skills, and so on). From an evolutionary perspective, hierarchical social categorization – an ability to recognize people as part of a certain social group associated with high or low social rank – is an evolved adaptation that facilitates the navigation of social hierarchies and thereby increases the chances of survival and reproductive prospects, at least in our ancestors.

It is now proposed that the ease, fluency, and desirability with which we perceive the social rank of others and identify our own status in the process of social comparison point to human preference in hierarchical social relations, although people may claim the opposite (Zitek and Tiedens 2012). Perhaps this is because the hierarchical principle for social group organization is an efficient way to maximize group cohesion and productivity (Koski et al. 2015). As Qu

and colleagues emphasize: “Not only are there benefits to obtaining a dominant position within the hierarchy, but the accurate representation of dominance relationships can help individuals form effective social alliances” (Qu et al. 2017, p. 893).

However, in contemporary society hierarchical social categorization may cause prejudice, biased perceptions, and stereotyped attitudes. This is so because we have often based our social classifications on signals and cues that do not match modern contexts. For example, we can ascribe leadership to those who are tall and physically strong. Such traits were important for leaders of our ancestors in savanna environments but are not very important for managers of modern organizations (the mismatch hypothesis, see, e.g., Li et al. 2017, Van Vugt et al. 2008).

Motive Systems for Navigating Social Hierarchies

Motive systems that stimulated humans to obtain and maintain high social rank can be different (more about this below), but all of them have a common evolutionary foundation. High status was a guarantee of reproductive success in ancestral communities. The recent studies demonstrate that even in modern society, men (but not women) with high social rank (measured by personal income) have more offspring than those with low incomes (Hopcroft 2015).

Dominance (force or the threat of force) and prestige (freely conferred deference) are considered dually evolved strategies for navigating social hierarchies (Henrich and Gil-White 2001).

The dominance strategy is historic first and is held in common with nonhuman primates, while prestige appeared later and is unique (or less developed in other animals) to human society. The dominance pathway “arose in evolutionary history in response to agonistic conflicts over material resources (e.g., food, mates), which were common among nonhuman species, but also persist in contemporary human societies in the form of psychological conflicts.” (Cheng and Tracy 2014, p. 5).

The prestige strategy emerged when our ancestors lived in relatively small hunter-gatherer communities (Maner and Case 2016, p. 7). Henrich and Gil-White consider prestige status a product of the changes in selective environments when cultural transmission was manifested in “abilities to identify and preferentially to copy models wh[ich] are likely to possess better-than-average information” (Henrich and Gil-White 2001, p. 167), which became important for our ancestors’ survival. Those whom others copy as skilled/knowledgeable models (the variant of paying deference) achieve their status through knowledge, expertise, performative skills, and the like. Such preferred models have prestige (Henrich and Gil-White, p. 167). Thus, prestige is a consequence of the evolution of direct social learning capacities (*infocopying* ability imitation) that differ from the analogous capacities in other species (Henrich and Gil-White, p. 173, with reference to others).

Besides the differences in phylogenetic history, dual strategies for navigating social rank hierarchies differ according to the source of deference, mechanisms of influence, nature of group hierarchies, role of social bonds, and personality correlates (Maner and Case 2016).

Deference to the dominant person is based on force or threat of force, whereas it is freely conferred by others to prestige status persons (e.g., Maner and Case 2016; Henrich and Gil-White 2001).

Henrich and Gil-White emphasize that prestigious people are never feared. The domain of words associated with prestige includes terms such as influence (not authority, or dominance, or power), honor, reputation, homage, reference, deference, and the like (Henrich and Gil-White, p. 168). The mechanisms of influence for prestige are admiration, respect, liking, and social modeling and for a dominance strategy are coercion, intimidation, aggression, and manipulation of reward and punishment (Maner 2017; Maner and Case 2016; Cheng and Tracy 2014; Henrich and Gil-White 2001).

Dominance and prestige adaptations for navigating social hierarchies are observed in different social environments. The maintenance of dominant social rank suggests steep

hierarchical relations with large and rather fixed distances between the top and lower positions. The prestige strategy is associated with relatively flat social relations and a domain-specific hierarchy (Maner and Case 2016).

The core of a dominance strategy comprises the social skills to form temporary coalitions to achieve certain goals for improving and maintaining high status. Navigating prestige in hierarchical relations involves the proposed abilities to form and maintain trusting social bonds for a long time (Maner and Case 2016).

The differences in personality correlates are also fixed. Thus, according to Maner, being “high in narcissism, hubristic pride, aggressiveness, disagreeableness, Machiavellianism, and psychopathy” is associated with a dominant status person, while being “high in agreeableness, self-esteem, need for affiliation, social monitoring, fear of negative evaluation, and conscientiousness” are the traits of a prestige-based high status person (Maner 2017, p. 2). Moreover, researchers (e.g., Van Vugt 2006) point to a substantial genetic component in such personality traits as extraversion, intelligence, empathy, and ambition that are associated with leadership. At the same time, nowadays it is emphasized that no clear evidence exists concerning genes that exclusively promote social dominance or subordination (van der Kooij and Sandi 2015).

Suessenbach and colleagues add leadership to dominance and prestige motives for obtaining high status. Although leadership itself can be achieved through dominance or prestige strategies, the authors state that the desire to be leader, i.e., “a desire to take initiative and responsibility in one’s group to direct it to a common group goal” (Suessenbach et al. 2019, p. 9), can be a functionally autonomous motive promoting hierachal organization in social groups. Add to that the idea of Van Vugt, who developed an evolutionary theory of leadership. Using empirical data he has proved that under selection pressure – the necessity to solve problems in a coordinated way – the behavioral role strategies were formed in leader and followers (e.g., Van Vugt 2006). Thus, such basic role distinction also contributes to promoting social rank hierarchies in human society.

Van Vugt (2006) and others (e.g., Bastardoz and Van Vugt 2019) also propose that leadership (following implies voluntarily deference) and dominance (following does not freely confer influence) are different evolutionary pathways to attaining high status. The main adaptive function of leadership is achieving coordination and collective action by a group of individuals (King et al. 2009). The contemplated followership strategy for navigating social hierarchies is less studied. However, in research already conducted (Bastardoz and Van Vugt 2019), following the right leader is considered as an usefully evolved adaptation in the ability to reap benefits from coordinated action.

Communicating Systems Signaling Social Rank

Emotions, verbal and nonverbal communication signals, cues, etc. are also considered as evolved adaptations to hierarchical social relations and a result of solving certain adaptive problems.

In Steckler and Tracy’s (2014) research, the facilitated role of emotions in individuals’ navigation of the social hierarchy is examined. First, experiences of a certain emotion motivate individuals to attain, improve, or maintain social rank. Second, displaying status-relevant information to others through status signals and cues suggests that “emotion expressions may help individuals avoid costly disputes that can arise when rank levels of the various parties are unknown” and “may allow both parties to quickly know how the social interaction should proceed” (Steckler and Tracy 2014, p. 202). Third, recognizing others’ emotions promotes adaptive behavior, for example, deferring to high-level status (Steckler and Tracy 2014, pp. 201–203).

Henrich and Gil-White emphasize that prestigious people do not initiate grudges in subordinates but love, respect, awe, and deference (Henrich and Gil-White 2001). Those who have a dominant status experience “hubristic” pride (marked by arrogance and conceit, correlated with aggression and even antisocial behavior), whereas with prestige, “authentic” pride is manifested in accomplishment, confidence, and

successful social relationships (Cheng et al. 2010; Tracy et al. 2009).

Pride is considered as part of the affective-motivational suite underlying different avenues of rank attainment (Cheng et al. 2010). Among other factors relevant to attaining, maintaining, and communicating social rank emotions (e.g., shame, envy, contempt, admiration, disgust, anxiety, fear, happiness, sadness), pride is considered as an evolved adaptation that plays a central role in the orchestration of hierarchical social relations (Tracy et al. 2010).

Although the majority of research does not differentiate between communication systems of dominance and prestige, the adaptive pathways for obtaining rank seem to have differences. Thus, Witkower and colleagues have recently demonstrated that people with dominance and prestige strategies communicate their status through different nonverbal displays. Generally, dominance strategies are associated with expansive behavioral displays (including expressions of pride) that feature “arms extended out from the body, with hands either on hips or raised above the head with clenched fists, chest expanded, head tilted slightly upward, and a small smile” (Witkower et al. 2019, p. 5), whereas prestige entails “expansiveness, smiling, and an upwards head tilt” (Witkower et al. 2019, p. 62).

Finally, language skills are also considered as instruments for obtaining high social positions via both coercive and prosocial strategies. For instance, Massey-Abernathy and Haseltine (2019) revealed that the more vocal an individual was, the more dominant he/she was rated by others. Cheng et al. (2016) demonstrated that in face-to-face group interactions, raising and deepening vocal pitch were associated with low and high rank accordingly.

Conclusion

From an evolutionary perspective, the human mind comprises many functional psychological adaptations specifically designed to solve the particular adaptive problems of ancestral group life (e.g., Van Vugt et al. 2008). Among such problems is the challenge of collectively coordinating

action in achieving certain goals that facilitated the survival of the human species. Adaptations for navigating social hierarchies were one of those evolved decisions.

It is proposed that evolved behavioral patterns, cognitions, emotions, and underlying motive systems comprise dual strategies for navigating social hierarchies: dominance (based on fear and force) and prestige (stems from expertise and skills). The biological predisposition to form hierarchical social relations based on leadership and followership is also considered among such basic evolved adaptations.

Social categorization according to hierarchical criteria is one of the elements of social cognition needed for maintaining social rank relations. Communicating signals and cues allow the correct categorization of others according to their social rank. They also allow a display of own status. Finally, emotions (as an element of communication systems) motivate attainment, improvement, or status maintenance.

A

Cross-References

- [Biosociology of Dominance and Deference](#)
- [Dominance Hierarchy](#)
- [Dominance in Humans](#)
- [Male Dominance Hierarchies](#)
- [Navigating Social Relationships](#)
- [Nonverbal Indicators of Dominance](#)
- [Primate Dominance Hierarchies](#)
- [Social Hierarchies](#)
- [Status Hierarchies](#)

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Adaptations for Reciprocal Altruism

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Synonyms

Reciprocal cooperation; Reciprocity; Social exchange

Definition

According to Hamilton (1964), altruism entails suffering a cost to confer a benefit. Trivers (1971) defines reciprocal altruism as an exchange of altruistic behaviors between individuals so as to produce a net benefit to both individuals. Traits that enhance reciprocal altruism, including punishment of nonreciprocators, have been defined as reciprocal altruism adaptations.

Introduction

There is a long-standing misconception that evolution is based on a fierce competition and

therefore rewards only selfish behavior. On the contrary, cooperation can be observed across life, including among genes, cells, individual organisms, and groups of organisms, including diverse human societies ranging from hunter-gatherer tribes to nation states.

In his seminal work *Inclusive Fitness*, Hamilton (1964) describes the evolution of altruism among genetically related individuals. Trivers (1971) suggests that reciprocal cooperation can be favored between unrelated individuals, calling the circumstance wherein individuals help one another in turn and preferential aid those who helped them in the past, reciprocal altruism. He proposed three prerequisite conditions for the evolution of reciprocal altruism. First, the fitness benefits to the recipient of help must outweigh the costs to the benefactor. Second, the probability of repeated interactions among the same individuals must be very high. Third, there must be a symmetry of donor role-recipient role exchanges, with a sufficiently frequent reversal to yield roughly equal experiences at both roles.

Nowak (2006) suggests that the aforementioned reciprocal altruism is a type of direct reciprocity, wherein the probability of another encounter between the individuals exceeds the cost-to-benefit ratio of the altruistic act. Additionally, there can be indirect reciprocity and network reciprocity. Indirect reciprocity is thought to promote cooperation only when the probability of one's reputation being known exceeds the cost-to-benefit ratio of the altruistic act. Meanwhile, network reciprocity is thought to be favored when the benefit-to-cost ratio exceeds one's average number of neighbors. Some scholars argue that reciprocal altruism is a mutual behavior that should be distinguished from altruism because it can initiate a causal chain of events that lead to a net benefit for both actors and recipients. For this reason, several authors suggest that it would be more appropriate to adopt the term reciprocity or reciprocal cooperation in place of reciprocal altruism (West et al. 2011).

Reciprocal altruism raises intriguing questions about human nature, such as why people help each other and how cooperation can evolve in a competitive world, in which selfish behavior is supposed to ensure survival. These questions

have attracted the attention of researchers from various disciplines, including game theorists, psychologists, and biologists. A useful model of two-party reciprocity is the prisoner's dilemma (PD) game. In PD games, an always cooperate strategy (unconditional cooperation) in which one cooperates at every opportunity regardless of partner reciprocation is beaten by an always defect strategy, and thus individuals engaging in unconditional cooperation and always defect eventually disappear from the population. Conversely, a tit-for-tat strategy (conditional cooperation) can be maintained by natural selection and is evolutionarily stable as long as there is sufficient probability of future interactions among participants (Axelrod and Hamilton 1981).

The existence of conditional cooperation as an adaptive human behavior would presuppose that the human brain has specialized mechanisms mediating conditional cooperation that would have been selected for in human ancestors living in social groups and engaging in social interactions for millions, and probably tens of millions, of years (Cosmides and Tooby 1992). Such mechanisms, which may constitute adaptations favoring reciprocal altruism, would appear to have had a profound influence on human behavioral tendencies. Adaptations favoring reciprocal altruism are presented below.

Conditional Reasoning

The concept of conditional reasoning entails an "if P then Q" construct that posits Q to be true if P is true. People have been found to perform poorly on Wason's four-card selection task, a standard paradigm for investigating conditional reasoning, with only 5–30% of normal subjects responding with the logically correct answer under most conditional rule experiments, even when the rule describes familiar content drawn from everyday life (Cosmides and Tooby 2007). However, when the conditional rule involves reciprocal altruism and detection of a violation corresponds to looking for cheaters, 65–80% of subjects detect violations accurately in the Wason selection task (Cosmides and Tooby 1992, 2013). Cosmides and

Tooby (1992, 2013) suggest that this propensity may be due to innate social contract algorithms that are adaptive for detecting cheaters. For example, there is no logical inference by which “If P then Q” implies “If Q then P.” However, if P and Q refer to benefits and requirements, it is natural to infer that “If you accept benefit B from me, then you must satisfy my requirement R” also implies “If you satisfy my requirement R then you are entitled to receive benefit B from me.” Thus, one that chooses the “benefit accepted” card with the “requirement not satisfied” card can be readily classified as a cheater, regardless of whether the selection pair is logically correct in a particular Wason selection task.

Recent brain imaging studies (Fiddick et al. 2005) have shown that brain damage can impair one’s ability to detect social-contract cheaters selectively, while leaving intact the ability to detect violations of precautionary rules. Such observations confirm that the brain engages in conditional reasoning processes that are specialized for detecting cheaters in the reciprocal altruism.

Trust and Trustworthiness

Trust and trustworthiness are crucial components of human cooperation behaviors in reciprocal altruism. Trust can be studied with sequential PD games, involving serial trust-reciprocity-feedback stages (Krueger and Meyer-Lindenberg 2019). In behavioral economics, trust has been defined as making oneself vulnerable to exploitation with the expectation that their trust will lead to a return benefit. According to a traditional economic analysis, no participant should ever trust an anonymous participant in a one-off game (Dunning et al. 2012). However, people do exhibit trust in economic games and the people who are trusted frequently honor that trust by returning money, thereby demonstrating trustworthiness.

Trust and trustworthiness can lead people to form spontaneous relationships with new partners and therefore to develop general trust (Yamagishi 2011). Specifically, Yamagishi (2011) suggests that a high opportunity cost in an environment of

social uncertainty favors investment of cognitive resources into the development of social intelligence. People who have acquired social intelligence can be more attentive to detecting information about others’ trustworthiness, enabling them to have a high level of general trust. Accordingly, general trust can be treated as a by-product of acquiring social intelligence and has been shown to be adaptive (Yamagishi 2011). Meanwhile, not taking opportunities to exploit others in circumstances of high social uncertainty can lead to rewards for trustworthiness by way of the social capital of a good reputation. In this sense, reputation, which can be rewarding or punishing, can moderate a person’s actions, fostering continued reciprocal cooperation. Thus, trust and trustworthiness may serve to enable reciprocal altruism by facilitating the formation of spontaneous relationships with new partners. Accordingly, potential cooperative partners may be identified, either by labeling or by reputation, based on their trustworthiness increasing the likelihood of future cooperation. Note that these impacts of trust and trustworthiness are represented in the direct and indirect modes of reciprocal altruism, respectively: labels allow for direct reciprocity, whereas reputation allows for indirect reciprocity.

Fairness and Fairness-Based Morality

A basic principle of fairness in cooperation is that those who have contributed more should receive more. Indeed, a sense of fairness can lead individuals to give resources to individuals whose welfare is not beneficial to their own (Baumard et al. 2013). Such behavior occurs in environments beyond the scope of mutualistic social behaviors, wherein the giving behavior may have no direct or indirect benefit for the actor. Some authors suggest that fairness-based choices may reflect an adaptation of reciprocal cooperation that has evolved into the development of a pillar of morality in the form of a sense of fairness (Baumard et al. 2013).

According to the mutualistic model of cooperation (Baumard et al. 2013), individuals will maximize mutual benefits in reciprocal cooperation by

choosing partners who provide a fair distribution of benefits. There are two major types of mutualistic models of cooperation: partner control and partner choice. Partner control models encompass a tit-for-tat strategy, wherein participants can penalize partners who fail to cooperate in subsequent trials of an iterated PD game (Axelrod and Hamilton 1981). In partner choice models, individuals are only able to promote cooperation by choosing and being chosen by a cooperative partner. Consistent with partner choice models, humans do have the psychological dispositions necessary for effective partner choice (Pradel et al. 2009). Moreover, people can distinguish good cooperators from bad cooperators (Tooby et al. 2006), and people do exchange information about the cooperativeness of partners in hunter-gatherer societies (Wiessner 2005). Thus, the evolution of fairness-based morality would be expected to have occurred in two stages (Baumard et al. 2013). First, individuals favoring partners who share the costs and benefits of cooperative interactions evenly would be motivated by selfish reasons and a Machiavellian psychological calculus. Subsequently, competition among cooperative partners can lead to the selection of an intrinsically motivated psychological concern for fairness.

In this evolution process, partner choice leads to fairness-based behavior, and the distribution of benefits in mutualistic cooperation is constrained by the pool of potential partners. That is, individuals would not establish cooperative relationships in which the benefits they receive are inferior to the average benefits they see others receiving in the same pool of potential partners. This principle of a market of potential partners leads to the selection of a sense of fairness, a psychological adaptation of reciprocal cooperation (Baumard et al. 2013).

In summary, the mutualistic theory of morality claims that reciprocal cooperation is sustained on the evolutionary level by mutualistic morality on a psychological level. Furthermore, according to the mutualistic theory of morality, this biologically evolved moral sense enables the cultural evolution of morality via the aforementioned mechanism of partner choice.

One-Shot Generosity, a Bedrock Feature of Human Nature

A

A well-known prediction of a one-shot cooperative interaction is that the equilibrium strategy would be to always defect (Delton et al. 2011). However, predictions of traditional economic models of rationality are often contradicted by empirical observations. That is, individuals often exhibit generosity, violating the expectations of fitness maximization that predict selfishness (Fehr and Henrich 2003). Agent-based computer simulations indicate that generosity in one-shot interactions is a predictable byproduct of the selection for cooperation in the brain's decision-making systems.

Indeed, repeated social interactions are quite different from a one-shot interaction owing to the potential for the production of net benefit to both partners in future series of cooperation (Axelrod and Hamilton 1981). Under the circumstances of repeated interaction, individuals may tend to be generous because the potential for benefit in future cooperation exceeds the benefit of an immediate defection (Axelrod and Hamilton 1981). Therefore, individuals are faced with the problem of distinguishing one-shot interactions from repeated interactions, a problem that has been systematized in the standard Neyman-Pearsonian decision problem. In this paradigm, a false-positive error occurs when one mistakes a one-shot interaction for a repeat interaction, and a miss occurs when one mistakes a repeated interaction for a one-shot interaction (Delton et al. 2011). The outcomes of these two types of errors are asymmetric because the cost of a miss (losing all benefits of future cooperation) is far greater than the cost of a false positive (risking a single incident of being exploited). As a result, individuals will cooperate "irrationally" even when it is exceedingly probable that they are having a one-shot interaction (Delton et al. 2011). In summary, the conditions of potential repeat interactions and there being a great potential benefit of cooperation, which promote the evolution of reciprocity, will also tend to promote one-shot generosity secondarily.

Revenge and Forgiveness

Revenge and forgiveness result from psychological adaptations that became species-typical because of their efficacy in enabling human ancestors to solve recurrent social problems during the course of evolution (Williams 1966). McCullough et al. (2013) defined revenge on a functional basis as:

a targeted imposition of costs or withholding of benefits, in response to a cost-inflicting (or benefit withholding) event, that results from a cognitive system designed (i.e., selected) for deterring other organisms from imposing costs (or inducing other organisms to confer benefits) upon oneself or other individuals in whom one has fitness interests. (p. 4)

To the extent that such a cognitive system can boost lifetime reproductive fitness, the ability to change others' incentives toward the self may evolve (Tooby and Cosmides 1996). In this context, four types of deterrence have been described: (1) direct deterrence of cost imposition; (2) indirect deterrence of cost imposition; (3) direct deterrence of benefit withholding; and (4) indirect deterrence of benefit withholding (McCullough et al. 2013).

Revenge carries costs that can potentially offset its deterrence benefits. In most cases, a critical cost of revenge lies in others' also having revenge systems. In the sequential PD paradigm, defecting when players are using a tit-for-tat strategy yields a cycle of mutual defection, known as the echo effect (Axelrod 1984), which reduces payoffs drastically for both participants.

Forgiving strategies, such as "generous tit-for-tat", can reduce the chance of getting trapped in defect-defect spirals. Forgiveness has been defined as a set of motivational changes whereby an individual becomes less motivated to retaliate against and maintain estrangement from an aggressor, while becoming more motivated by good will for the aggressor (McCullough et al. 2013). Thus, revenge and forgiveness have complementary biological functions, wherein mechanisms for revenge can deter harm, while forgiveness mechanisms can lead to problem-solving related to the preservation of valuable relationships despite prior harm. Both sets of mechanisms help to consolidate reciprocal altruism.

Gratitude

Gratitude refers to an emotional appreciation typically evoked by the perception that one has benefited from the generosity of another (McCullough et al. 2008). Assumed to be an important facilitator of reciprocal altruism (Trivers 1971), gratitude appears to mediate at least three functions in reciprocal altruism. First, gratitude can signal the transmission of a benefit. The intensity of the gratitude would be particularly high when the beneficiary recognizes that (1) the benefactor acted intentionally, (2) the altruistic action was costly to the benefactor and/or highly valuable to the beneficiary, and (3) the action was not driven by kinship obligations (McCullough et al. 2008). Second, gratitude may trigger reciprocal behavior. That is, the greater the intensity of gratitude evokes, the higher the possibility the beneficiary will want to provide the benefactor something in return. Hence, gratitude can introduce psychological states that support generosity and cooperation (McCullough et al. 2008). Moreover, the expression of gratitude from beneficiaries may reinforce prosocial behavior in benefactors. Thankfulness expressed by recipients conveys a signal to the benefactor that his or her support is acknowledged and thus likely to be reciprocated in the future. In this way, gratitude in beneficiaries can make them appear to be safe targets for future investments of the benefactor (McCullough et al. 2008).

Anger

Actual or intentional exploitation or harm from others triggers anger (Izard 1977). If a transaction is judged to be unfair, anger could motivate one to perform retaliatory actions, inflicting costs on the transgressor. Such sequelae may force the target of anger to augment their view of the angered individual's welfare and reduce the possibility of such a transgression in future (Sell et al. 2009; Trivers 1971).

The aggression caused by anger can have ramifications that exceed the cost of the offenses committed (Trivers 1971) and sometimes even

destroy a cooperative relationship. Such over-reaction is logical if one considers that a too-low punishment for the current offense may encourage an offender to cheat in the future. The natural selection for a strong exhibition of aggression in response to exploitation may thus deter cheating (Trivers 1971). Individuals in a position to enact greater benefits or harms on others may be more prone to expressing anger when dealing with reciprocal fairness grievances than those in less influential positions. Such influence could become an important bargaining chip, and individuals with these powers may expect the beneficiary to attach heightened importance to their benefits in accordance with their contribution (Sell et al. 2009).

Guilt

The sense of guilt is a negative emotional state that occurs when one realizes that s/he has violated a moral or social standard (Tangney et al. 2011). Typically, guilt is elicited when one realizes s/he has inflicted harm on another, either intentionally or unintentionally (Keltner and Buswell 1996). In the context of reciprocal altruism, a beneficiary may feel guilt after cheating a feedback expectation, an act that induces punishment when it is discovered to have been perpetrated intentionally (Trivers 1971). Functionally, guilt directs the transgressor's attention toward the harm imposed on another, introducing emotional discomfort and motivating one to compensate and behave reciprocally in the future to prevent disrupting a reciprocal relationship. Moreover, the anticipation of guilt prevents social transgressions, leading one to focus on the self-harm that would come from the potential degradation of a cooperative relationship (Fessler and Haley 2003).

Empathy and Sympathy

Empathy encompasses multiple related capacities: the capacity to share in the emotional state of another; the capacity to use reason to

understand the cause of another's state; and the capacity to understand and adopt another's perspective to be in line with that person. Empathy may have arisen from intensive parental care and then been applied to a wider network of social relationships. Consistent with reciprocal altruism theory, individuals tend to show empathy to cooperators, but empathy may be suppressed, or even replaced with schadenfreude, for defectors (de Waal 2007).

In psychology, three levels of empathy are recognized (de Waal 2007). The lowest level is emotional contagion, which refers to being affected by another's emotional or arousal state. For example, one may experience aversive vicarious arousal when seeing others in pain, which may motivate him or her to engage in altruistic behavior to reduce such feelings. The second level of empathy is sympathy or sympathetic concern, which refers to feelings of sorrow or concern for the distress or need of others. Finding and helping those in need of help underlies the building up of reciprocal relationships. Individuals in distress now might offer reciprocal support in the future. The greater the potential benefit to the recipient, the greater the sympathy and the more likely one is to engage in an altruistic gesture. Trivers (1971) suggests that sympathy can facilitate detection of people in need and motivate altruistic behavior based on the needs of beneficiaries. The third level of empathy is empathic perspective-taking, which refers to the capacity to understand another's specific situation and needs, combined with vicarious emotional arousal. The main manifestation of empathic perspective-taking is targeted helping of others according to their specific situations and goals.

In conclusion, human mind contains specialized mechanisms (adaptations) designed for reciprocal altruism.

Cross-References

- [Ability and Willingness of Victim to Retaliate](#)
- [Altruism Norms](#)
- [Anger Proneness](#)
- [Be Forgiving](#)

- ▶ Benefit to Another at Cost to Self
- ▶ Cheater Detection
- ▶ Cheater Detection Adaptations
- ▶ Cooperation Varies with Genetic Relatedness
- ▶ Costly Signaling and Altruism
- ▶ Evolution of Cooperation
- ▶ Evolution of Morality
- ▶ Evolution of Reciprocal Altruism
- ▶ Evolved Moral Foundations
- ▶ Fairness in Primates
- ▶ Food Sharing and Nonhuman Reciprocal Altruism
- ▶ Frans de Waal
- ▶ Game Theory
- ▶ Game Theory as a Foundation of Evolutionary Psychology
- ▶ Gratitude, Sympathy, and Empathy
- ▶ Hamilton's Rule and Theoretical Implications
- ▶ Helping and Genetic Relatedness
- ▶ Helping and Inclusive Fitness Benefits to Helper
- ▶ High-Cost Altruistic Helping
- ▶ Ingredients of Reciprocal Altruism
- ▶ Iterated Prisoner's Dilemma Model
- ▶ Leda Cosmides and John Tooby (Founders of Evolutionary Psychology)
- ▶ Moral Emotions
- ▶ Morality Is Cooperation
- ▶ Prisoner's Dilemma and Cooperation
- ▶ Problem of Altruism
- ▶ Problem of Cheating
- ▶ Psychology of Reciprocal Altruism
- ▶ Puzzle of Altruism, The
- ▶ Recalibration Theory of Anger
- ▶ Reciprocal Altruism (Middle-Level Theory in Evolutionary Psychology)
- ▶ Reciprocal Altruism and Cooperation for Mutual Benefit
- ▶ Reciprocal Altruism and Cooperation for Mutual Benefit
- ▶ Reciprocal Altruism and Group Living
- ▶ Reconciliation
- ▶ Repeated or Iterated Prisoner's Dilemma
- ▶ Reputation and Altruism
- ▶ Rescuing Friends and Relatives
- ▶ Rescuing Strangers

- ▶ Robert Axelrod's (1984) *The Evolution of Cooperation*
- ▶ Robert Trivers
- ▶ Science and Morality

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Adaptations to Avoid Ostracism

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Synonyms

Shunning; Social exclusion

Definition

Humans evolved strategies to avoid being ignored, left out, or ostracized. By avoiding ostracism, our evolutionary ancestors were better suited to their environment. Such adaptations helped ensure our survival and reproduction.

Introduction

The need to belong is a basic feature of human psychology and characterizes us as a species (MacDonald and Leary 2005). Ostracism threatens this need. To help our ancestors achieve their survival and reproductive goals, people evolved adaptations to prevent ostracism. Below, examples of adaptations to avoid ostracism are listed.

Social Pain

Physical pain evolved to alert us to environmental threats and to serve as a preventative force against physical injuries (Bolles and Fanselow 1980). *Social pain*, the aversive experience associated with ostracism, arose from an evolutionary push to co-opt the physical pain system to respond to social injuries (e.g., ostracism; Chester et al. 2012). Much like physical pain, individuals with a blunted sense of social pain exhibit greater ostracism in their daily lives (Chester et al. 2015). The prospect of ostracism's sting prevents people from doing things that could cause them to experience ostracism.

Conformity, Obedience, and Norm Adherence

Group members who disobey group norms often experience ostracism (Kurzban and Leary 2001). This tendency is even observed among our close Chimpanzee relatives (Goodall 1986). Thus, it behooves people, especially those at the lower rung of the social ladder, to act in ways that conform to group standards. Our powerful tendency to conform to group norms and obey authority figures likely reflects the need to prevent ostracism across our species' history (Latané 1981).

Reciprocity and Free-Loading

For society to flourish, people must cooperate and pool resources. Distressing times often propel people to help rather than hurt others. But people also seek to maximize their personal outcomes. Rather than giving their fair share, people rely on others' generosity. To prevent people from enjoying the benefits of group membership without contributing, humans have evolved cheater detection mechanisms that serve to identify and ostracize free-riders (Price et al. 2002). To prevent ostracism, group members must reciprocate assistance from others and contribute equally to collective tasks.

Self-Control

We'll never know if people were born to be bad or good. What we do know is that selfish, antisocial actions can cause ostracism. To restrain egocentric tendencies, individuals must use self-control, the ability to place higher-order goals above immediate desires (Baumeister et al. 2007). Self-control processes arise from the prefrontal cortex, a brain structure that is disproportionately large in humans (Dunbar 2002). The prefrontal cortex likely evolved to prevent selfish impulses from translating into ostracism from the group.

Conclusion

Early humans evolved in small groups, relying heavily on each other for their well-being. In that context, ostracism was a death sentence. As a result, humans evolved adaptations to avoid ostracism. Through social pain, adherence to group norms, contributing equally to group goals, and using self-control to restrain our selfish impulses, we can avoid being ostracized.

Cross-References

- [Avoiding Stigmatization](#)
- [Stigmatization and Ostracism](#)

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Adaptations to Human Sperm Competition

- ▶ History of Sperm Competition in Humans

Adaptations to Sperm Competition

- ▶ Sperm Competition Tactics

Adaptations: Product of Evolution

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Definition

Structure or behavior of an individual that is the long-term outcome of the process of natural selection.

Introduction

The word adaptation has a vernacular and two technical senses. In a vernacular sense, an

individual's adaptation is simply the adjustment of this individual to new conditions. For instance, when the temperature at the place you are located increases sufficiently, you start sweating. Your temperature adjusts or adapts to this new temperature. This is an adaptation in the vernacular sense, which is different from what evolutionary biologists and psychologists are referring to when they use the word "adaptation," although a link between the vernacular and the technical senses exists. An adaptation, for an evolutionary scientist, is both a structure (for instance, an organ) or a behavior which is the outcome of the process of natural selection, and the evolutionary process by which such a structure was produced. Thus, one technical meaning of the term "adaptation" in evolutionary sciences refers to the product of natural selection, while the other refers to the process by which such a product is obtained.

The Process of Adaptation

One of the greatest achievements of Darwin's (1859) theory is that it can explain how complex structures to which we attribute functions are the products of an unguided process. William Paley, a famous theologian, is well known for having formulated a version of the "watchmaker analogy" in his influential book *Natural Theology* written in 1802, one version of which is the following. If you stumble upon a rock on the beach, it is unlikely you will ask who designed the rock and whether the rock has a purpose. But if you now stumble upon a watch, you will want to know who produced the watch, as well as the purpose of this complex object. Design calls for a designer, in this case a watchmaker, according to Paley. Natural selection can explain complex "watch-like" structures, ones which appear to bear the hallmarks of intentional design, without recourse to any sort of intentional designer. This type of reasoning led Richard Dawkins (1986, p. 21) to claim that "[n]atural selection is the blind watchmaker, blind because it does not see ahead, does not plan consequences, has no purpose in view. Yet the living results of natural selection overwhelmingly impress us with the appearance of design as

if by a master watchmaker, impress us with the illusion of design and planning.”

How can natural selection achieve this result without invoking a designer? Suppose you have a population of individuals that all differ in their characteristics. For instance, some individuals are able to detect light, while others are not. Suppose also that being able to detect light produces an advantage in terms of survival or reproduction, so that on average light-sensitive individuals have a larger number of offspring than light-insensitive individuals. The reason for this advantage could be because seeing light permits an individual to detect some movements and consequently escape predators more often than light-insensitive individuals. Finally, suppose that individuals transmit their ability to detect light to their offspring with some fidelity. On average, light-sensitive individuals produce light-sensitive offspring more often than light-insensitive individuals do. At the next generation, we expect the population to have a higher proportion of light sensitive individuals than it had in the previous generation. This recipe for evolution by natural selection, which at its cores invokes variation, difference in fitness (reproductive output), and heredity has been proposed a number of times ever since Darwin presented his own version in the *Origin* (for a review of them see Godfrey-Smith 2009; for a famous version see Lewontin 1970). It embodies the principles by which a population can adapt to its environment. Yet, all one gets after one generation is a population in which individuals are slightly better able to escape predators than they were in the previous generation, nothing like complex structures such as an eye.

But suppose now you repeat this process over and over again for thousands of generations, with some individuals exhibiting new variation (acquired by random or blind mutations) at each generation. For instance, one mutation could increase or decrease the number of cells able to detect the light, change their position, etc. With such a process of blind variation (i.e., random from the point of view of the individual bearing this difference in terms of the advantage or disadvantage it will produce), the population will start

exhibiting increasingly complex structures. And, in fact, this is precisely what Nilsson and Pelger (1994) demonstrated. Using a computer simulation, they showed that by random mutations increasing or decreasing in different ways the optical quality of a patch of light-sensitive cells, a structure similar to that of the mammalian eye or eye of an octopus can evolve in less than 2000 steps (1829 to be precise), where each step can modify one element of the structure of the patch by one percent. Given the fidelity with which traits are typically transmitted from generation to the other, they estimated that it would take less than 400,000 generations to evolve an eye. This is, according to them, a pessimistic estimate since natural selection would typically work on several elements of the structure of the eye at once, while their simulation only tweaked one element at a time.

Nilsson and Pelger’s simulations represent a proof of concept: With a simple process producing blind or random variation, differential success, and transmission of characteristics over time, complex structures or behaviors can emerge. These structures are adaptations.

Adaptive, Maladaptive, and Adaptation

How many steps does it require for a structure to become an adaptation? In the case of the eye presented above, this is equivalent to asking for the threshold point at which the structure is sufficiently different from the patch of light-sensitive cells so that we can call it an adaptation to detect and escape from predators (assuming the bearer of the structure is prey). There is no definitive answer to this question. But recognizing that it has no definitive answer leads to some interesting distinctions, especially in the context of human cognition in its modern environment. An adaptation, as we characterized it, is the product of natural selection. Yet, we also saw that after one generation natural selection already produces a difference: the proportion of the most successful variants will increase (of course this assumes that genetic drift can be neglected). Should we call the difference an adaptation?

Strictly speaking one might want to do so and accordingly call this a *simple* adaptation (or one-step adaptation). In some contexts, this is exactly what is done. For instance, being a heterozygote with the sickle-cell variant of hemoglobin, which results from a single mutation from normal hemoglobin, is regarded as a classical adaptation against malaria (Kwiatkowski 2005). Unfortunately, being a homozygote with the sickle-cell variant leads to a disease known as “sickle-cell anemia.” That said, when the structure or function is more complex, such as an eye, a small difference improving the success of individuals when compared to others is called “adaptive” rather than an adaptation. This distinguishes cases in which a structure has been selected for millions of years in an ancestral environment and yet has a negative effect on fitness in the modern environment – think about the adaptive role of liking sugar in an ancestral environment and its current role on obesity and cardiovascular diseases – from cases in which the adaptation still has an advantageous role in the modern environment. In the latter case the adaptation is also adaptive, while in the former it is not; the adaptation is now maladaptive.

Furthermore, the adaptive/adaptation distinction permits us to account for structures that had no previous function (something known as an evolutionary by-product) and suddenly become advantageous. In such a case, the structure is adaptive without being an adaptation. For instance, some scholars have argued that the beliefs in supernatural agents encountered in many religions started originally as a by-product of an adaptation to detect agency in the environment (Boyer 2001). Since it is costlier not to detect an agent when there is one than to detect an agent when there is none (think about the consequence of not detecting a predator or opponents when there is one), the thesis that beliefs in supernatural agency are a by-product of our evolved cognition is a plausible hypothesis. From this by-product, some people have argued that specific beliefs about supernatural agents, for instance that they are interested in human morality, have an adaptive value without necessarily being an adaptation: it might currently increase the fitness of people more prone to have such

beliefs without having been selected for in the past (for a review of these different hypotheses see Bourrat 2015). If an adaptive process goes on for many generations, an adaptive structure will become an adaptation.

Conclusion

Adaptation is a fundamental concept of Darwinian apparatus. Without this concept, it would be extremely difficult to make sense of the biological complexity around us. In particular, it plays an important role in evolutionary psychology since many complex behaviors, despite their lack adaptiveness in the current environment (or even their deleterious effects, a phenomenon known as evolutionary mismatch), are often regarded as adaptations for an ancestral human environment, known as the environment of evolutionary adaptedness (EAA). Despite the perils of having an adaptationist story for every trait (known as “just so stories”), as forcefully argued by Gould and Lewontin (1979), by and large, the success of evolutionary sciences rests upon generating such stories and then rigorously assessing whether they withstand diverse empirical tests.

Cross-References

- [Adaptationist Program, The](#)
- [By-Products of Adaptations](#)
- [Maladaptations](#)
- [Mismatch Between Evolved Morality and Modern World](#)

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Adapted Mind, The

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Synonyms

[Adaptation](#); [Conceptual integration](#); [Evolutionary psychology](#)

Definition

One of the seminal books in the establishment and development of evolutionary psychology as a distinct method of inquiry in the behavioral sciences.

Introduction

The Adapted Mind (Barkow et al. 1992) outlined two major goals: the introduction of evolutionary psychology and the connection between evolutionary psychology and fields such as biology, anthropology, sociology, economics, and history. One of the overarching themes present in the work is the push for collaboration, or conceptual integration, amongst the social sciences. As the physical sciences, such as chemistry and physics, have compatible theories for the workings of the world, the social sciences should adopt a similar system

for compatibility and common language between them. Doing so would allow for converging lines of evidence for scientific discoveries and help alleviate the present problem with reproducibility in the social sciences (see Brase 2014 for an explanation of one such framework).

Barkow et al. (1992) explains the basic mechanisms of evolution by natural selection, wherein heritable variations in individuals that provide an advantage for the propagation of genes to future generations is the driving force. Importantly, adaptations take many (e.g., thousands of) generations to spread throughout a population. More simply, evolution is a very slow process, and it does not respond to rapid environmental changes. Instead, adaptations are built to solve very specific and persistent problems; they are domain specific (Tooby and Cosmides 1992). A common misconception, as addressed in the chapter by Symons (1992), is that a trait which is an evolved adaptation does not imply that that trait is presently adaptive. An adaptation was designed to solve a specific problem that existed across many generations in the past, and present technologies may have rendered such an adaptation neutral or even maladaptive. For example, sugar tastes sweet and the taste of sweetness is an indicator of fruits at their most nutritious. Presently, with the abundance of refined sugar, our propensity to seek sugar-rich foods may be maladaptive. However, if industrialized people were to be faced with conditions that required foraging for food in order to survive, the attraction to sugar would, once again, become adaptive to satisfy caloric needs.

The remainder, and vast majority, of the adapted mind is dedicated to providing examples of how evolutionary psychology can be integrated into specific research areas within the behavioral sciences. These include chapters on nonhuman primate origins of social interaction and cooperation (by McGrew & Feistner), on mating and sexual behaviors (by Buss, by Ellis, and by Wilson & Daly), on caring for offspring (by Boulton & Smith, by Fernald, by Mann, and by Profet), on language and perception (by Pinker & Bloom, by Shepard, and by Silverman & Eals), on environmental preferences (by Kaplan and by Orians & Heerwagen), on intrapsychic processes (by Nesse

& Lloyd), and on new approaches to studying culture (by Barkow). Each topic incorporates the need to collaborate across disciplines and the same push to approach investigation from an adaptive, domain-specific stance.

Conclusion

After more than two decades, the main arguments from this work: pushing for collaboration and a domain-specific approach to research, are still relevant. The Standard Social Science Model (a term introduced by Tooby and Cosmides 1992) still exists in contemporary texts purchased by undergraduate students, and Barkow et al. argued that this model isolated the behavioral sciences from other fields. By implementing a more collaborative approach, fields like psychology stand better equipped to earn credibility from other sciences and from the layperson.

Cross-References

- ▶ [Adaptationist Program, The](#)
- ▶ [Founders of Evolutionary Psychology](#)
- ▶ [Jerome H. Barkow](#)
- ▶ [Leda Cosmides and John Tooby \(Founders of Evolutionary Psychology\)](#)

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Adaption

- ▶ [Assimilation](#)

A

Adaptive Benefits of Matriliney and “Walking Marriages” in Mosuo Culture

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Synonyms

[Culture](#); [Kin](#); [Mating](#); [Matriliney](#); [Paternity uncertainty](#); [Resources](#)

Definition

Arguably the last known surviving matrilineal tribe in China, the Mosuo offers interesting insights into familial and mating arrangements to support reproduction.

Introduction

Due to its unconventional relationship norms and family structure, the Mosuo tribe is typically seen as a sociocultural puzzle. The evolutionary perspective, however, assumes that social structures that can exist or have existed are likely to be functional and supported by adaptations that enable their sustained functioning. Therefore, the Mosuo pose an interesting case study of alternative reproductive arrangements and elucidate the evolutionary motives facilitated by such arrangements. More specifically, Mosuo practices can work because they enable the Mosuo to overcome a variety of adaptive problems typically faced by individuals in more conventional pair-bonded

relationships. In this entry, we describe the features of the Mosuo, discuss some hypothesized adaptive benefits of Mosuo mating and familial practices, review the available evidence for those hypothesized adaptive benefits, and suggest areas for further research.

General Characteristics of the Mosuo

Although rare, matrilineal societies can be found in various places around the world, including Africa (e.g., the Akans), India (e.g., the Nair), and Australasia (e.g., the Vanatinai). Matrilineal society, also called matriliney, refers to a socially ordered community that adheres to a kinship system in which ancestral descent is traced through maternal instead of paternal lines (the latter being termed patrilineage or patriliney). The Mosuo represent the last matrilineal society in China and are among the few left in the world that are still somewhat thriving and gaining considerable public attention in recent decades. They consist of a population of approximately 40,000 minority Chinese living on the border of Sichuan and Yunnan provinces in the Himalayan Mountains (Walsh 2005). How long they have practiced their way of life is disputed, with experts believing the culture to be somewhere between a few hundred to over 2,000 years old (Dawson 2018; Wen et al. 2004). While the Mosuo have both matrilineal and patrilineal subpopulations due to intermingling with other cultures and the influence of modernization, the current entry will focus on the matrilineal Mosuo residing near Yongning and Lugu Lake, both of which are situated in Yunnan Province (Mattison 2011).

Until recently, the majority of Mosuo were subsistence agriculturalists, raising crops such as buckwheat, corn, wheat, potatoes, and garden vegetables mainly for their own consumption and engaging in animal husbandry of livestock as a significant sideline (Shih 2010). Starting in the 1980s and increasingly through the 1990s, a subset of the Mosuo inhabiting the stretch along Lugu Lake have carved out a living from profits driven by tourism (Mattison 2011; Walsh 2005).

Although family-owned hotels and shops have also resulted in substantial income variation among households, most families residing in areas away from the lake retain agricultural traditions as their major source of subsistence (Mattison 2011).

Among traditional Mosuo, family property and resources are controlled by female heads of households and are normally handed down to their daughters and their daughters’ children (Holden et al. 2003). Mosuo men do act as temporary co-stewards of resources, but whatever rights they have to resources, nominal or real, will be transferred to their sisters’ children. Mosuo men are expected to prioritize and dedicate labor to their natal households rather than their romantic partners’ households (Cai 2001). As we will see later, Mosuo men and women romantically consort in the woman’s home, after which the men return to their own residences to continue investing in their natal households, providing caregiving in particular to their sisters’ children. As lineage affiliation among the Mosuo is matrilineal, children of both sexes fall under their mother’s lineage and typically reside with her throughout their lives. The most important inherited resource shared by a household until recently was land, but money and other durable goods have increasingly become more important, especially in areas where tourism is prevalent (Mattison 2011).

Reproductive Practices of the Mosuo

The Mosuo practice a system of romantic pairing known as “walking marriage” or *sese* (Cai 2001; Mattison 2011; Shih 2010). When females come of age at approximately 13 years old, they can start to take lovers from men within the tribe, having as many or as few as they desire over their lifetime. Male companions spend their days helping in their own homes or carrying out jobs such as fishing, farming, or construction and visit the women’s homes at night, often secretly (Shahtlyn 2010). Thus, throughout the course of their unions, men visit their lovers mostly at night while retaining separate residences.

According to ethnographers of the Mosuo, walking marriages involve no contract between lovers, paternity is not assured but is also unimportant, and multiple concurrent unions are possible and do not incite jealousy (e.g., Cai 2001; Shih 2010). Moreover, not only do men engaging in *sese* have no obligation to participate in their partners’ lineages, but they are also expected to refrain from doing so due to potential tensions that may arise between their own families and their partners’ relatives (Cai 2001; Mattison 2011). For instance, a man who spends too much time at a partner’s household risks being judged as neglecting his own family or as interfering in the partner’s household. As such, the children that result from walking marriages are seldom raised by their biological fathers; instead, the brothers of the mother (i.e., the maternal uncles) take on paternal responsibilities and serve as father figures. It can also be said that paternal investments are irrelevant in the Mosuo context. As the typical duties of a conventional father, such as the provision of resources and nurturance of offspring, are provided by the mother’s kin in her natal household, investments from biological fathers are rendered unnecessary. Correspondingly, there is also no stigma attached to not knowing who a child’s father is (Shaitlyn 2010).

Challenges to Relationship Orthodoxy

From an evolutionary perspective, adaptations are features and characteristics that exist to promote the reproductive success of organisms (Williams 1966). These adaptations also include psychological traits such as mate preferences and mating strategies, which guide individuals toward acquiring mates who are most likely to bring them the highest chance of reproductive success (Buss and Barnes 1986).

For instance, reproduction hinges critically on women’s valuable reproductive resources, such as their limited eggs and heavy investment in offspring (e.g., internal gestation and lactation). Yet, the processes of reproduction (e.g., pregnancy, childbirth, childrearing) can be very costly to

women and render them highly vulnerable (Trivers 1972). Thus, while men may have evolved a preference for cues to fertility and reproductive potential in prospective mates (e.g., youth, health, physical attractiveness), women evolved a preference for partners who can offer resources and protection (Symons 1979). In addition, as females are the more heavily investing sex, women tend to be on average more cautious than men when selecting potential mates. In contrast, men are much less biologically constrained, and they can also directly increase their overall reproductive success by increasing the number of partners that they inseminate – a generally undesirable strategy for women who, especially during ancestral times where birth control did not exist, must incur pregnancies and are potentially bound to several years of maternal investment for any given sexual encounter (Li and Yong 2018). Therefore, whereas men stand to benefit by pursuing multiple mates, women benefit more from being choosy about the quality of their partners and are less interested than men in having multiple partners. Lastly, across various human societies, fatherhood is the norm as the support afforded by fathers in addition to mothers increases the survival and reproductive viability of offspring (Geary 2005). As such, women tend to prefer men with fatherhood qualities, such as the ability to protect them and their offspring, provide resources, and nurture young (Buss and Barnes 1986). The benefits of having both parents raise children increases the desire for long-term pair-bonding in humans. Reflecting these preferences, monogamous heterosexual marriages prevail across the world (Herlihy 1995).

The mating preferences and approaches of the Mosuo differ substantially from those widely adopted or practiced in other cultures. Specifically, the concept of fatherhood does not exist among the traditional Mosuo or exists instead in the form of care from maternal uncles. Mosuo women also may not be as concerned about a potential mate’s resources and social status as would be predicted by evolutionary theories of human mating. Moreover, Mosuo women do not expect their romantic partners to commit to the relationship and are themselves open to having

multiple partners. These unconventional practices of the Mosuo pose a significant challenge to our beliefs about family structure, in particular the common practice of nuclear families comprising children and pair-bonded parents, as well as what we know about the dynamics of human mating and attraction.

Mosuo Practices as Solutions to Adaptive Problems

By doing away with fatherhood and keeping the lineage within the maternal side, Mosuo familial and relationship arrangements may help to solve a range of adaptive problems otherwise faced by people in more conventional marriage arrangements. The following is a list of hypothesized adaptive solutions afforded by traditional Mosuo practices.

Solution to Women's Problems of Assessing the Commitment and Quality of Mates

Evolutionary theories of mating suggest that women are confronted with the adaptive challenge of assessing prospective partners' willingness to commit and ability to provide protection and resources, primarily because the survival prospects of a woman and her offspring hinge critically on the male partner's commitment and provisioning (Symons 1979). In Mosuo contexts, however, women who are childbearing or childrearing have their needs met through the resources, protection, and nurturance provided by their natal households (Cai 2001; Shih 2010). With her and her offsprings' welfare taken care of through the help of kin, a Mosuo woman is unlikely to incur the typical costs associated with partner desertion or the selection of an inept mate. Consequently, she can afford to exert less effort in mating assessments, which also carry the burdensome secondary challenge of determining whether potential mates are being deceptive about their mate quality (Tooke and Camire 1991). Moreover, Mosuo women are relatively freer to make relationship choices based on other factors such as physical attraction or personality compatibility.

Solution to Men's Problems of Demonstrating Mate Quality and Intrasexual Competition

Conversely, given that Mosuo women's requirements in mate selection are less stringent than those of women seeking conventional relationships, Mosuo men do not have to incur the costs associated with protracted courtships and displays of worth and formidability in order to attract mates (Grammer 1989). The intensity of intrasexual competition between men will also likely be reduced, at least on the basis of outdoing each other through the accumulation and display of resources and status (Buss 1988).

Male intrasexual competition can be harmful not only to the men themselves but also to the society wherein these men compete. Among males vying for female attention, the motive to compete produces a preoccupation with gaining resources, status, and dominance, which can translate into a variety of outcomes ranging from injuring or killing mating rivals (Wilson and Daly 1985) to increased risk-taking (Ronay and von Hippel 2010) to an acute obsession with work and income (Yong et al. 2019), all of which can put men's health at risk. At a societal level, the male desire to accrue resources in order to compete intrasexually may exacerbate status disparities between men who have resources (and are thus capable of accruing even more resources) and those who do not, leading to a host of societal problems related to social and economic inequality (Wilkinson and Pickett 2009). The inherently aggressive nature of male intrasexual competition has also been argued to be an underlying cause of societal instability, such as gang violence (Wilson and Daly 1985) and even terrorism (Kanazawa 2007). Thus, Mosuo practices that diminish men's need to compete for mates may reduce men's exposure to harm as well as promote societal stability and peace.

Solution to Men's Problem of Increasing Sexual Access to Multiple Mates

As men stand to directly improve their reproductive success by increasing the number of females they can inseminate, men may have evolved a preference for sexual variety and to desire multiple partners in short-term sexual relationships

(Li and Kenrick 2006). The orthodox female preference for relationship exclusivity and long-term commitment, however, often constrains men’s ability to enact a quantity- and variety-driven reproductive strategy. As men in Mosuo contexts are not expected to commit to their romantic partners, they are free to fulfill their desire for sexual quantity and variety – an approach that negates the problems otherwise confronted by men who try to seek extra-pair matings while in conventional relationships. Given the potentially severe consequences of being caught having a sexual affair, such as physical retaliation from the cheated partner’s family or the legal repercussions of infidelity, men are typically careful to seek additional partners only surreptitiously. In contrast, Mosuo men are permitted to do so without fear of those repercussions as the preferences of the opposite sex are not violated.

Solution to the Problem of Paternity Uncertainty

As human reproductive biology entails internal female fertilization, men face the problem of being cuckolded, that is, investing care and resources in children who are actually sired by other men – an adaptive problem not faced by women. The uncertainty over whether offspring are theirs increases to some extent the incentive for men to focus more on mating than on parenting (Geary 2005). Given the freedom and acceptability for Mosuo women to mate with as many men as they wish, Mosuo men’s confidence in paternity over children produced through walking marriages is relatively low. However, because Mosuo men are not required to raise their own putative offspring, paternity no longer becomes a concern (Cai 2001). Indeed, although Mosuo men may sometimes opt to care for their own offspring (whom they cannot be certainly sure are theirs), they primarily channel their caregiving efforts to their sisters’ children instead. As women are almost certainly sure that the offspring they produce are theirs, the brothers of Mosuo women have a reliable degree of certainty over the relatedness of the nephews and nieces they help raise, thereby eliminating the possibility of investing in unrelated children.

Doing away with the need for relationship commitment therefore allows both men and women in the Mosuo tribe to sidestep the problems that emerge from potential as well as actual infidelity in conventional relationships. For instance, it is unlikely that Mosuo individuals feel the need to expend substantial effort in mate guarding, nor would they be as prone to the troublesome experience of romantic jealousy as would couples in conventional relationships who fear the loss of investment from their valued partners (Shahtlyn 2010; Yong and Li 2018). On the flipside, being subjected to intense mate guarding can also be extremely harrowing. As men have a strong desire to avoid being cuckolded and raising unrelated children, they may take extreme actions to deter or punish mates for sexual infidelity which can sometimes lead to serious physical injuries or even death (Goetz et al. 2008). These are all effectively avoided by the Mosuo.

Matriliney as daughter-biased investment may also function as an adaptive solution by parents to optimize allocation of resources in terms of inclusive fitness (Holden et al. 2003; Hamilton 1964). Many societies pass on wealth and property through the male line because men’s but not women’s mate value is intricately tied to status and resources. As such, bequeathing wealth and property to sons promises higher reproductive returns as sons can be made more desirable and thus stand to benefit more than daughters from being endowed with such resources (Trivers and Willard 1973). However, because paternity uncertainty tends to be high for the Mosuo, transmission of wealth and property through males may lead to loss of resources to nonkin. Therefore, paternity uncertainty may have served as a historical antecedent for early Mosuo parents to adopt matrilineal practices and bias investment of wealth and property toward daughters rather than sons so that these resources will be channeled toward actual progeny.

Solution to the Problem of Familial Instability

In most formalized long-term relationship contexts, people officially marry into families, and this often involves the female marrying into the male household. This practice creates obstacles to

cooperation and avenues for rifts due to genetic unrelatedness between the household and incoming individuals. For instance, given that the female is nonkin, her affines may minimize cooperation with her or even exploit her. When the couple have children, the female may also be more inclined to view herself and her children as a genetically related unit distinct from her partner's household and then value the interests of her unit over those of the household. These misalignments in genetic self-interest can lead to familial instabilities as evidenced by the numerous instances of infighting in imperial families throughout recorded history (Soulliere 1988). The Mosuo avoid such rifts by not having contractual marriages and emphasizing involvement and commitment primarily to one's natal household (Cai 2001); as such, Mosuo households minimize "contamination" from the intrusion of nonkin with divergent genetic interests, so to speak. Indeed, Mosuo individuals have expressed that they prefer not entangling daily life and responsibilities with love affairs, with one woman saying "who wants a mother-in-law?" (Dawson 2018). Hence, the consistently high degree of genetic relatedness in Mosuo households due to the relative absence of lowly related individuals and high certainty of relatedness through the maternal line strongly facilitates familial solidarity and cooperation.

Solution to the Problem of Conflict over Whom to Invest in

People in conventional relationship and familial contexts may also face the dilemma of having to choose between one's natal family and their romantic partner (which may include affines) in situations of conflict. This is often difficult to resolve because both parties are typically important in conventional contexts – the natal family is genetically related; therefore helping them is directly beneficial for inclusive fitness (Hamilton 1964); at the same time, the romantic partner is a reproductive mate and co-parent; therefore helping them is directly beneficial for reproductive success and indirectly beneficial for inclusive fitness (Pillsworth and Haselton 2005). This conflict

may manifest as, for example, the dilemma over who to give one's limited resources to or the dilemma of deciding who to save in a life-threatening situation. Failure to finesse this quandary can result in anger and distrust from the side that feels shortchanged (Sell 2011). Among the Mosuo, the norm of returning to and investing in the natal family makes clear that one's kin should be prioritized, thus eliminating the burden of having to make such choices and reducing the potential for conflicts and undermined relationships.

Empirical Evidence for the Adaptive Benefits of Mosuo Practices

Despite growing awareness and media coverage of the Mosuo in recent decades, surprisingly little research has been conducted that allows us to confirm the hypothesized benefits of Mosuo practices as an alternative to conventional relationships structured around formal marriage. To our knowledge, only two studies have been conducted that directly validate the benefits we proposed. First, a study by Thomas et al. (2018) found that costly cooperation among the Mosuo, such as traveling over long distances to provide help, varied most strongly and positively as a function of kinship or genetic relatedness over other factors such as need, affinal relations, or proximity, thus confirming that inclusive fitness indeed underlies Mosuo helping and cooperative behaviors.

Second, Mattison (2011) examined matriliney as a possible group-level adaptation and proposed that daughter-biased transmission of wealth may serve as a solution to the problem of resource loss due to paternity uncertainty. She predicted that, all things being equal (e.g., males and females would equally benefit from inheriting wealth), complete certainty over paternity in sons' offspring would be needed in order for resources to be transmitted equally to sons and daughters. As paternity certainty is likely to be low among men engaging in walking marriages, her framework predicts daughter-biased investment of resources, which is indeed generally the case for the traditional

Mosuo. Hence, daughter-biased resource transmission through matriliney appears to be an adaptive solution to the problem of potential resource losses under conditions of high paternity uncertainty. When viewed from another perspective, a shift toward daughter-biased investment may have been a key factor that enabled the Mosuo to do away with fatherhood and unlock the benefits associated with not having to depend on the commitment of romantic partners.

Future Research

Albeit scarce, the available evidence so far suggests that our predictions of the advantages of Mosuo practices are in the right direction. More empirical research is certainly needed to examine our numerous speculations and, in all likelihood, uncover further adaptive benefits brought about by such unorthodox practices. This will not only enlarge our perspective on the possibilities for human relational arrangements – including their various pros and cons – but also contribute further to our understanding of mating psychology and behavior.

The Mosuo and other cultures with atypical mating rituals and practices also allow us to identify potential shifts in mate preferences and selection criteria and thus promise interesting and novel insights. For instance, given that Mosuo men do not need to attract women using status and resources, Mosuo women are likely to select men based on other traits such as physical attractiveness. Correspondingly, we may also predict high levels of physical attractiveness in Mosuo men due to the selection pressure exerted by women on this trait.

Although it is commonly assumed that matriliney shifts the balance of power in favor of females and thus offers more benefits to females, the current analysis also suggests that males can benefit tremendously from matrilineal practices. Some of these insights can be borrowed to engender further investigations into how conventional or modern familial and relationship structures can be modified to benefit both sexes.

Conclusion

The current entry demonstrates the utility of the Mosuo tribe as a case study of alternative reproductive arrangements. Through this analysis, we elucidated a range of benefits afforded by Mosuo practices, thereby showing that conventional long-term relationships structured around monogamous marriages may not necessarily be the most ideal despite their ubiquity across the globe. Although this analysis does not suggest that we do away with conventional marriages, it brings to light many of the costs we may incur in conventional marriages and expands our understanding of the effects as well as pros and cons of alternative mating arrangements.

Cross-References

- ▶ [Genetic Relatedness Affects Aid to Kin](#)
- ▶ [Benefits of Commitment and Marriage](#)
- ▶ [Benefits to Kin](#)
- ▶ [Children without Paternal Investment](#)
- ▶ [Cultural Differences](#)
- ▶ [Cultural Evolution](#)
- ▶ [Cultural Variation](#)
- ▶ [Female Mate Choice](#)
- ▶ [Genetic Relatedness Affects Aid to Kin](#)
- ▶ [Grandparental Investment and Genetic Relatedness](#)
- ▶ [Inclusive Fitness](#)
- ▶ [Kin Selection](#)
- ▶ [Marriage](#)
- ▶ [Mate Preferences](#)
- ▶ [Mate Value](#)
- ▶ [Maternal Investment](#)
- ▶ [Mating Strategies](#)
- ▶ [Mating Systems](#)
- ▶ [Multiple Matings](#)
- ▶ [Parental Effort Versus Mating Effort](#)
- ▶ [Parental Investment](#)
- ▶ [Paternal Care](#)
- ▶ [Paternal Investment](#)
- ▶ [Paternal Investment Relative to Maternal Investment](#)
- ▶ [Paternal Role](#)

- ▶ Paternity Certainty
- ▶ Paternity Uncertainty
- ▶ Paternity Uncertainty and Investment in Sons and Daughters
- ▶ Seeking Extra-Pair Partners
- ▶ Sexual Conflict and Sex Differences in Parental Investment
- ▶ Trivers-Willard Hypothesis

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Adaptive Hypotheses of Infanticide

- [Infanticide in Nonhumans](#)

Adaptive Lag

- [Mismatch Between Evolved Morality and Modern World](#)

Adaptive Learning

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Synonyms

[Adaptive plasticity](#); [Associative learning](#); [Cultural learning](#); [Cultural transmission](#); [Optimal imitation](#); [Optimal learning](#)

Definition

A category of learning strategies which promotes an individual's assimilation of successful behaviors, traits, and skills, increasing an individual's level of fitness in a given environment

Introduction

A construct of interest to both the fields of developmental and evolutionary psychology is *Adaptive Learning*, sometimes referred to as adaptive plasticity, which some researchers have labeled as an overarching category of learning strategies that contribute to an individual's level of fitness in a given environment (Kameda and Nakanishi 2002). Currently, adaptive learning has been reviewed within the context of its relationship to

the Baldwin effect, which states that the utilization of *Adaptive Learning* increases the rate at which a species undergoes evolutionary changes to the phenotype (Sznajder et al. 2012). However, this entry seeks to provide a broader overview of the area of research investigating *Adaptive Learning* and the strategies that it comprises. These learning strategies include prestige-biased learning (Atkisson et al. 2012; Chudek et al. 2012; Henrich and Broesch 2011), majority-biased copying (Evans et al. 2018), conformity (Haun et al. 2014; Kameda and Nakanishi 2002; Morgan et al. 2015; Muthukrishna et al. 2015), and play (Lew-Levy and Boyette 2018). These strategies explain the adaptive nature of learning and subsequent evolutionary benefits. This entry seeks to provide an analysis of these *Adaptive Learning* strategies, primarily focusing on the broader categories of *Conformity and Imitation* and *Prestige Bias*.

Conformity and Imitation

To be successful in an environment, it is often necessary to conform to the demands of the majority in order to receive acceptance into the community. Additionally, individuals that do not have the resources to devote to individual learning may opt to selectively copy the majority if the behavior displayed is shown to improve culturally significant skills. One example of imitation was shown in a study conducted by Lew-Levy and Boyette (2018) in which the authors observed learning through imitation in Aka and Ngandu village children in the form of work-themed play. They found that children spent less time engaging in work-themed play as they got older, because they begin to engage in these real work tasks more as they mature. Lew-Levy and Boyette also found that a child's ethnicity and gender were associated with the types of roles they practiced; they adopted the roles that were most representative of their own identity, despite having access to models of different gender and ethnicity. For example, the researchers found that children were only practicing activities that were relevant to life in their village and did not incorporate play based on skills of foreigners or those from other villages.

Lew-Levy and Boyette inferred that play has an adaptive learning function as it helps children develop necessary skills consistent with life in their immediate environment.

An earlier work conducted by Kameda and Nakanishi (2002) investigated the cost of social learning in unstable environments. The researchers used a game called “where is the rabbit” where participants were asked to judge the location of the rabbit for 60 rounds. They found that as the cost of individual learning increased, participants became less likely to conform. Kameda and Nakanishi state that the increase in the cost of individual learning creates an imbalance where fewer people become information generators, and therefore if the environment is changing over time and fewer people are generating new information about the environment, it is not beneficial to conform to potentially outdated information. This shows the adaptive nature of this strategy, as the individual evaluates the sources of information within the evolving context of the immediate environment.

Additionally, Haun et al. (2014) investigated differences in conformity likelihood across human, orangutan, and chimpanzee children. They found that human children were more likely to conform to the actions performed by a majority of demonstrators, even if this action was just as effective as an action previously used by the child. The other great ape children did not adjust their actions to conform to the demonstrators. In addition, children were more likely to conform when they were in the presence of the demonstrator and less likely in their absence. Children also conformed to a new action just as frequently when there were one or three demonstrators. This shows an individual’s drive to model effective behaviors as well as to conform to the cultural expectations of their environment.

In a similar study, Morgan et al. (2015) investigated how children conform in uncertain environments. They found that children in the 3- to 4-year age range had a strong drive to conform to an action performed by a total majority of demonstrators, but not the actions of a less than total majority. Six-year-olds conformed in an equal proportion to the number of demonstrators, and

7-year-olds showed a similar drive to conform to total majorities, as well as an increased drive to conform to less than total majorities. These results led Morgan and colleagues to infer that as children age, they begin to develop the ability to utilize and interpret different social and asocial information when making their own decisions, much like the decision-making competencies of an adult.

A study by Muthukrishna et al. (2015) investigated conformist social learning biases in an experiment requiring participants to indicate the longest line presented in an array of varying size and number (similar in design to Asch’s 1951 experiment). They found across their two studies that very few participants in each respective study showed no signs of conformity. Muthukrishna et al. propose that these findings may reflect an underlying adaptive benefit to conformity in that it may be beneficial to the survival of a group to improve cooperation. Also, through observation (i.e., social learning), an individual can learn potentially costly information by witnessing another perform a dangerous task (e.g., watching someone eat an unknown berry that could be poisonous).

Finally, Evans et al. (2018) investigated selective copying and the utilization of “optimal” imitation in children. In their study, children watched demonstrators perform varying levels of relevant actions in order to retrieve a capsule from a “sweeper box” device. They found that when children witnessed a single method being performed by every demonstrator, the children were more likely to copy the relevant actions. In addition, children were also shown to copy less than total majorities, but not as often as total majorities and primarily when performed unanimously. However, when an irrelevant action was demonstrated unanimously, children were shown to only copy the irrelevant action in the next immediate trial. Additionally, 6-year-old children were less likely than 4-year-old children to copy irrelevant actions when performed by a less than total majority. Evans and colleagues interpret these findings as evidence of children becoming “optimal” imitators, meaning that children will examine the usefulness of a copied behavior in practice and then determine if the behavior is worth adopting.

Collectively, the findings presented in this section show the processes used by both children and adults to develop the skills necessary for the survival of themselves and their community. This is done through selective copying of observed behaviors and evaluating their usefulness through practice to determine their real benefit. Additionally, children and adults show a reliance on the consensus of the community to help determine what skills are desirable and beneficial.

Prestige Bias

Individuals may selectively choose to learn from sources of information deemed to be the most prestigious source available. A prestigious individual is deemed to have expertise in multiple domains even if they are only adept at a single skill or trade. Henrich and Broesch (2011) investigated the role of cultural transmission networks present in Fijian villages through a series of individual interviews. They found that when a potential model excelled in fishing, they were more likely to be chosen as a model for growing yams, but not a model for learning about medicinal plants. Additionally, those who excelled at growing yams were more likely to be sought after as a source of information on fishing as well as medicinal plants. However, the authors noted that individuals with more formal education were deemed to be a poor source of information for all three domains assessed. This is perhaps due to a belief that the skills being taught in schools do not translate well to success in the village community.

In another study investigating the impact of prestige, Chudek et al. (2012) found that across two experiments, children were more likely to model their behavior after a demonstrator that received at least 10 seconds of preferential attention from “bystanders” while modeling the behavior over a demonstrator that did not receive the same amount of attention. This pattern was particularly strong when modeling the use of an object, with a slightly weaker effect for food preferences and no effect for language learning. Findings from a second experiment led Chudek et al. to conclude that prestige may be derived

from attentional biases, as children are shown to preferentially attend to the demonstrator that received more attention from other “bystanders.” The researchers believe these findings are potentially important for survival purposes, as the implications of choosing a poor model for food preferences could have life-threatening consequences.

In a study that focused on the prestige bias present in adults, Atkisson et al. (2012) investigated social learning with adults participating in a hunting simulation with temporally-varying environments. They found that as individuals transition into novel environments, they improve in their ability to determine when it is the most beneficial to learn from someone else. Additionally, the authors found that participants were more likely to engage in social learning when performing poorly. As participants begin to become accustomed to the novel environment, they also begin to more accurately differentiate between successful and unsuccessful behaviors for the environment, choosing to persist in the performance of successful behaviors. However, Atkisson and colleagues note that they did not find any supporting evidence for an increase of reliance on prestige bias in novel environments over stable environments. The authors believe that incorporating a stronger transition from a stable to a novel environment in their experiment might increase a participant’s reliance on prestige-biased transmission in novel environments. Furthermore, this lack of reliance on prestige information may be due to a changing environment; if the new environment requires different adaptations, information from prestigious sources could be of lesser value. Atkisson et al. also note that the amount of attention a specific model receives impacts the participant’s decision to adopt the behavior exhibited by that model. The authors infer that the presence of prestige information in real-world settings can be a useful indicator of whom to trust and imitate.

Prestige bias can be a valuable *Adaptive Learning* strategy as an individual will be able to learn a set of skills that have been demonstrated to be successful in the current environment relatively quickly and at a low cost to the learner. The benefit

of selecting a prestigious source of information can help develop an individual's proficiency at hunting, gathering and growing food, and recognizing potential threats in the environment. However, prestige-biased transmission may become less viable as the environment changes, as some of these skills may no longer be effective in the new environmental conditions. In such a case, the individual should be capable of determining the prestigious source's information and then selectively attend to a new source as better information becomes available.

Related Findings and Conclusions

These studies indicate some modern and evolutionary advantages of acquiring successful and environment-specific skills. Either through conformity and imitation or through prestige-biased transmission, the benefits generated from utilizing these adaptive strategies can have a significant impact on an individual's level of fitness. Researchers have also studied the potential role of adaptive learning strategies in other aspects of daily life, including the acquisition of religion (Beck and Forstmeier 2007; Gervais and Najle 2015). These studies investigate the cultural role of developing religion as a species, as well as the potential adaptive advantages to be gained through the sometimes costly obligations of following a religion that may hinder an individual's level of fitness (i.e., celibacy). Adaptive learning strategies show clear real-world implications as they can help in a variety of environments. In an evolutionary context, it is beneficial to conform to the will of the group to receive their support and learn from them. This is also true for imitation, as it is critical to survival that an individual copy the most successful designs available for tools, such as arrows (see Atkisson et al. 2012), as choosing a poor model can be costly and potentially life-threatening. To conclude, whether an individual seeks to improve their work performance or provide for their family with improved hunting skills, seeking out the best source of information will help refine and develop their skills.

Cross-References

- [Associative Learning](#)
- [Cost-Benefit Analysis](#)
- [Cultural Evolution](#)
- [Cultural Inheritance](#)
- [Cultural Transmission](#)
- [Development of Adaptations](#)
- [Evolution of Adaptations](#)
- [Imitation](#)
- [Imitation and Mimicry](#)
- [Increasing Longevity](#)
- [Learning](#)
- [Learning Versus Imitation](#)
- [Play and Social Learning](#)
- [Play and Tool Use](#)
- [Religion](#)
- [Religious Beliefs](#)
- [Social Learning](#)

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Adaptive Memory

► [Evolution of Memory, The](#)

(Adaptive) Phenotypic Plasticity

► [Adaptive Plasticity](#)

Adaptive Plasticity

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Synonyms

(Adaptive) Phenotypic plasticity; Developmental plasticity; Flexibility; Malleability

Definition

Property of a given genotype to produce different phenotypes depending on different environmental conditions, thereby enhancing organisms' fitness.

Introduction

The relationship between organism and environment is highly dynamical and can be thought of as a trade-off between the demands imposed by the environment and the organism's adjustments to those demands. On the one hand, the environments change; on the other hand, organisms fit the requirements posed by the new conditions "in the struggle for life." Phenotypic plasticity, the capacity of a genotype to give rise to different phenotypes in response to different environmental conditions, is crucial if organisms are to adapt to new environments. Adaptive plasticity is simply the phenotypic plasticity that enhances the organisms' fitness.

Although plasticity has been known for over a century, until recently it was taken to be uninteresting or even irrelevant. Currently, however, it arouses great interest; proof of this is the fact that while <10 papers were published per year before 1983, about 1300 papers were published in 2013 (Forsman 2015: 282). This exponential growth was promoted by the recent questioning of the traditional evolutionary framework (see below).

This entry will show why adaptive phenotypic plasticity is currently of such importance and will introduce its main characteristics. In addition, it will illustrate this property with the most paradigmatic instance of plastic phenotype, i.e., learning, the evolutionary consequences of which are emphasized by the so-called Baldwin Effect.

What Is Adaptive Plasticity?

Phenotypic plasticity, which comprises very different phenomena (Bateson and Gluckman 2011; Pigliucci 2001), is the property of a specific genotype to give rise to different phenotypes in the face of different environmental circumstances. This property is one of the two main adaptive mechanisms possessed by organisms, the other being population-level allele frequency change. However, as pointed out by Sultan (2017: 4), the emergence of favorable new genetic variants is rare and random, whereas plasticity has the great

advantage that it provides the organism with immediate adaptive variation and in many individuals at the same time.

The key tool for the analysis of phenotypic plasticity is the notion of norm of reaction, defined as “the set of phenotypes produced by a given genotype in a specified range of developmental circumstances” (Sultan 2015: 21). However, it should be noted that the two notions are not equivalent: the norm of reaction is a function describing the genotype-specific relationship between environments and phenotypes, whereas plasticity is an attribute of the norm (Pigliucci 2001: 7).

Plastic responses to environmentally induced factors presuppose cue-response systems (see Sultan 2015), in which an organism perceives some aspects of the environment as information and is able to respond to the cue through specific phenotypic effects. The cues, which cover a huge typology, may be anticipatory (an environmental change is predictable through reliable cues) or immediate (direct environmental influences) (Sultan 2015).

As regards the kinds of plasticity, a distinction is widely acknowledged (see Sultan 2015 and references) between adaptive and inevitable plasticity. The former encompasses phenotypic responses to the environment that are functionally adaptive, whereas the latter characterizes the factors that limit physiological or developmental processes (for instance, organisms developing in environments with scant nutrients experience only limited growth). Another distinction worth considering (partially related to the former) is that which exists between active (anticipatory phenotypic changes in response to environmental cues) and passive plasticity (direct influence exerted by the environment on chemical or physiological processes) (for discussion, see Forsman 2015).

Unfortunately, the exact relationship between phenotypic plasticity and adaptive evolution remains unclear. Obviously, any instance of phenotypic plasticity that increases fitness in response to new environments or new environmental conditions is beneficial for the organism, in relation to nonplastic beings. However, this situation cannot be automatically conflated with an adaptation. Furthermore, it should be remembered that the notion of adaptation is poorly understood

(Pigliucci 2001: 160). It is, therefore, extremely difficult to draw the line between adaptive and nonadaptive plasticity.

Plasticity provides organisms with an obvious advantage to successfully cope with new environments or environmental conditions, thus reducing the threat of extinction; consequently, it allows “a better phenotype-environment match across multiple environments than would be possible by producing a single phenotype in all environments” (DeWitt et al. 1998: 77–78). In contrast, if the environments remain constant over time, the aforementioned benefit does not apply.

However, it is also obvious that plastic organisms cannot adapt to any environmental conditions, and consequently no organism exhibits a perfect or infinite plasticity (DeWitt et al. 1998: 78). The lack of such a “Darwinian monster” (Pigliucci 2001: 174), i.e., an organism that copes perfectly with any environment, shows that (the evolution of) plasticity depends on the existence of associated costs. In this sense, DeWitt et al. (1998: 78) establish the distinction between costs and limits: “A cost of plasticity is indicated in a focal environment when a plastic organism exhibits lower fitness while producing the same mean trait value as a fixed organism. In contrast, a limit of plasticity is evident when facultative development cannot produce a trait mean as near the optimum as can fixed development.” These scholars make reference to five costs (maintenance costs, production costs, information acquisition costs, developmental instability, and genetic costs) and four limits (information reliability limit, lag time limit, developmental range limit, and the epiphenotype problem; for discussion, see DeWitt et al. 1998). While acknowledging the theoretical value of those costs and limits, Pigliucci (2001: 175ss.) argues, however, that those constraints on plasticity can hardly be distinguished from an empirical perspective.

Finally, a further point in question is the deep implications of phenotypic plasticity for evolutionary theory, as emphasized by West-Eberhard (2003). This scholar argues that phenotypic plasticity strongly influences adaptive evolution through phenotypic accommodation, which integrates developmental and evolutionary change without the need for genetic change to take

place. According to West-Eberhard's (2003) framework, the evolution of a new adaptive trait through natural selection begins with a genotypically or environmentally induced phenotypic change. The initial viability of the change is increased through adaptive plasticity (phenotypic accommodation), this step being followed by genetic accommodation through natural selection. Accordingly, "Genes are followers, not necessarily leaders, in phenotypic evolution" (West-Eberhard 2003: 158). In other words, genetic changes follow (i.e., do not necessarily precede) phenotypic change, in such a way that genetic novelties are not required in order for phenotypic novelty to evolve. Therefore, according to West-Eberhard (2003), phenotypic plasticity has a prominent role in facilitating and accelerating three main evolutionary processes: the origin of novelty, speciation, and macroevolution.

The following section illustrates the property of phenotypic plasticity with its most powerful instance, i.e., learning, by showing how learning capacity can give rise to new directions of evolutionary change. This aspect is known as the Baldwin Effect.

A Brief Overview of the Baldwin Effect

The Baldwin Effect (Baldwin 1896) is a (controversial) mechanism which speeds up natural selection (for discussion, see Weber and Depew 2003; Longa 2005). It can be broken down into two steps. The first one has to do with phenotypic plasticity, which enables an organism to develop new behaviors when exposed to new environmental conditions, or to adapt itself, through learning, to behaviors observed in the environment (for instance, by mimicking the phenotypic result of a mutation arising in another individual). Phenotypic plasticity thus provides the organism with fitness, which in turn enables it to stave off extinction. Therefore, the starting point of the process is a phenotypic change arising as a consequence of an ontogenetic adaptation made possible by the organism's plasticity. However, for the Baldwin Effect to apply, a second and crucial step is required, namely the genetic assimilation of the phenotypic trait previously learned as a response to a given stimulus. In

this step, the plastic learning mechanism for the phenotypic trait is replaced by a rigid mechanism based on heredity. It is in this sense that learning can guide evolution.

If the learning of a given phenotypic trait varies within a population, some individuals will be capable of learning the trait better than others. Natural selection will favor those who acquired the ability more easily (for example, on the basis of limited exposure to the stimulus), because those individuals will increase their fitness. Further down the evolutionary line, mutations will occur (in a non-Lamarckian sense) which will produce the same type of trait without the need for learning, the outcome being the reduction (or the deletion) of phenotypic plasticity for the trait. In other words, natural selection will tend to act on plasticity, by confirming and accelerating the evolutionary change which originally began via learning. It is for this reason that the Baldwin Effect speeds up evolution.

For a full understanding of the Baldwin Effect, it is also crucial to bear in mind that learning presupposes a trade-off between the costs and benefits associated with such a capacity. Although learning has undeniable advantages, it also has clear disadvantages. For example, it requires time, attention, and effort, and the learned behavior is exposed to dangerous contingent factors that might well be deleterious. Yet the disadvantages disappear if the learned behavior becomes inherited. The Baldwin Effect, therefore, reduces the costs of learning.

To sum up, the Baldwin Effect is another instance that shows, in agreement with West-Eberhard's framework, that genes are followers, not leaders, in evolution.

Conclusion

The traditional evolutionary framework completely ignored phenotypic plasticity because this property did not fit in with the evolutionary assumptions of the Evolutionary Synthesis and the resulting Neo-Darwinist thought. The reason is clear: because evolution was taken to be a mere change in allelic frequencies, environmental conditions and phenotypic plasticity were put aside, for neither aspect was genetic and they were,

therefore, considered to be irrelevant from an evolutionary point of view.

However, such traditional Neo-Darwinian assumptions are now being strongly challenged. In fact, there exists a wide range of extragenetic factors that do become inherited, many of them passing environmental information to the offspring (Sultan 2015) and producing nongenetic although inherited adaptations. This means that the genotype cannot dictate the adaptation to the environment (i.e., there cannot be a single predetermined developmental outcome); rather, the phenotype becomes actively generated through the developmental process (Sultan 2017). Accordingly, the environmentally induced phenotypic variation has a crucial role in creating the conditions that produce an adaptive genetic response (let us remember genes as followers, not as leaders). To sum up, the status of the environment greatly surpasses the role of a mere selective filter (Sultan 2015: 41). It is for this reason that phenotypic plasticity will presumably gain an increasingly important role in evolutionary biology in the years to come.

Cross-References

- ▶ [Adaptation](#)
- ▶ [Adaptation and Natural Selection](#)
- ▶ [Adaptive Learning](#)
- ▶ [Development](#)
- ▶ [Development of Adaptations](#)
- ▶ [Differential Reproductive Success](#)
- ▶ [Ecological Factors and Rape](#)
- ▶ [Environmental Unpredictability](#)
- ▶ [Learning](#)
- ▶ [Ontogenetic Adaptations](#)

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Adaptive Play Behavior

- ▶ [Evolution of Play](#)

Adaptive Polymorphisms

- ▶ [Alternative Adaptive Peaks](#)

Adaptive Problem of Detecting Kinship

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Synonyms

Altruistic behavior; Coresidence; Genetic relatedness; Incestuous behavior; Kin detection system; Maternal perinatal association; Nepotism;

Definition

Evolution of cues used by humans to detect kin in order to avoid incest and promote altruistic behavior toward genetic relatives.

Introduction

As a highly social species, humans interact and cooperate with many individuals; however cooperation among relatives tends to be greater than among unrelated individuals (Hamilton 1964). Throughout history, humans of all known cultures have always tended to feel and behave differently toward family members than to individuals to whom they were not genetically related. This behavior, which is not exclusive to humans, is distinguished by two important traits: on the one hand, the display of a highly altruistic behavior in which their own welfare could be sacrificed to help family members and, on the other hand, an innate aversion to any sexual contact with genetic relatives. From the evolutionary point of view, natural selection has favored this behavior because it conferred a selective advantage to the individuals displaying it. These desirable features increased in frequency to the point that nowadays they have become a universal feature of the species.

Species' typical traits have been favored by evolution because they solved an adaptive problem for the organism that displayed it. Therefore, it is correct to infer that the behaviors displayed by humans toward family members have been selected because they solved an adaptive problem, at least in the environment of evolutionary adaptiveness. However, it is important to note that thousands of species display social behaviors that are influenced by genetic relatedness. Altruistic behavior or nepotism correlates with the amount of shared genes that are identical by descent. Therefore, organisms display this behavior in response to cues of genetic relatedness. In humans, genetic relatedness correlates with the willingness to help in a hypothetical situation and the amount of imbalance tolerated in a reciprocal relationship (Burnstein et al. 1994).

Avoiding Interbreeding

Social groups and closeness to relatives lead to two entirely different adaptive problems, avoidance of inbreeding and willingness to support kin. Breeding with relatives increases the probability of conceiving individuals with two copies of recessive deleterious genes. These genes tend to produce either an *in utero* early death or the birth of offspring with congenital abnormalities. Therefore, genes that coded for behaviors that led to incestuous behavior have eventually caused their own disappearance by being present in always fewer handicapped bodies. On the other hand, genes that promoted behavior that avoided sex with genetic relatives have been favored by natural selection. This have led to their increased presence in offspring that would have been healthier and reproductively more successful than the ones produced by incestuous sex. As a result, the successful genes have spread in the population to a point of ubiquity in human populations.

Development of Altruism

The second adaptive problem associated to genetic relatedness involves the ability to identify kin in order to support them. Altruistic behavior toward kin is a consequence of genes aiming to spread themselves; thus natural selection has favored the permanence of motivational systems that, in an all else equal situation, increase the willingness to help close genetic relatives as opposed to unrelated ones. A genetic makeup that encourages helping relatives so that they reproduce more effectively would increase the probability of spreading new copies of those genes in the population. This means that genetic designs that promote altruistic behaviors will always be favored as long as the cost to the individual's own reproduction is offset by the benefit to the reproduction of its kin member. The degree of relatedness between relatives has a great impact on the expression of this behavior since the more closely related two individuals are the higher the probability that they share the same genetic makeup.

Kin Detection Systems

In order to effectively solve the above adaptive problems, organisms would have developed the ability to identify who is and who is not a genetic relative and estimate the closeness of this relatedness. Detecting genetic similarity is therefore an important adaptive problem, and not an easy one to solve. Organisms cannot “see and compare” DNAs. It appears that the problem has been somehow solved by the development of a *kin detection system*. By analyzing and outweighing several unrelated cues, this system seems to generate an internal index of relatedness. Based on the results, the system then feeds two different motivational systems, one that promotes sexual attraction/aversion and the other family-directed altruism. It is important to note that familiar relationships do not seem to be identified in the same way, for instance, the system uses different cues to determine relatedness between parents and offspring when compared to siblings.

One of the main cues used to establish relatedness to offspring is similarity. People tend to rate strangers that look similar to them as more trustworthy and less sexually attractive. Mammalian mothers have almost 100 % confidence in their maternity. Therefore they regard any infant who is present after birth as their own child even if they do not resemble her. Fathers on the other hand must use other cues such as phenotypic similarity. A study by Apicella and Marlowe (2004) found that fathers favor children who look more like them (Apicella and Marlowe 2004). This not only refers to physical similarity (ancestral males would have had very little exposure to their own image) but nonvisual cues of self, such as personality, behavioral traits, and smell. In addition, since his mother and sibling share a proportion of his genes, a male could also use their faces as templates.

To gauge relatedness to siblings, the system has evolved to detect mainly two cues: maternal perinatal association (MPA) and duration of coresidence during the period of parental investment. MPA is established when an individual sees their mother caring and nursing a newborn; this means with a high probability that the newborn is

his sibling and will be tagged as such. As a consequence, the motivational systems will be promoting high levels of altruistic behavior and high levels of sexual aversion. It is obvious that MPA only works for older siblings. Thus, in order to detect genetic relatedness to older siblings, the brain uses a different cue which takes into account the coresidence period with other children when growing up (approximately between ages 0 and 18). In hunter-gatherer societies, the duration of childhood coresidence is highly correlated with the degree of kinship (Lieberman et al. 2007). There are several studies that have shown that early coresidence causes sexual disinterest between siblings and even unrelated individuals raised together from childhood (Westermarck effect) (Wolf 1995). Interestingly time of coresidence is proportional to the degree of aversion to incest; thus, the longer a youth coresides with an older sibling, the more disgust elicited by the thought of incestuous sex. This extends to moral judgments of third parties where the length of coresidence predicts how morally wrong youngsters find third-party incest.

The MPA cue is overly predominant over coresidence; in other words they are not additive. MPA is enough to generate high levels of altruism and sexual disinterest which do not seem to be modified by time of coresidence. In order to obtain similar levels of altruism and sexual aversion in younger siblings, 14–16 years of coresidence are needed. Thus, coresidence only has an effect if the MPA cue is absent. Since both cues are not additive, they must somehow be associated; it has been suggested this is done by a “kinship estimator.” The kinship estimator combines the cues in a non-compensatory way, following a decision tree pattern. In addition the kinship index seems to be generated in an unconscious way and therefore not affected by conscious beliefs. This is evidenced by cases of step or adoptive siblings. In this case coresidence generates altruistic behavior and sexual aversion despite the fact that the individuals know they are not genetically related. This shows that the criteria used by the kinship estimator prevail over conscious beliefs. Although the two cues mentioned above seem to be the strongest ones,

in their absence other cues such as physical resemblance and olfactory signals indicating similarity of the major histocompatibility complex are also taken into account by the system. This is especially relevant in case of distinguishing for instance, maternal half-siblings from full-siblings (DeBruine et al. 2008).

Conclusion

It is important to note that the mechanisms described above are prevalent across species. Nowadays modern humans possess other more sophisticated means of assessing kinship which have been added, not replaced, to existing ones (Geary 2005). These processes seem to be controlled by the neocortex and tend to be complemented and overridden by aforementioned more primitive ones (Park et al. 2008).

As discussed above, animals are not born with knowledge of which individuals are kin. Kin-recognition mechanisms are dependent on learning, enabling individuals to acquire the association between specific members of the group and kin-relevant responses. As a consequence, kin recognition is susceptible to mistakes. A minority of individuals are still inclined to engage in incest. This could arise from the lack of exposure to cues of kinship during upbringing. For instance, opposite-sex siblings that had been separated for considerable time during childhood are more likely to engage in incestuous activity (Bevc and Silverman 2000). In this case these behaviors can occur with intact brain mechanisms. Another explanation for this behavior could be a malfunction of the kin detection system in which due to damage, the motivational system that causes sexual attraction is not turned off by cues of kinship.

Although the presence of a kinship estimator seems to agree with an evolutionary premises, some issues are worthy of consideration. The evolutionary approach bases its assumptions on contemporary hunter and gatherer societies. All these societies express on one way or another incest taboos, but there is evidence that not all ancestral groups conformed to the structural organization of

the groups alive today. Modern hunter and gatherer lifestyle is quite restricted to few areas that share similar landscapes and limited immigration/emigration. Our ancestors, on the other hand, occupied a wealth of different habitats ranging from the African savannah to arctic regions. As a consequence of this, it is very likely that social structures were quite diverse among those groups.

It is reasonable to deduct that the kinship model of incest avoidance is more adaptive in societies that do not involve significant immigration/emigration. Here kin detection is important in order to favor altruistic behavior and an increase in the number of kin.

In many animal species that live in social groups, this excess of kin members is usually solved by emigrating before mating season. Usually as soon as males reach reproductive age, they move away from the familiar unit reducing the risk of inbreeding. In these cases there is no evolutionary pressure to develop an incest avoidance mechanism. In the case of humans, it is not well known if this was the case during ancestral times. Although there is some evidence that at least in some early *H. sapiens* groups, males moved away, it is not known whether this happened in the majority of groups. It has been argued that without this information the adaptive benefit of evolving a kinship detector is not well supported (Richardson 2015).

Cross-References

- ▶ [Altruism in Kin Selection](#)
- ▶ [Benefits to Kin](#)
- ▶ [Cooperation Varies with Genetic Relatedness](#)
- ▶ [Facial Resemblance and Kinship Detection by Strangers](#)
- ▶ [Genetic Relatedness Affects Aid to Kin](#)
- ▶ [Grandparental Investment and Genetic Relatedness](#)
- ▶ [Hamilton's Rule and Genetic Relatedness](#)
- ▶ [Hamilton's Rule and Kin Investment](#)
- ▶ [Helping More Likely with Close Kin than More Distant Kin](#)
- ▶ [Incest Avoidance](#)
- ▶ [Kin Detection by Odor](#)
- ▶ [Kin Recognition](#)

- ▶ Kin Recognition and Classification in Humans
- ▶ Kin Selection
- ▶ Parental Investment
- ▶ Paternity Uncertainty and Investment in Sons and Daughters
- ▶ Presence of Siblings
- ▶ Resemblance
- ▶ Sex Differences in Ability to Assess Fighting Ability
- ▶ Westermarck Effect

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Adaptive Problems

- ▶ Sex Differences, Initiating Gossip

Adaptive Solutions to Socialization

- ▶ Robert Kurzban on Group Processes

Adaptive Specialisations

- ▶ Carruthers on Massive Modularity

Adaptive Variation

- ▶ Alternative Adaptive Peaks

Adiposity

- ▶ Obesity

Adjunct Mother

- ▶ Aunt Care

Adjustment

- ▶ Assimilation

Adjustment of Copulatory/Ejaculatory Investment

- ▶ Male Prudence and Sperm Limits

Adolescence

- ▶ Genetic Influences of Puberty
- ▶ Puberty in Girls

Adolescent Issues

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Synonyms

[Issues related to adolescent development](#); [Teenage issues](#)

Definition

Adolescence is the developmental period between childhood and adulthood. It is a unique time characterized by dramatic social transformations (e.g., friendships become more intimate) that occur alongside significant physical, cognitive, and psychological changes.

Introduction

Adolescence (broadly spanning 10–22 years old) is a unique period in development characterized by rapid and dramatic biological, cognitive, and social changes. For instance, most adolescents go through puberty, which involves hormonal shifts that trigger the development of primary and secondary sex characteristics and physical growth, in addition to changes in emotionality and behavior (e.g., Connolly et al. 1996). The adolescent brain also undergoes important structural and functional changes, including increased synaptic pruning (which contributes to growth in cognitive abilities) and further development of the prefrontal cortex (a brain region implicated in processes such as decision-making and personality expression, e.g., Casey et al. 2008; Steinberg 2010). Both resulting from and amidst these changes, adolescents' social worlds begin to evolve. For instance, beginning in early adolescence (10–14 years old), youth spend the majority of their waking time with their peers (rather than

their families, e.g., Collins and Laursen 2004; Montemayor 1982).

Over the years, adolescents' peer experiences have garnered significant theoretical and research attention. Often, the focus is on the ways in which peers can cause *harm* (e.g., vis-à-vis peer pressure and victimization). However, many adolescents form positive and supportive relationships with their peers that foster *healthy* development and well-being. This entry will explore the unique features of adolescents' peer experiences, distinguishing between those at the dyadic- (i.e., experiences between two adolescents, such as friendships) and group-level (i.e., experiences involving the larger peer group, such as popularity and peer victimization) of social complexity. Different perspectives on the significance of peers in the lives of adolescents will be offered, including an evolutionary perspective that emphasizes the positive and negative trade-offs (Buss 1995; Hawley 2011).

Friendships

Beginning with the peer experience of *friendship* (i.e., voluntary relationships between two same-age peers that are characterized by mutual affection or liking), it is well established that the large majority of adolescents, at any given time point, have at least one *mutual* friendship as determined by reciprocated friendship nominations (i.e., Zoe nominates Sophia as a friend and Sophia nominates Zoe as a friend; Parker and Asher 1993; Rubin et al. 2015). Most of these adolescent friendships, especially those considered by both adolescents to be a *best* friendship, are with same-sex peers. In fact, a robust finding in the developmental sciences literatures is that the majority of friendships across the lifespan tend to be with same-sex peers (Hartup and Stevens 1997). This is perhaps best explained by the *homophily hypothesis*, such that individuals are most attracted to, and subsequently form friendships with, those who are similar in observable characteristics, such as sex, race, and behavior (Kandel 1978). That said, there is a significant increase in the frequency of *other-sex* friendships throughout

the adolescent developmental period (Poulin and Pedersen 2007). In fact, a gradual *coming together* of boys and girls occurs during adolescence whereby adolescents first develop crushes on and begin to interact with other-sex peers and then later form other-sex friendships and mixed-sex peer groups. This coming together of the sexes, in turn, helps facilitate the formation of adolescents' first heterosexual *romantic* relationships, thus beginning the evolutionarily important process of mating.

The features or qualities of friendships also begin to change during the adolescent period. For instance, relative to friendships during childhood, adolescent friendships become more intimate (Buhrmester and Furman 1987). This developmental change is particularly pronounced for girls and is mostly due to adolescents' engaging in increased levels of *intimate disclosure* to their friends (i.e., telling each other secrets; Rose and Rudolph 2006). Although friendships become increasingly intimate during adolescence, they also become increasingly characterized by jealousy and other negative relationship processes (i.e., *co-rumination* or repeated discussion of negative feelings and problems by both relationship partners; Rose 2002), which may explain, in part, why adolescent friendships become particularly vulnerable to conflict and break-up (Benenson and Christakos 2003; Bowker 2011). Indeed, a recent study found that approximately 50% of adolescent friendships dissolve across a single school year (Meter and Card 2016). Thus, many friendships during adolescence would not be considered *reliable* alliances. And, many adolescents report stress and sadness when their friendships end, likely because many adolescents experience friendship dissolution as a significant *interpersonal loss* (Bowker 2011). Another rarely discussed reason, however, for the fragility of adolescents' friendships is that adolescents have greater choice over their peer relationships than they did when they were children, and thus, many may *choose* to end friendships that are not satisfying, fulfilling, or promoting of resources. In this regard, the *self-initiated* termination of certain adolescent friendships may be advantageous for individual growth and development, but very little

research has evaluated this more positive aspect of friendship dissolution.

Moving beyond the prevalence and characteristics of adolescents' friendship experiences, friendship is a central construct of study in the adolescent literature because of its influence on adjustment outcomes. In other words, there is a large, ever-growing body of research showing that friendships impact adolescents in numerous and significant ways. For example, adolescents with mutual friends report higher levels of self-esteem and psychological well-being relative to those without mutual friends (for recent review, see Rubin et al. 2015). Importantly, the effects of adolescent friendships on psychological well-being appear to be both immediate *and* lasting. Bagwell et al. (1998), for instance, found that having a friend in early adolescence predicted positive psychological well-being in young adulthood. These effects were found after controlling for peer acceptance (at the group-level of social complexity, as explained in more detail below), findings consistent with those from many other studies showing that the effects of friendship on psychological and other types of adjustment during adolescence are *unique* (e.g., Erath et al. 2008). Of course, there is significant variability in the ways in which adolescents' friendships impact individual adjustment. For example, the *characteristics of the friends* matter such that adolescents whose *friends* are suffering psychologically or are delinquent are likely to be *negatively* influenced by their friends over time through *socialization* processes (e.g., Poulin et al. 1999; Zalk et al. 2010). From an evolutionary perspective, forming successful friendships (especially with prosocial peers) likely fulfills needs to belong and promotes access to resources (i.e., sources of help and support), above and beyond those available to an individual acting alone, while forming friendships with those in distress interferes with the benefits of friendships (Buss 1995). Finally, it should be acknowledged that individuals of all ages vary in their abilities to form and maintain friendships, and some individuals, including adolescents, find themselves in less desirable and maladaptive friendships because they are rejected, excluded, and

victimized by their peers (peer difficulties at the group-level of social complexity, which are described in the following section), and thereby left without any other options.

The Peer Group

Friendships during adolescence are oftentimes embedded in larger peer groups, such as *crowds* (i.e., large, reputation-based groups such as “populars,” “jocks,” and “brains”; Prinstein and La Greca 2002) and *cliques* (e.g., smaller groups composed of multiple friendships; Urberg et al. 1995). Crowds and cliques are important to study, as research shows that adolescents are not only influenced by their close friends but also these larger peer group experiences. For instance, Hussong (2002) found that adolescents (aged 16–19 years old) were more likely to use drugs and alcohol if their best friends did, and *also* if the cliques and crowds with which they affiliated were frequent substance users. In addition, affiliation with highly regarded/valued crowds, such as the “populars” or “jocks,” has been found to promote positive psychological well-being (i.e., high self-esteem, low levels of loneliness) whereas low-status crowd (e.g., “burnouts”) affiliation appears to have the opposite effect (La Greca and Harrison 2005; Prinstein and La Greca 2002). From an evolutionary science perspective such findings are not too surprising, as being a part of a larger group has its advantages (i.e., in terms of resources, protection, etc.), especially a larger group with power (e.g., Buss 1995). Nevertheless, the aforementioned findings nicely illustrate that it is not only friendships that matter during adolescence but larger peer groups do as well.

In addition to cliques and crowds, researchers oftentimes study adolescents’ levels of popularity, rejection, and victimization, all of which reflect how adolescents *fare* with the larger peer group. Adolescents are uniquely aware of their peers and the social dynamics in their schools, and thus, researchers often ask them to report on who is highly popular, rejected, and victimized in their grade and school. Such procedures (also

known as *sociometric* and *peer nomination* procedures; see Cillessen 2009) allow researchers to determine who receives the most nominations for these group-level experiences, and from there to understand how variability in such experiences is associated with outcomes such as psychological well-being. For instance, adolescent *popularity* has garnered considerable theoretical and empirical interest, in part because it peaks in terms of importance during early-to-middle adolescence (LaFontana and Cillessen 2010). Adolescents who are perceived by peers as popular tend to be well-adjusted in a number of ways (e.g., socially skilled, attractive, athletic, Cillessen et al. 2011) and are well-known and highly visible in the larger peer group. As a result, they are oftentimes powerful and influential among peers (Cillessen et al. 2011). Obtaining high levels of popularity is considered *adaptive*, from an evolutionary perspective, as it increases individual access to or control over tangible, social, and sexual resources. Popular youth, however, often use a combination of aggressive and prosocial (e.g., kind and helpful) strategies to achieve their popularity (Archer and Coyne 2005; also see *Resource Control Theory*, Hawley 1999); this tendency toward aggression causes them to not always be highly *accepted*, or well-liked, by peers (Parkhurst and Hopmeyer 1998). Popular youth also commonly achieve high status by engaging in other “norm-violating” behaviors (i.e., substance use, rule-breaking) that can be harmful to their individual development and to their peers but, at the same time, are viewed as cool and mature during adolescence (Cillessen et al. 2011; also see *Maturity Gap Hypothesis*, Moffitt 1993). As such, there appear to be trade-offs associated with achieving high status among peers during adolescence.

Of course, not all adolescents fare well with their peers, and instead, some adolescents are *rejected* (i.e., disliked) and *victimized* by their peers. Adolescents may be rejected if they display traits or behaviors that are not highly valued by the peer group, including shy or withdrawn behavior or aggressive behavior (Parkhurst and Asher 1992); the same adolescents might also be highly victimized by their peers. Other

adolescents, however, might be victimized because they are perceived as weak or vulnerable in some way (and therefore, an “easy” target for bullies). For example, adolescents without friends, who appear psychologically distressed, are obese, or have a developmental or learning disability, experience high levels of peer victimization (Hong and Espelage 2012). Victimization takes many forms, including physical (e.g., kicking, hitting, pushing), verbal (e.g., threatening, insulting, name-calling), and relational (e.g., excluding, ignoring, spreading rumors/gossip; Archer and Coyne 2005; Dodge et al. 2006) and can occur in person or online (Salmivalli and Peets 2018). Although bullying and peer victimization are common during childhood, they increase during early adolescence for a number of reasons, including less adult supervision and new links between rule-defying behavior and social status (Cillessen and Mayeux 2004; Moffitt 1993). Not surprisingly, both rejected and victimized youth tend to suffer psychologically (e.g., elevated levels of loneliness, depressive symptoms, anxiety), although some of these negative outcomes may be mollified by protective factors such as having a close friendship (Parker and Asher 1993). Beyond mental health outcomes, peer victimization and rejection have also been found to negatively impact physical health (e.g., dysregulated cortisol responses) and to interfere with academic functioning (e.g., Erath et al. 2008; McDougall and Vaillancourt 2015). As such, over the past few decades there has been widespread interest in prevention and intervention efforts targeting peer rejection and victimization, many of which are school-based and call on peers to assist and intervene (e.g., Yeager et al. 2015). However, such programs, especially those focused on peer victimization and those in the United States, have been limited in effectiveness, in part because many adolescents are reticent to protect their peers out of fears for becoming targets themselves (Salmivalli and Peets 2018). Thus, negative group-level peer experiences continue to be a serious concern during adolescence.

Conclusion

Despite seemingly obvious applications of evolutionary science to understanding adolescent issues, developmental psychologists have been slow to adopt this framework. Just a few years ago, one prominent psychologist observed: “...at the time of this writing, Google Scholar located only four articles with the word ‘evolution’ or ‘evolutionary’ in the title from all the English language journals on adolescence. This gap is extraordinary in light of the reproductive maturity of the average 15-year-old and evolutionists’ interest in reproduction” (Hawley 2011, p. 307). For the most part, developmental research on adolescent issues has taken a risk-based approach focused on elucidating when and why problems occur (e.g., how behaviors such as aggression contribute to peer and psychological problems). Evolutionary scientists, however, have cautioned against the tendency to strictly pathologize adolescent “problem” behaviors (e.g., aggression/bullying, substance use, sexual activity) and instead have suggested a more balanced perspective that allows for the possibility of both positive and negative trade-offs for any behavior. In addition, it has been suggested that many “problem” behaviors during adolescence occur because they are high risk/high reward. For example, substance use can be considered risky as it could lead to detrimental or even fatal outcomes, but, it can also be viewed as potentially adaptive/rewarding by fostering improved group standing and belongingness (Ellis et al. 2012). As such, drawing upon an evolutionary science perspective could enrich the study and understanding of adolescent development by focusing on such trade-offs.

Beyond striving for better integration of evolutionary and developmental sciences, there is still much to be learned about the varied issues pertaining to adolescent development, only a small subset of which were discussed in this entry. For instance, many issues related to adolescence are changing with the proliferation of technology, and researchers have been slow to catch up. In the future, there will be a great need to better

understand the ways that social media has impacted adolescents' social worlds, including problems with peers (e.g., cyberbullying, peer exposure and influence; Hawley 2011), and also potential benefits (e.g., reduced loneliness, the facilitation of intimacy between friends). Furthermore, given our increasingly connected world, cross-cultural variations and similarities in adolescent development and peer experiences are imperative to better understand and could lead to an deeper knowledge of which aspects of adolescent development are universal (and thus biologically or evolutionarily based) versus context-bound. In addition to cultural differences, it is also important to consider that many individual-level differences (e.g., in personality and other traits) may impact or alter the types of friendships and group-level experiences adolescents have. For example, there is a growing literature revealing variability in the reasons that some adolescents choose to withdraw or keep away from their peers (e.g., shyness versus preferences for solitude), and how these differences impact how they are perceived by peers and their psychological well-being (see Rubin et al. 2009). Finally, more multidisciplinary research that cuts across disciplines is needed to fully understand the complex ways that adolescents' social, biological, and cognitive functioning interact to predict short- and long-term outcomes.

Cross-References

- ▶ [Altruism Defined by Benefits Conferred](#)
- ▶ [Fair-Weather Friends Versus True Friends](#)
- ▶ [Bullying](#)
- ▶ [Cognitive Changes in Adolescence](#)
- ▶ [Friendship](#)
- ▶ [Peer Competition and Cooperation](#)
- ▶ [Peer Feedback and Norms](#)
- ▶ [Peer Groups](#)
- ▶ [Peer Pressure](#)
- ▶ [Peer Rejection](#)
- ▶ [Peer Rejection, Sex Differences in Initiation of](#)
- ▶ [Peer Socialization](#)

- ▶ [Same-Sex Friendships](#)
- ▶ [Sex Differences in Same-Sex Aggression](#)

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Adolescent Parenthood

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Synonyms

Parental investment; Teenage pregnancy

Definition

Producing and caring for an offspring by a parent who is under the age of 20 years-old.

Introduction

Adolescent parenthood has been associated with many negative outcomes, such as decreased physical and mental health of the offspring (Pinzon and Jones 2012). Although there have been fluctuations in the rate of teenage pregnancies in the United States, there has been a relatively steady decline in the number of children born to adolescents through the 1990s and 2000s (Pinzon and Jones 2012). This entry will discuss some of the negative outcomes associated with adolescent parenting as well as some of the evolutionary psychological theories behind human mating and parenting. A large portion of evolutionary research on parenting focuses on the paternity uncertainty hypothesis, the mating opportunity cost hypothesis, and parent-offspring conflict theory.

Paternity Uncertainty Hypothesis

Because males can never be certain about whether they are the biological father of their putative offspring, they may engage in behaviors to decrease their uncertainty and/or conserve their resources by decreasing their resource expenditure on their offspring (Trivers 1974). Human female fertilization is internal, indicating

that maternity is 100% certain, but paternity is oftentimes in doubt. Facial resemblance and odor recognition are two cues men use to familiarize themselves with the child (Alvergne et al. 2009). Fathers of children whose faces resemble their own reported greater levels of emotional closeness with them than those lacking facial resemblance (Daly and Wilson 1988). Fathers also showed more affection and attachment to children whose smell they can easily recognize. Men invest more resources, time, and affection in children who are genetic offspring than those who are genetically unrelated offspring (i.e., stepchildren). In addition, fathers who have a romantic relationship with the mother and/or cohabit with the mother are far more likely to invest in parenting than fathers who are not currently romantically involved, or cohabitating, with the mother of their offspring (Daly and Wilson 1988). A number of factors play a role in this dynamic, including the type of romantic involvement the couple had during the pregnancy and after birth, paternal ability to provide and support kin, as well as the father's level of education, socioeconomic status, relationship with his family of origin, ethnic background, cultural values, moral values, and spirituality (Jones and Pinzon 2012).

Mating Opportunity Cost Hypothesis

The mating opportunity cost hypothesis indicates that males are less likely to take on parental care because, in doing so, they risk missing additional mating opportunities. Although females can acquire many mates, they are not able to reproduce as frequently as males because of the 40-week gestation period of pregnancy (Buss 2012). During these 40 weeks, the pregnant female is not able to reproduce again, but males could seek extra mates to increase their reproductive opportunities. The reproductive success of males is limited to the available number of fertile females that can successfully conceive. Adolescent males are typically not ready to settle with just one female and are very aware of the possibility of potential mates.

Parent-Offspring Conflict Theory

Parent-offspring conflict occurs when parents' perceived needs of their offspring differ from the offspring's perceived needs and desires (Trivers 1974). Because of adolescents' lack of experience and resources, they are less likely to raise a child effectively and correctly. Infants are completely dependent upon their parents for survival, which calls for the parents to consistently be available and prepared. The theory of parent-offspring conflict predicts that each child will generally desire a larger portion of the parent's resources than the parents want to give (Daly and Wilson 1988). With both the parents and the offspring being young, one would expect conflict between the two to be more frequent than if the parent was of an adult age and mindset. This could lead to negative outcomes for the offspring. For example, a young parent may not have the patience to raise a young child or be willing to sacrifice certain activities or resources – such as developing relations with friends via social gatherings, or spending money on desired but unnecessary items (e.g., jewelry and other convenience items) – that may be necessary to forego when raising a child. Parent-offspring conflict may also arise if a parent decides to secure a new mate. Acquiring a new mate may lead to a decrease in available resources, which could lead to greater competition for these dwindling resources and, therefore, greater conflict. Parent-offspring conflict over the parent's mating decisions remains a topic that is not often explored empirically (Buss 2012).

Decreased Life Expectancy

Adolescent parents' offspring often suffer from decreased life expectancy. There are many cases of child neglect and infanticide brought on by the pressures of life that adolescents do not effectively handle in their best judgement. The proportion of births leading to infanticide are highest among women between ages 15 and 19 years-old (Bugos and McCarthy 1984). Teenage mothers show the highest rates of infanticide, more than three times higher than any other age group (Daly and Wilson 1988). Infants of adolescent mothers also have an increased risk of adverse health outcomes including higher incidences of perinatal

mortality, low birth weight, preterm birth, developmental disabilities, and poorer developmental outcomes (Jones and Pinzon 2012).

Paternal desertion is also cause for concern regarding the offspring's health and life expectancy. Child mortality rates significantly increase when the father is not present (Hurtado and Hill 1992). When abandoned by the father, adolescent mothers are left with few choices, including abandoning or giving up the child for adoption, killing the child and investing available resources toward mating, or simply living with it and raising the child alone. Younger and/or unwed mothers are more likely to commit infanticide, devoting their efforts more toward other adaptive problems, such as surviving or attracting men who are willing to invest resources in them (Buss 2012).

Many cases of inadequate care of infants born to adolescent parents can be explained by drug usage, domestic violence, psychological disorders, and potential socioeconomic problems. Research conducted in Sweden illustrated the long-term socioeconomic effects of adolescent parenthood (Vinnerljung et al. 2007). Specifically, adolescent parents possess an increased likelihood of low educational attainment, single living arrangements, and welfare dependency – supporting the view that childbearing during adolescence is a risk factor for poverty in later life.

Violence during pregnancy is most recognized between the ages of 12 and 24 years old. Approximately 61% of the subjects in their study have experienced IPV, with 37.5% reported having experienced it during pregnancy (Mylant and Mann 2008). Studies conducted in urban areas revealed that homicide is the leading cause of death of reproductive aged women (Daly and Wilson 1988).

Infants of adolescent mothers have an increased risk of adverse health outcomes, including higher incidences of perinatal mortality, low birth weight, and developmental disabilities (Jones and Pinzon 2012). In fact, infant mortality rates are significantly greater for infants of adolescent mothers under the age of 15 (Phipps et al. 2002).

Having multiple children during adolescences has also been associated with several

negative outcomes. Repeat births have been linked to decreased educational achievement, increased dependence on governmental support, increased infant mortality, and low birth weight (Jones and Pinzon 2012). Research has revealed that a repeat or second pregnancy occurs in 19% of adolescent mothers within 1 year of the first birth. That probability increases to 38% within 2 years of the first birth, with higher rates for those with low socioeconomic status (Partington et al. 2009).

There are also many factors that contribute to improved outcomes of adolescent mothers that are recognizable. Studies have shown that having completed school before becoming pregnant, actively participating in a program for pregnant adolescents, having a sense of control over one's life, experiencing little social isolation, and limiting the number of children one produces are all factors associated with improved outcomes of adolescent mothers (Jones and Pinzon 2012). Another study showed that although these factors improve an adolescent mother's success outcome, it did show negative effects concerning the offspring. More than two-thirds of women in that study had completed high school, had regular employment, and were not dependent on the government for income. However, even with these positive effects for the mother, there may still be negative outcomes for the offspring. That same study found the offspring of those adolescent mothers displayed greater rates of difficulties at school and behavioral problems at home than did offspring of adult mothers (Jones and Pinzon 2012).

Conclusion

Ultimately, adolescent parenting can produce many risks for offspring. However, this is not to say that negative outcomes afflict all adolescent parents. Adolescents are still developing, which may impede their progress as a parent. Although there are many negative outcomes for infants of adolescent parents, there are many family factors associated with improved outcomes for both adolescent mothers and their children. These include early childcare for the infant provided by the

infant's family of origin, social and familial support that also allows the adolescent parent to finish school, playful interaction between the infant and father, and stability of marital status for the adolescent mothers (Jones and Pinzon 2012).

Cross-References

- [Abstinence](#)
- [Adolescent Issues](#)
- [Oral Sex and Sexual Debut](#)
- [Prevalence of STDs](#)
- [Sex Education in Schools](#)
- [Sexual and Reproductive Development](#)
- [Sexual Coercion and Dating](#)
- [Sexual Debut](#)
- [Sexual Intercourse](#)
- [Sexual Socialization](#)
- [Sexual Stigmatization](#)

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numerous factors that influence an adoption, including cultural norms, parent's traits and resources, and the social and legal parameters surrounding adoption. One important potential influence on parents' decision to adopt is information about the children themselves. In particular, cues of resemblance/kinship, age, and child attributes can all influence the desire to adopt a child. From an evolutionary perspective, each of these traits can influence the costs and potential outcomes of an adoption, making them highly relevant to adoption decisions.

Adolescents

► Goals

Adoption

- Evolutionary Paradox: Adoption
- Paternity Uncertainty and Investment in Sons and Daughters
- Resemblance

Adoption Preferences

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Synonyms

Adaptation; Alloparenting; Facial cues; Family

Definition

What child traits influence parents' desire to adopt?

Introduction

Adoption is a complex behavior that can take many forms and offer many functions. There are

Resemblance/Kinship

Evolutionary theory suggests that parents should invest in related children so long as the cost to themselves (i.e., their own genes) is offset by the benefit to the shared genes in the related children (Trivers 1972). This means that for many parents, cues of resemblance or kinship will be high on the list of preferred traits in an adoption (Volk and Quinsey 2002). The most likely circumstances for this form of adoption are when one or both of the parents die (Halbmayer 2004), a not uncommon event in the evolutionary past (Volk and Atkinson 2008), or when they are incapable of caring for a child (a more recent likelihood; Scelza and Silk 2014; Stolley 1993; Testa 2004). Under these circumstances, the related adopting parent functions enable the survival of the related child (a large benefit) for a relatively modest cost (a smaller cost than birthing and raising one's own child – particularly if the child is older). This is likely a relatively ancient pattern of behavior as chimpanzees have been observed to adopt younger siblings if they are maternally related (Hobaiter et al. 2014). In these circumstances, resemblance is likely to exist to some degree due to shared genetics. In North America, just under half of all adoptions are by kin who are supporting children with a living parent (Stolley 1993), while 31 % of fostered children are raised by kin (Testa 2004). These numbers might well be higher as many families rely on informal systems of adoption and fosterage to support ill-equipped

biological parents. Thus kinship appears to be an important motivating factor in adoption.

But clearly, known kinship is not the only motivation behind adoption given that at least half of adoptions in North America occur with parents adopting unrelated children. Under these circumstances, cues that suggest resemblance and kinship may still matter. Many adoption practices are well aware of most parents' desire to adopt children who resemble them physically and/or behaviorally and often attempt to simulate or generate that resemblance (Hamilton et al. 2007; Howell 2006). A North American social worker was quoted by Wegar (2000, pg. 367) as saying "We also try to match physical appearance. I had one family that I was able to match a child, a little girl, with a family that the mother looked remarkably like a biological parent. I mean, if you look at the pictures you would think that they were related... It was a fantastic match...because the child looks like she belongs to the family...we make an effort to match people in terms of physical appearance, in terms of values...religious beliefs, those sorts of things."

Both men and women express a greater desire to hypothetically adopt a child that resembles them (Volk and Quinsey 2002, 2007). Families invest more in offspring who are genetically related than in unrelated children (Gibson 2009). Facial cues have received the most attention, in part because they are at least moderate predictors of actual genetic relatedness (Alvergne et al. 2007).

Interestingly, numerous studies have documented that men value cues of resemblance more than women do in a hypothetical adoption paradigm (Volk 2009; Volk and Quinsey 2002, 2007). From an evolutionary perspective, this may be due to the fact that men face paternity certainty risks, while no such risks occur for birth mothers, making men in general more sensitive toward cues of paternity (Alvergne et al. 2009). Anecdotally, during the 1990s when Western adoption of Chinese infants was highly pervasive, it is widely believed that the Chinese government deliberately matched children with adoptive families based on the resemblance of the child to the adopting father (Volk 2011).

Age

Another crucial cue for adoption is age. From an evolutionary perspective, older children are much more likely to survive than younger children (Volk and Atkinson 2013). Thus, it is something of a paradox that adopting parents strongly prefer to adopt younger children (Howell 2006; Stolley 1993; Volk 2011). Adults also show a preference toward hypothetically adopting children with younger-looking faces (Luo et al. 2011; Volk et al. 2005). Among older children, adults prefer cues of immature behavior (Blasi et al. 2015). Older adopted children are more likely to be raised by kin than non-kin (Volk 2011), presumably to offset the costs of adopting an older child with the benefits of adopting one who is genetically related.

Thus, child age presents an apparent paradox – why would adults prefer to adopt younger children who are less likely to survive? One proposed answer is that younger children allow parents more flexibility in shaping a child's behavior and identity to fit their own (Hamilton et al. 2007; Howell 2006). This may be less important for kin, explaining part of the reason why they would be willing to adopt older children (Talle 2004). An alternative answer is that infants have evolved facial cues that are more effective in soliciting parental care than older children because of their greater need for parental care (Volk et al. 2007). Lorenz (1943) termed these cues as "kinderschema" and noted that they are present in nonhuman species as well. In all likelihood, the influence of age likely represents a combination of these factors, as adults prefer the malleability of younger children while simultaneously being more affected by more effective solicitation of care by younger facial cues.

Health

Health is another important cue for parents as it is a signal that relates to both the potential costs (investment) and benefits (survival) of parental care (Volk and Quinsey 2002). Given the very levels of infant and child mortality in the

environment of evolutionary adaptedness (~26 % and 47 %, respectively; Volk and Atkinson 2013), it is not surprising that cues of good health are positively associated with a desire to adopt while cues of poor health are not (Volk et al. 2005; Waller et al. 2004). Most national (vs. international) adoptions in Western countries tend to involve children who are at a higher risk of having physical and/or mental issues (Stolley 1993). In contrast, international adoptions are often used as a means of reducing or even eliminating the higher health risks associated with national adoption (Howell 2006; Miller 2005). Among hunter-gatherers and pre-modern societies, cues of low health were potentially lethal signals that could result in infanticide or abandonment of infants (Cunningham 2005; Silk 1990). Nevertheless, it is worth noting that in comparison to cues of youthfulness, that are themselves associated with lower health, health is a weaker predictor of adoption preferences (Volk et al. 2007).

Cuteness

Yet another important cue for parents in adoption scenarios is cuteness or attractiveness. Anecdotally, cuter children are more likely to be adopted than less attractive children in actual adoptions (Volk 2011). This is backed up by research showing a cross-cultural preference for cute children (Volk 2009; Volk and Quinsey 2002). In contrast to resemblance, the appeal of cuteness appears to be stronger for women than for men (Volk and Quinsey 2002). The appeal of cuteness may relate to the display of good genes that signal a valuable investment (Volk and Quinsey 2002). It is therefore not surprising that cues of cuteness are strongly correlated to both younger age and positive health (Volk et al. 2007).

Conclusion

To summarize, adoption is a complex behavior that can have multiple forms and functions. It appears to be influenced by a range of infant and

child characteristics including relatedness, age, cuteness, and health. Generally speaking, adults appear to be motivated both by cues that signal the benefits of adoption (e.g., genetic relatedness), the costs of adoption (e.g., poor health), and the mitigating factors on those costs and benefits (e.g., cuteness as an indication of good genes and young age as an indicator of familial malleability). These preferences are undoubtedly only part of a complex decision process that involves other parental, social, and economic factors. Nevertheless, it does appear that there are consistent patterns of adoption preferences that hold across cultures and history and that these preferences are generally aligned with adaptive evolutionary outcomes.

Cross-References

- ▶ [Consolidating Familial Power](#)
- ▶ [Evolutionary Paradox: Adoption](#)
- ▶ [Forms of Adoption](#)
- ▶ [Function of Adoption](#)
- ▶ [Resemblance](#)

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- ## Adrenaline
- Epinephrine
-
- ## Adrenogenital Syndrome
- Congenital Adrenal Hyperplasia (CAH)
-
- ## Adult Attachment
- Attachment in Adulthood
 - Pair-Bonding in Other Mammals
 - Romantic Attachment
-
- ## Adult Sex Ratio
- Sex Ratio and Men’s Long-Term Mating
-
- ## Adultery
- Frequency of Infidelity
 - Infidelity Risk
 - Seeking Extra-Pair Partners

Advanced Age

► [Senescence](#)

Advanced Tool Use

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Synonyms

[Utilization of complex instruments](#)

Definition

The ability to develop and utilize objects, such as long blades and primitive sickles in order to better hunt, process prey, and survive.

Introduction

It is believed that the first *Homo sapiens* tools were originally developed approximately 250,000 years ago. Tools developed within this timeframe lacked the characteristics that would classify them as advanced. Advanced tools, and their use, is believed to have begun roughly 100,000 years ago. Examples of these tools include spears with spearheads, longer blades, and sickles. These are considered to be improvements and demonstrate a higher process of thought among *Homo sapiens*.

The Importance of Advanced Tool Use and Its Practicality

Advanced tool use is a very important milestone in evolution. The departure from primitive tools, i.e., clubs, primitive spears, is an important distinction with regard to *Homo sapiens*. Prior to the development of advanced tools, tools were quite simple. These included simple oval stones

fashioned into “hand axes,” among other primitive tools. When comparing these two different kinds of tools, this shows an increased cognitive ability, as well as demonstrates an increased physiological ability to use them. The utilization of advanced tools came with many benefits. For example, processing hunted prey, which can involve removing edible food, furs, bones, or anything else that could serve a use, and the cleaning process for food itself became easier. Another benefit of advanced tools is the ability to hunt game of all sizes. Prior to this development, only small- and medium-sized game was effectively hunted for food. Obviously, this change had a huge impact on the diet of the *Homo sapiens*. For example, “Toolmaking would have facilitated access to a wider range of foods and the ability to process those foods more intensively or efficiently, likely making them more palatable and yielding more calories” (Pobiner 2016). With the increased ability provided via the advanced tools, the means to hunt larger game and even aquatic game arose. It is important to note that not all advanced tools were used solely for hunting purposes. Tools that had sharp, flat edges would most likely be not as useful as a sharp, pointed edge for hunting, but perhaps useful in helping to remove hide from hunted animals, which would provide a benefit of its own.

Conclusion

In conclusion, the development of advanced tools ultimately allowed *Homo sapiens* to better adapt to their environment. The ability to not only gather more food but also a greater variety of food provided a significant advantage to the *Homo sapiens*. Furthermore, the ability to better process hides and other materials certainly helped to improve the quality of life for *Homo sapiens* as well.

Cross-References

- [Advanced Tools of Neanderthals](#)
- [Evolution of Tool Use](#)

- ▶ Human Tool Making
- ▶ Stone Hammers

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Advanced Tools of Neanderthals

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Synonyms

Device; Implement; Instrument; Utensil

Definition

An instrument of manual operation; an implement, usually held in one's hand, for performing or facilitating.

Introduction

Tool use in hominins is considered a leap in our evolutionary history. It indicated both an understanding of symbolic learning and how to use the environment to one's advantage. For Neanderthals, tools were usually simple, made of either bone or stone, and frequently specialized for one or another use, typically using the same set of techniques to create them. There is well-documented evidence that tool use did exist at Neanderthal sites; however, there is still debate over whether or not Neanderthals invented their own tools, or if they learned them from the encroaching Anatomically Modern Human populations migrating from Africa (Soressi et al. 2013; Tyron and Faith 2013).

The time period when Neanderthals were living in Europe and making these tools is known as the Middle-Paleolithic (Simek 1998; Villa et al. 2008). This era is compared with the Upper-Paleolithic, which is usually more associated with human migration in to Europe from Africa.

A

Toolmaking

Typically, tools in Europe were made of flint, whereas in Africa tools tended to be made of flint, quartz, and sandstone (Lazuen 2012). Two main tool-making practices were utilized by Neanderthals. For stone, the levallois technique was used, which involved flaking pieces of stone off of the core to create a sharp edge or point (Lazuen 2012; Tyron and Faith 2013). A different form called the Lissoir Style, lissoir being French for “to make smooth,” describes the specific method by which the Neanderthals would have prepared bone (as opposed to stone) tools for use, usually preparing animal skins to be worn (Soressi et al. 2013).

While most Neanderthal tools appear to have been made for scraping and toughening animal hides (Vos 2015), research done by Bodea et al. (1999) suggests that they may have also been used for hunting. Remains from a wild ass, found in Syria, included the point of a levallois tool embedded in the vertebra. The angle and depth at which the tip was buried suggests that it is unlikely that the tool was used for cutting or preparing the animal for meat or wear. The authors discussed whether or not the tool was attached to a handle (hafted), or if it had been the tip of a projectile. Overall, this tool is suggestive of some of the other uses that levallois tools may have served for Neanderthals (Villa et al. 2008; Bodea et al. 1999).

One valuable discovery made at some middle Paleolithic sites includes bitumen, that was likely fired and used as glue for hafting purposes. The birch used to make this material would likely have been sourced from several kilometers away from the site at which this evidence was found, which provides remarkable clues about Neanderthal creativity and ingenuity (Villa and Soriano 2010).

The hafting process would have consisted of creating a stone tip that was pointed on both the upper and lower sides of the long edge, with a flat back. The flat back was mounted on to a wooden shaft, which would have been shaved to an angle at the edge. The stone was then secured using the bitumen glue and/or muscle sinew from previously hunted fauna (Villa and Soriano 2010).

Examples

It appears as though Neanderthals were likely good hunters, contrary to what was believed several years ago, especially considering the evidence above featuring the wild ass. As such they had a variety of stone tools at their disposal for everything from killing, butchering, and preparing animal hides (Villa and Soriano 2010; Villa et al. 2008). Several stone tools found have been examined for various technical elements as well as for a better understanding as to what they were used for and how. It was clear based on the evidence that the tools had been created using the levallois technique. Notches on some of the tools indicated that they may have been hafted, or mounted onto a handle, for more efficient use. Overall, two different hunting tools were found. One larger, and one smaller, assumedly used differently (Tyron and Faith 2013).

Soressi et al. (2013) discussed four different tool fragments found at known Neanderthal sites, suggesting that these are some of the first and oldest tools to be associated with these hominins. They appear to show little wear from carnivore or other potential sources of modification other than the Neanderthals who shaped them. The bones likely come from the ribs of large hooved animals, and all included striations that suggest a consistent method, the lissoir, for polishing and grinding the bones into the desired shape. The authors suggest that the likely use for these bones would have been to prepare animal skins (Soressi et al. 2013; Barras 2013).

The researchers made a point to compare these bone tools with others to ensure that environmental wear, which can sometimes produce similar objects, was not the source of the shaping of the

bones. It was found that these bones were very likely shaped intentionally, and would have served the very specific purpose of toughening animal hides to be worn and preserved, making these tools highly specialized. This adds to the debate about whether or not Neanderthals invented these tools independently, or if they were learned from modern humans migrating from Africa (Soressi et al. 2013; Barras 2013).

Smaller stone tools have been discovered in Europe in increasingly larger numbers. It appears as though they were intentionally manicured to be smaller in size. They date to the approximate period when Neanderthals would have inhabited this area, between 400 and 40 kya. Central Europe revealed large numbers of these unique tools, which researchers have called Taubachian, to distinguish them from other tools of the era (Borel et al. 2016).

Borel et al. (2016) conducted research on these smaller tools in order to ascertain what they may have been used for. Comparing features of the environment from geography, to flora and fauna, the researchers sought to get a full understanding of the context under which these tools were made. Dating approximated the era of these tools to be roughly between 116 and 70 kya. It appeared that the size and shape of the tools was clearly intentional, and the edge that was used for a specific task was consistent, meaning that the opposite side of the tool was likely the part that was gripped by the user. However, shapes between tools were not consistent, and there was no way to effectively categorize the tools for use, based on this feature. It appears as though most of the tools were used for scraping; however, there is no way to be certain that that was the only use tools at a given site may have had. It is relatively clear that the makers and users of these tools were Neanderthals. Some tools may have been attached to various other materials, such as handles, to make the tool more effective (Borel et al. 2016).

Another feature that is yet unclear is whether or not, in more forested areas, use of stone tools coincided with the use of wooden tools as well. Four wooden spears were found in the mud of the banks of a lake in what is now Germany, along with the skeletal remains of a family of horses

(Villa et al. 2008). Cuts on the bones of the horses match the spears as well as tools that are similar. The wooden spears were all made of spruce, and one of pine; however, the consistency with which they were made suggests an understanding of the raw materials of the area. Other impact scars on the tips of certain tools indicate use as projectiles, either attached to thrusting or throwing spears (Villa and Soriano 2010). Naturally this lends more support, as well, to the idea that wooden tools may have been part of the Neanderthal toolbox (Borel et al. 2016; Villa et al. 2008).

The expertise with which these tools were made suggests that they were made by craftspeople who understood well their purpose and materials, as well as knowledge of the raw materials in the area (Borel et al. 2016; Villa et al. 2008). The fossilized tools we see today suggest a consistency through which they were made and used, suggesting that the hominins who made them understood the various textures of bones and stones, well enough to create this successful method for creating these tools (Soressi et al. 2013; Barras 2013). This idea is supported by the other tools found at the site, made from stone, include hand-axes, and knives, showing that Neanderthals likely had several kinds of tools in their repertoire.

Controversy

It is still a topic of debate whether or not Neanderthals began producing tools before or after the arrival of *Homo sapiens* into Africa. Fossil records from the Arcy-sur-Cure site in France date one of the youngest Neanderthal sites known, at 34,000 years ago. The authors assert that the hominins that lived here were, in fact, Neanderthals, based on a series of features related to skeletal remains. This helps indicate that Neanderthals lived up until relatively recently in our evolutionary history, which implies that coexistence or at least contact between Anatomically Modern Humans and Neanderthals, was likely given the temporal and geographic overlap between them in Western

Europe (Hublin et al. 1996). Rossano (2010) claims Neanderthals were expert “toolmakers,” meaning that it is possible that they made tools independent of human influence. Additionally, the age of most of these tool remains suggests that they were made by Neanderthals before humans arrived (Tyron and Faith 2013).

Modern human tools were much more advanced and could be categorized by many different functions, more so than the Neanderthal tools could. Additionally, (Klarreich 2004; Klein 2003) suggests that Neanderthals may have been able to copy the toolmaking of modern humans, but they did not seem to do much to pass them further. If it was the case that Neanderthals learned tool use from modern humans, why wouldn’t they have learned to master all of the complex tools that the humans made, instead of just a simple few, especially when the evidence suggests that Neanderthals did have the mental capacity to master craftsmanship (Villa et al. 2008).

However, lack of evidence, in some cases, makes it difficult for bone remains to be identified as being a true tool, or simply bones that have been modified by other parts of the environment (Soressi et al. 2013). What does appear to be clear is that there are tools of many kinds all over Europe, suggesting that tool production and use in Neanderthals was not limited to one particular geographic climate or one particular group of hominins, which could easily suggest their inventiveness independent of modern humans (Borel et al. 2016).

Conclusion

Part of the important implications of toolmaking in Neanderthals and other hominins is the fact that they represent symbolic thinking and social learning. Tool use was likely passed on from one person to another via observational learning by the student (Barras 2013). The cognitive demands of symbolic thinking likely helped the development of working memory in Neanderthals, and could have potentially helped with other forms of communication, such as language (Gibson 1991; Rossano 2010).

There are other cultural practices that do not seem to have a clear origin, such as the burying of the dead, which marks a significant milestone in hominin cognition as it establishes differentiation between life and death (Barras 2013). Villa et al. (2008) argue that more research on hunting tools in Europe during the middle-paleolithic period is necessary for having a better understanding of the behavior of Neanderthals at the time.

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Advantageous Side Effects

► Beneficial Side Effects

Advantages of Having Close Blood and Affinal Relationships

► Benefits of Profound Kinship Connectedness (and Problems from a Lack Thereof) Through an Evolutionary Mismatch Lens

Adverse Effects of Alcohol in Utero

► Teratogenic Effects of Alcohol Exposure on the Fetus

Advertisements

► Advertising

Advertising

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Synonyms

Advertisements; Research methods; Data

Definition

Advertisements, which are widely available, can provide insights into the evolved preferences of target audiences and serve as a useful supplement to other methods in evolutionary psychology research.^t

Introduction

Advertisements present an important source of data for evolutionary psychologists. Advertising is ubiquitous in our fast-paced, modern world, and people living in urban places are exposed to hundreds, if not thousands, of advertisements daily. Yet, little research exists that describes how advertisements can be prudently utilized. This chapter discusses how advertisers create content that strategically exploits consumers' values and preferences and how advertising content can provide insights into various aspects of our evolved psychology.

Advertising: More Than Meets the Eye

Advertising refers to a paid, mediated form of communication from an identifiable source, designed to persuade the receiver to take action, either now or in the future. The selection of advertising content by advertisers and marketers is far from arbitrary, as marketers seem to know that advertising that appeals to people's intrinsic preferences or beliefs, such as their values, attitudes, and tastes, is more attention grabbing, influential, and persuasive (Yong et al. 2016).

As advertising tends to appeal to individuals' intrinsic preferences and values, the content of advertisements and commercials offers researchers an important source of empirical data. Advertisements exploit the intuitions or insights that marketers have about their target audiences, which allow researchers to infer particular psychological features of these target audiences.

Advertisements Reflect Evolved Psychology

At a fundamental level, advertisements reflect evolved psychological preferences and present a window into human nature. The following sections describe some important inferences that can be made of our evolved psychology from advertisements.

Mate value traits. Men and women prefer traits in a mate that can improve their own reproductive success. Because women's fertility declines as a function of age, men's reproduction is constrained by their access to reproductively valuable or fertile mates (Trivers 1972). In response to this adaptive challenge, men evolved to prefer physical features that signal youth, health, and fertility in sexually mature women, including firm skin, breasts, and buttocks, and a low waist-to-hip ratio (Buss and Schmitt 1993). In contrast to women, men face a slower decline in fertility across the life span, so identifying fertile partners is less crucial for women. Instead, because ancestral men varied in their ability to provide resources that aid the survival of women and their offspring, women, more than men, evolved to value a partner's social status, which is closely related to his ability to provide resources and protection (Buss and Schmitt 1993).

The content of advertisements provides a unique avenue to examine the validity of these mate preferences. More specifically, the theory of evolved mate preferences predicts that advertisements will tend to portray men and women according to their relevant mate value traits in advertisements, specifically senior and high-status men and young and physically attractive women. Indeed, a variety of studies analyzing a wide range of magazine advertisements, television commercials, and other forms of mass media have found that exemplary women are typically shown as being young and physically attractive and exemplary men as having high status (Saad 2004). Female characters in advertisements are more likely to be distinguished by their looks, such as being physically attractive and dressing provocatively, while male characters tend to be portrayed as demonstrating skill or having important occupational roles (Yong et al. 2016). The display of

older age also appears to be more acceptable for men than women, as women are less likely to be shown on prime-time television with gray hair compared to men.

Another source of evidence for mate value traits can be found in personal advertisements, where individuals attempt to entice the interest of potential mates. One study analyzed over 300 personal advertisements in a respectable Californian singles digest and found that women advertised their appearance-related traits much more than men did, whereas men emphasized their status-related traits more than women did. A more recent study examined online personal advertisements and found that little had changed; men are more likely than women to exaggerate their income and social status, while women are more likely than men to misrepresent their physical appearance and underreport their age (sometimes both at the same time by using photos taken 10-plus years ago).

Relationship duration preference. Compared to women, who are required to invest heavily in the production of offspring because of internal gestation and postpartum suckling, men are physiologically required to make a relatively smaller contribution of only a few sex cells during sexual intercourse. Therefore, children carry much higher costs to women than men, especially in ancestral times when access to food and health care was scarce, if they result from sex with a partner who is unwilling or unable to provide resources and protection (Trivers 1972).

These differences in the costs of short-term, uncommitted sexual relationships meant that men, more so than women, could maximize their reproductive success by acquiring more mates. Therefore, men, more than women, evolved to have a range of psychological mechanisms that facilitate a short-term mating strategy and increase their access to a wider pool of sexual partners, such as proclivity for sexual variety and heightened sensitivity to cues of sexual receptivity (Buss and Schmitt 1993).

Advertisers indeed exploit this preference for short-term mating by depicting women, but not men, as attractive sex objects (Saad 2004). The

presentation of sexually attractive and receptive females can make an advertisement more attention grabbing and influential. For instance, one study utilized a visual cueing task in which participants had to focus on a particular stimulus and then shift their attention to a different point on the computer screen. Men had greater difficulty disengaging their attention to the new point on the screen when the initial stimulus was an attractive woman, while women did not experience this effect when the initial stimulus was an attractive man (Maner et al. 2007).

Presenting images of sexually attractive and receptive females in advertisements also increases men's cognitive disinhibitions and impulsivity (Yong et al. 2016). One study found that male participants increased their likelihood of discounting the future—regarded as a disinhibited, impulsive preference for immediate gratification—when exposed to pictures of attractive members of the opposite sex, while this effect was not found for female participants or participants who were exposed to pictures of unattractive opposite sex members (Wilson and Daly 2004). Disinhibition has consequences for reduced self-control and deficiency of deliberative decision-making and also has been shown to increase the likelihood of spending or acquiescing to persuasive messages. Indeed, in a study of loan advertisements conducted on a South African sample, advertisements that included a photograph of an attractive woman led to increased demand for the loan, and this effect was driven by male consumers. Thus, when attractive, skimpily clad women are recruited as models by organizers of car showroom events, advertisers are exploiting men's short-term mating psychology to make their messages more effective. These differences in the portrayal of the sexes have been found to span generations and time periods as well as across cultures, suggesting a consistent trend (Yong et al. 2016).

Advertisers have also historically taken advantage of women's preferences for committed, long-term relationships. For instance, it has been argued that appealing to the family ideal and the importance of love in advertisements can create

the belief that shopping provides a solution and relief to these unfulfilled needs. Further research can be conducted to see if appeals to long-term relationships still persist in advertisements aimed at women today.

Gains and losses. Kahneman and Tversky's (1979) seminal prospect theory provides an important model for understanding human decision-making behavior under risk. Prospect theory stresses that gains and losses are evaluated relative to the status quo as a reference point. As our ancestors likely operated close to subsistence level as their status quo, resource losses often entailed a high chance of starvation and death. Thus, for most humans, resource losses generally loom larger than gains. By manipulating the "reference points" that enter decision rules or preferences, consumer choices can be influenced, and invoking potential losses is a particularly powerful stimulus for demand if it triggers loss aversion (Kahneman and Tversky 1979).

Various studies have found that loss-framed appeals in advertisements and persuasion messages tend to be more effective than gain-framed appeals when loss aversion was triggered. In a direct marketing field experiment to persuade people to use a particular credit card in Israel, people were approached and told that there are either "many disadvantages in using cash instead of ZionCard" (loss frame) or "many advantages in using ZionCard instead of cash" (gain frame). Indeed, loss-framed messages induced higher credit card usage than gain-framed messages (Ganzach and Karsahi 1995). Similarly, advertisers influence female consumers by exploiting loss aversion in intrasexual competition contexts (Yong et al. 2016). Advertisers often deliberately highlight women's physical shortcomings and insinuate that if women do not purchase their products and services, they will bear the consequences of retaining their physical flaws. Indeed, as early as the 1920s, advertisements for products such as mouthwash and soap have unabashedly stated that women who do not care about their looks (e.g., maintain good oral or skin hygiene) will fail to attract and retain a mate. The wildly successful cosmetic industry is a testament to the

effectiveness of such advertising messages that play on female physical attractiveness and mate value, as women spend more than men on goods and services that enhance appearance (Saad 2004). During economic crises, while most industries suffer losses, beauty and cosmetic industries (where females are the primary consumers) either are unscathed or may even experience a boom, as the number of financially stable men drops and intrasexual competition for such men intensifies (Hill et al. 2012).

Status signaling. Just as advertising can inform theories and hypotheses about evolved psychology, an evolutionary perspective may provide insight into how advertising has played a major role in shaping the materialistic values around which modern societies and economies function. In particular, advertisements may exploit a fundamental need for men and women to signal high social status to others. Having a high relative position in the local social hierarchy is evolutionarily important as it was linked to resource access and likely conferred survival and reproductive advantages in the ancestral past (Buss and Schmitt 1993). Social status is dependent not only on one's own skills and accomplishments but is ultimately something that is conferred by others. That is, others must see and acknowledge a person's standing in order for him or her to have a level of status. Given the evolutionary importance of status and the role that others' perceptions play, people may have evolved to display markers of their social status to others when possible.

In modern economies, advertising and product marketing have helped create a plethora of consumer avenues through which individuals can signal their social status—for example, widely recognized brand names in handbags, automobiles, watches, clothing, phones, schools, and holiday destinations are among the thousands of material products and services through which status can be signaled. Indeed, material luxuries are a highly viable means of status signaling underlying conspicuous consumption. Importantly, the status that individuals signal with each material purchase is only fleeting, as more and more people also acquire the same items, and product life

cycles become increasingly shorter (Li et al. 2015). Studies have indeed demonstrated that advertising across television and print media has increasingly depicted and appealed to a materialistic lifestyle among consumers in cultures as diverse as the United States and Japan.

Conclusion

In summary, advertisements present an abundant and convenient source of empirical data for evolutionary psychologists. By examining psychological traits in advertising content, researchers can make inferences about human nature and use advertisements to gauge the validity of evolutionary theories on human psychology. At the same time, an evolutionary psychological perspective can shed light on why advertising works and how it has contributed to the materialism that pervades modern society.

Cross-References

- ▶ [Conspicuous Consumption](#)
- ▶ [Intrasexual Competition](#)
- ▶ [Long-Term Mating](#)
- ▶ [Men's Mate Preferences](#)
- ▶ [Preferences in Long- Versus Short-Term Mating](#)
- ▶ [Sex Differences](#)
- ▶ [Sexual Strategies Theory](#)
- ▶ [Short-Term Mating](#)
- ▶ [Social Status](#)
- ▶ [Social Status and Economic Resources](#)
- ▶ [Women's Mate Preferences](#)

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Advertising Effects

- ▶ [People's Responses to Personal Ads](#)

Aesthetic Display

- ▶ [Art Production, Appreciation, and Fitness](#)

Affair

- ▶ [Sex Differences for Pursuing](#)

Affective Bond

- ▶ [John Bowlby and Attachment Theory](#)

Affiliation

- ▶ Tend and Befriend Adaptations

Affiliation and Sexual Behavior

- ▶ Sex as Bonding Mechanisms

Affiliation and Sexuality

- ▶ Sex as Bonding Mechanisms

Affiliative Bonds

- ▶ Cost of Same-Sex Friendships
- ▶ Same-Sex Friend

After Life

- ▶ Spiritualism

Age

- ▶ Risk Variation with Parent Age
- ▶ Youth and Fertility

Age Categories

- ▶ Categorization by Age

Age Categorization

- ▶ Categorization by Age

Age Differences in Marriage Partners

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Definition

Age differences between spouses have been observed across different cultures, such that men are usually older than their marriage partners. Such arrangements are more prevalent than both same-age and women-older marriages.

Introduction

The age gap between partners has been a popular topic of debate, filling tabloids with articles on celebrity couples with “huge age differences,” speculating whether they are truly happy and whether it is really love that bonds them together. Not surprisingly, age difference is one of the main aspects that individuals consider when selecting a romantic partner. In heterosexual relationships, men are on average older than their partners, a pattern observed across cultures, such that the age gap between partners is 2–3 years in developed countries (Kolk 2015). Such a pattern is observed even in gender egalitarian societies, such as Norway. These marriage arrangements are more common than same-age marriages and women-older marriages. For older men, marrying a younger woman can mean having a beautiful, adventurous, and dynamic partner. In contrast, older men are often perceived as more successful and confident, given that they have had more time to acquire resources and experience, a characteristic that is often attractive to women. In this entry, I will discuss consequences of dissimilarities between spouses and why men consistently prefer younger women than themselves, whereas women do the opposite.

Consequences of Age Disparity Between Spouses

The age differences between spouses may have consequences in different domains. For example, the age gap between parents has an inverted U-shaped association with number of children in a Polish sample (Kuna et al. 2018). Having a younger partner is positively associated with symptoms of depression in elderly people (Pradeep and Sutin 2015). Australian men and women reported to be more satisfied with a younger partner than with an older partner, suggesting that age-different couples are less resilient to problems in the relationship in comparison to same-age couples (Lee and McKinnish 2018). Age dissimilarity between spouses also affects other aspects such as commitment to the relationship (Lehmiller and Agnew 2008), infidelity, and risk of contracting sexually transmitted diseases (Maughan-Brown, Kenyon, and Lurie, 2014). Why then are such relationships prevalent across cultures, if there are so many apparent disadvantages associated with engaging in age-dissimilar relationships?

Theoretical Explanations of Age Differences Between Spouses

Sociocultural approaches argue that the preferences for men-older relationships are a result of social norms and gender roles (Klinger-Vartabedian and Wispe 1989). On the other hand, Bergstrom and Bagnoli (1993) further claim that the relative desirability of women as marriage partners becomes more apparent at an earlier age than do men, proposing an equilibrium model to explain the preferences for men-older marriages. In this model, educationally and professionally ambitious men choose to wait until they have achieved educational and economic success to get married. On the other hand, those men who do not believe they can enhance their educational and professional opportunities will offer to marry at a younger age. *In equilibrium*, women are expected to marry at a younger age than men; however, more desirable women will be more likely to marry older men in comparison with less desirable women.

An evolutionary perspective, a common explanatory model, predicts that individuals will generally pursue partners with attributes that can increase their reproductive success. As such, because women invest more heavily in reproduction (Trivers 1972), they will favor partners who are able to invest in them and in their offspring, can physically protect them, and are likely to be good parents (Puts 2016). Consistent with this view, Buss (2007) reviewed different studies showing women across several cultures tend to value attributes such as good financial prospects more than do men and attributes that are related to higher earning potential such as ambition, social status, and older age. Men, on the other hand, tend to value physical appearance, a cue of women's fertility and reproductive value, which are attributes associated with younger age and vitality. Such patterns help to explain the age gap between spouses and the sex differences on preferences for partner age. While women will prefer older partners, since they are more likely to have finished their education and built up a good career, men will prefer younger women because attractiveness and fertility are more apparent at an early age.

Conclusion

Men and women have different reasons for engaging in men-older marriages as a result of sex-specific partner preferences related to the reproductive value of women and the earning ability of men. While men prefer younger women because at a younger age the reproductive value of women is more apparent, women prefer older men because they are more likely to have acquired economic and other resources to provide for their partners and for the offspring.

Cross-References

- ▶ [Long-term Mating](#)
- ▶ [Mate Preferences](#)
- ▶ [Sex Differences in Long-term Mating Preferences](#)

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Age Disparity

► Older Men

Age Groups

► Categorization by Age

Age of Child

A

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Synonyms

Baby schema; Infant; Kinderschema; Parental investment

Definition

The developmental age of child that is associated with the highest parental investment.

Introduction

The age of a child is shown to have important effects on parental investment decisions. This is likely because the age of the child may be associated with the child's ability to survive (Volk et al. 2005; Hrdy 1999). For example, newborns are less likely to survive without parental care compared to older children due to lower levels of health-related development at that stage (e.g., less developed immune systems; Voora et al. 1982) and higher dependency on parental care compared to older children (Hrdy 1999; Volk and Atkinson 2008). Therefore, the offspring that shows the highest chance of survival, which is generally the older child, should typically receive the most parental investment as this child will more likely produce offspring and help propagate parents' genes (Trivers 1972). However, this would suggest that parent may be predisposed to make parental investment decisions more strongly based on parents' own interests of propagating their genes rather than the child's interest. On the other hand, younger infants are certainly more in need of parental care for survival compared to older children (Hrdy 1999; Volk and Atkinson 2008). Therefore, it could also be hypothesized that parents may be predisposed to make parental investment decisions based on what is best for the

child. If this is the case, then parents' investment decisions could be perceived to be more strongly dependent on children's interests rather than parents' immediate (evolutionary) interests. So who do parents actually invest in: younger or older children?

A close look at the data on parental investment based on age of the child suggests that parental investment decisions may be more complex than any of the above two theories would independently suggest. Franklin and Volk (2017) helped shed some light on this when they proposed an inverted "U" curve associated with child age and parenting decisions. This is based on evidence which suggests that adults may have the strongest caregiving predispositions toward children between 3 and 6 months old, which represents the peak of the inverted "U" curve (Franklin and Volk 2017; Franklin et al. 2018). The bottom left of the curve represents adults' least positive perceptions and caregiving behaviors toward newborns. This is presumably in part because the newborn stage is associated with the highest mortality rates across childhood and therefore may be the riskiest age for parental investment (Volk and Atkinson 2008). Finally, the bottom right of the curve suggests that adults' perceptions and caregiving behaviors tend to slightly reduce after 6 month stage (Franklin and Volk 2017).

The reason for adults' apparent peak in caregiving perceptions and behaviors at 3–6 months is likely because this is the stage at which there may be an optimal balance between children's robust health and need/dependency on parental care (Franklin and Volk 2017; Franklin et al. 2018). For example, compared to newborns, 3 and 6 month olds are more likely to survive illnesses and infections without serious medical intervention (Voora et al. 1982). Additionally, older children can more independently survive without parental care. Therefore parents may not ultimately evolutionarily benefit from investing in older infants at the expense of younger infants (Franklin et al. 2018). Therefore, investment in infants between 3- and 6-month-olds appears to be the safest investment that still allows parents to ensure infant survival without depleting too much of parents resources.

Conclusion

The underlying factors that are suggested to influence the peak in parental investment toward children between 3- and 6-month-old infant strengthen the idea that in cases of conflict between parents' and children's interests, evolutionary pressures may have favored parents' interests over those of children (Trivers 1974). More specific to parental investment based on child's age, it appears that parents may be predisposed to invest in offspring at an age at which the offspring will optimize parental parents' resources. Therefore, the age of the child may be an important factor to consider when trying to understand the complexity associated with caregiving decisions.

Cross-References

- ▶ [Parental Investment](#)
- ▶ [Parental Investment Theory](#)
- ▶ [Parent-Offspring Conflict](#)

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Age of Menarche

- Absence Prior to Puberty

Age of Mother at Birth of Her Child

- Maternal Age

Age of Parent

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Synonyms

Developmental psychology; Fertility

Definitions

Parental age. Although it might seem obvious what “parental age” refers to, it should be noted that age at first menarche, age at first sexual encounter, and age of first birth may not, indeed typically do not, coincide. Biosocial factors, such as status, must also be included. Also worthy of note is that humans are unusual mammals in that females can live for 25 or more years after maternal viability stops (at around age 50). Menopause may well be an adaptation to grand-parental investment beyond child-bearing years (Buss and Schmitt 1993).

Life History Theory. A mid-level biological account of the differential allocation of resources to growth or repair. In general animals can fall into fast (relatively high risk, low investment) or slow (low risk, high investment) patterns of child-bearing (Stearns 1976).

Introduction

Humans are obligate – indeed intensive – investors in their offspring, with the minimum potential parental investor being the male (Trivers 1972). Long gestation, and lengthy infantile dependence (including lactation – which is shortened compared to other primates) combined with a huge amount of social learning, with both status and resource inheritance, means that life history mechanisms can play out along a number of key areas. A key one of these is parental age. Theory needs to explain how these features cluster together, either as a complete package or as a mosaic of features (Bogin and Smith 1996).

Evolution and Parental Age

When Robinson Crusoe discovered that he was not alone, his economy changed from simple resource management to the need to understand a complex interplay of intentional forces (von Neumann et al. 2007). Humans are all similarly born into worlds which are highly complex in social terms. Their own species constitute some of their key rivals, and potential allies – both kin and nonkin. Although other primates are social, the need to adjust to a complex social world seems to be a key difference for our species that probably helps to explain a complex mosaic of effects. For example, while chimpanzees and gorillas have to put a lot of thought and resources into preventing infanticide, this is unlikely to have been a major selective factor in recent human evolution (Geary and Flinn 2001).

Instead, human males often, but not always, invest in offspring, and this investment can take the form of status, resources, skill acquisition, and so on. In this respect, older males tend to have more mate value than younger ones, all things being equal. However, younger male reproduction will be selected for in the standard life-history cases where males are less likely to invest and fit the general patterns of risk taking, and low parental investment (Stearns 1976).

When it comes to women, age is much more critical to offspring fitness, with females having to

trade off fertility (which usually peaks at around the age of 20, although this varies with respect to accelerated life histories) and reproductive value (which includes social resources, and the crucial ability to generate and sustain networks of allo-parenting) (Walker et al. 2006). In general, earlier menarche, age at first sex, age at first pregnancy, and shorter inter-birth intervals tend to cluster together, along with indicators of fast life history strategy such as lower birth weights, absent fathers, and increased birth complication risks (Nettle et al. 2011).

Conclusion

Although life history models do effectively predict and describe human parental age decisions, the picture is complicated by a set of interlocking factors surrounding the unique human capacity for social competition through coalition formation (Geary and Flinn 2001). Future research needs to be aware of the way these factors inter-related and are tackled in the unique niches that humans occupy.

Cross-References

- [Cooperative Breeding](#)
- [Fertility](#)
- [Life History Theory](#)
- [Parental Investment](#)
- [Reproductive Value](#)
- [Social Development](#)

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Age of Weaning in Human Evolutionary History

- [Duration of Breast Feeding in Ancestral Environments](#)

Age Perception

- [Social Categorization by Age of Faces](#)

Agency-Detection

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Synonyms

[Attribution of intentionality](#); [Identification of animated actors](#); [Mind perception](#)

Definition

The ability to identify intentional actors in the environment.

Introduction

Agency detection is an evolutionarily based psychological capacity to see an event to be motivated by an action tendency. This perception is universal among humans, and it may be widely shared among nonhuman animals. In the case of humans, however, to the source of this tendency, the agent, various mental states, including beliefs, feelings, and intentions, are readily assigned. These mental states may include dispositions of the agent, such as his or her attitudes and personality traits although cultures may differ widely in the degree to which these dispositions are prioritized. Here, we review evidence for these possibilities and argue that agency detection may be instrumental in promoting norm-abiding behaviors, including prosocial behaviors to ingroup members, and thereby in the formation of both modern religions and increasingly large societies based on them.

Agency Detection Is Adaptive

Personal agency implies an intention to act in some way toward objects, both real and imagined. Agency involves a behavioral tendency based on beliefs about the objects as well as feelings toward them. The experience of agency is fundamental to psychological functioning and well-being. Agency detection is the attribution of similar qualities of action to others. Being able to understand that what happens to us is in part the consequence of other agents' thoughts and feelings, as well as their action tendencies based on such thoughts and feelings, is a prerequisite for all meaningful responses to them and hence the basis of social interaction in general. These other agents do not necessarily have to be other humans. They could also be non-animals or even inanimate objects. Many researchers argued that humans are hypersensitive agency detectors, meaning that they are biased to overattribute intentional action as the cause of a current and ambiguous event. This hypersensitive agency detection tendency has sometimes been explained in terms of higher costs of failing to notice potentially dangerous

agents, relative to false alarms, during the ancestral past. Attributing intentions to others involves two mutually reinforcing steps. In the first step, the hypersensitive agency detection tendency recognizes an action tendency. The second step consists of attributing mental states such as beliefs, desires, and intentions to the source of the action tendency, the agent. This second step involves the capacity for mentalization (i.e., theory of mind). Both steps are thought to have evolutionary origins.

Agency Detection as an Early Step of Social Inferences

Many animals may be assumed to possess at least some rudimentary agency detection device for the abovementioned reason: They would be helpless victims of others without. For instance, escaping away from an attacking predator requires a perception of its action tendency. Such flight reactions may be brought about by automatic perception-behavior links and involve mainly subcortical structures. It may be safe to hypothesize that most animals detect action tendencies. These tendencies detected, in turn, inform subsequent coping actions.

However, in the case of higher primates, especially humans, the second step of mental state ascription may play prominent roles. This second step of agency detection serves more flexible regulation of social behaviors. Humans infer others' subjective mental states, such as their beliefs, intentions, and emotions to accommodate their actions to those of others. The capacity of inferring such mental states, called theory of mind, is crucial for both social coordination and cooperation.

This capacity comes into play even when seeing movement of geometrical figures. In their classic study, Heider and Simmel (1944) asked their participants to describe the movements of three geometrical figures (a square, a triangle, and a circle) in a video clip. The participants described the figures as though they were humans acting intentionally (e.g., "The big triangle is chasing the small one"). Thus, it is evident that

humans are highly primed not only to detect action tendencies in non-animate figures but also to ascribe mental states to them. This study is one of the first to demonstrate that once an intentionally behaving agent has been detected, people move beyond the initial detection of agency and ascribe mental states to the agent (although it is clear to everybody that squares or triangles do not have any mental experience at all).

The second step of agency detection (ascription of mental states to an agent or simply mentalization) is most prominent in humans and possibly unique to them. Indeed, there is reason to hypothesize that the human brain evolved to support this mental capacity. The neocortex ratio, i.e., the volume of the neocortex (the gray matter) to the volume of the entire brain, is much larger for humans than for any other known species. This big brain is remarkably costly: It makes up for only about 2% of the body weight yet consumes roughly 20% of the energy intake. So, there must be benefits of this costly big brain; otherwise, it would not have evolved. According to the “social brain hypothesis,” one of the central payoffs of that big brain comes from the fact that humans evolved *to be* social beings. Generally speaking the human brain evolved in order to increase the chances that the body that it inhabits will survive and produce offspring. For both purposes (surviving and breeding offspring), forming relatively large groups of individuals is conducive. Living in larger groups of people who share and exchange information and functional practices and pass them on from one generation to the next is such an evolutionary advantage. It provides protection against predators and allows the execution of larger joint tasks. Hence, from this perspective we may hypothesize that humans evolved to be social and cultural beings. Yet, the complexity of life in larger groups of individuals requires much more social coordination and cooperation, and accordingly, the mental devices that make this regulation possible may have evolved to be highly elaborated and efficient.

Consistent with this line of argumentation, Dunbar (1992) showed that across primate species the neocortex ratio correlates with the typical group size that these animals live in. The larger

the groups they form, the more mental capacity for social regulation is required which is reflected in the accordingly larger neocortex ratio. Mentalization plays an important role in this concern. Of course, the capacity of mentalization is only one of multiple mental tools that enable this social regulation and facilitates coordination in larger groups.

Universal vs. Culture-Specific Aspects of Social Inferences

It is important to note that the mental states that are ascribed to the agency detected may or may not be dispositional. Cultures vary in the tacit beliefs about the nature of “person” or the self (Markus and Kitayama 1991). In Western cultures, including North American cultures and West-European cultures, there is a belief in the independence of the self. The self is thought to be defined by a set of internal attributes, such as personality traits and attitudes. With this cognitive schema in mind, people may explain another person’s behavior by focusing on the most salient aspect of him or her, namely, the person’s traits and attitudes. In contrast, in many cultures outside of the West, there is a pervasive belief of the self as interdependent. The self is thought to be embedded in significant social relations, and as a consequence, it is defined by relational features, such as social expectations, roles, duties, and obligations. With this alternate cognitive schema in mind, people in non-Western cultures may explain the seemingly identical behavior of another person, not by his or her internal attributes, but instead by situational forces that impinge on him or her, such as social roles and expectations.

The cultural analysis above implies that, although people in all cultures infer mental states when having detected agency, the precise nature of the mental states that are inferred may show cultural variation. In Western societies, these mental states are likely to be dispositional. Hence, it may be quite common that people refer to another person’s personality traits and attitudes. However, the mental states that are inferred do not have to be dispositional. They can be cognitions,

perceptions, and beliefs regarding the surrounding, as seen from the agent's point of view. Indeed, in non-Western cultures, the mental states inferred during agency detection may be related more to the agent's perception of his or her surroundings. The agent may therefore be seen to have perceived social expectations, or norms, or to have been obligated or pressured to act the way he does.

To investigate the degree of dispositional inference, we may start by simply asking participants to explain another person's behavior. An early study finds that European Americans explain the other's behavior by referring to his or her traits and attitudes. But Indians refer primarily to social roles, duties, and obligations in doing so. Subsequent studies have used a similar paradigm and found that the weight of dispositional (vs. situational) causes is higher for Westerners than for people in non-Western cultures, including East Asians, South Asians, and Arabs.

Another way to investigate dispositional inference is to have participants observe another person's behavior and infer attitudes of this person. The question is whether the attitudes inferred would correspond to the behavior. If observers have an independent schema of the person or the self, then they may perceive the other person's behavior to have been caused by a trait or attitude that corresponds to the behavior. However, if they have an interdependent schema, they may be more attuned to situational forces, especially when such forces are salient. Under such conditions, the tendency to infer the corresponding attitude or traits may be attenuated.

In a classic series of experiments, American participants were provided with a brief essay expressing either a pro or con attitude on a political issue of the time. The participants then inferred what the author's real attitude on the issue would be. Not surprisingly, individuals who read a pro essay attributed a more favorable attitude to the author than those who read a con article. What is surprising is the tenaciousness of this effect. The inferences of the attitude that corresponded to the essay content occurred even when participants were explicitly told that the essay writer was requested to express the particular position expressed in it. It therefore appears

that participants were insufficiently attentive or cognizant of the social pressure that supposedly existed. Hence, the effect observed was considered a psychological bias. The claim was that people are primed strongly to infer dispositions of another person even in the presence of social pressures on him or her.

However, within this original experimental scenario, it is evident that the essay writer chose to comply with the request. Hence, it would seem reasonable to infer a degree of willingness the writer had to write the essay. This consideration might be especially relevant since the essays used in the original series of studies did include some arguments, which may have augmented the impression that the writer was willing to write the essays. Thus, the original series of studies did show robust correspondent inferences, but it is not all that clear whether these inferences would constitute any psychological bias. To mitigate this possibility, in some subsequent studies, participants were shown a video of another person who was merely reading an essay written by someone else. Even under these conditions, the correspondent inferences persisted.

Furthermore, within the original series of studies on the topic, the social pressure was described in a brief paragraph embedded in the experimental instructions. Hence, the social pressure may not have been psychologically salient enough. To address this possibility, researchers asked their participants to pose a social constraint on another person and then to judge the attitude of this other person. Specifically, the participants were to directly ask another person to state one position or another on certain topics and then to infer the real attitude the person would have on the topics. The researchers found a persistent tendency to infer the attitude corresponding to the attitude expressed. In short, at least in Western cultural contexts, the inference of another person's attitude that corresponds to his or her action seems quite strong to the point in which it is excessive. That is, this tendency may represent a genuine psychological bias.

Will this bias, called the correspondence bias, generalize to cultures outside of the West? If people in non-Western cultures believe the person or

the self to be interdependent with the surroundings, they may be sensitized to situational constraints as a determinant of behavior. If so, the correspondence bias may not be as robust as it demonstrably is in Western cultural contexts. Initial effort testing this possibility used the original attitude inference paradigm and did not provide support to this expectation. Remember, however, in the original attitude inference paradigm, it must have been very easy to dismiss the situational constraint (a request by someone) since, after all, the target person had agreed to comply with the request. Moreover, the situational constraint was embedded in experimental instructions and thus supposedly lacking in cognitive salience. Further, the essay contained substantive arguments, again suggesting that the target person willingly wrote the essay. What if dismissing the situational constraint were made more difficult?

One study examined this possibility by having participants actually experience the situational constraint (i.e., being asked to write an essay in support of a given political position). Without this experience, both Americans and East Asians inferred the same degree of corresponding attitudes. Even with the added procedure designed to make the situational constraint salience, Americans continued to make correspondent inferences. For Koreans, however, this effect was substantially attenuated under this condition. In another study, participants were asked to request a target person to read a pre-prepared essay written by someone else. Afterward, they inferred the real attitude of the target while watching the person reading the essay. As may be expected from prior work in the USA, Americans continued to show a reliable correspondence bias. Under this condition, however, Japanese showed no correspondence bias. In yet another experiment, Miyamoto and Kitayama (2002) prepared two kinds of essays. One was a standard essay that was typically used in this literature. As noted above, the essay was composed of several arguments that were reasonable. Another was a much-abbreviated version of the essay that was both short and devoid of any substantive argument. Consistent with prior American findings, American participants in the Miyamoto and

Kitayama (2002) studies continued to show a reliable correspondence bias even in the abbreviated essay condition. In contrast, but consistent with the prior cross-cultural evidence reviewed here, Japanese participants showed no correspondence bias in the abbreviated essay condition.

One theory of the correspondence bias holds that when observing another person's behavior, people infer an attitude corresponding to the behavior *automatically* (Gilbert and Malone 1995). This spontaneously inferred attitude becomes an initial anchor for subsequent reasoning. Thus, only later do they attend to situational factors and take them into account. The prominent correspondence bias evident among Americans can be explained by assuming that the situational adjustment is often secondary, more deliberate or optional, and thus insufficient. Thus, the initial anchor is not sufficiently adjusted by the situational constraint. Applying this anchoring-and-adjustment theory to the cross-cultural evidence reviewed above, one can argue that regardless of cultures, people automatically infer the agent's attitude that corresponds to the observed behavior. However, Asians may know that situations have powerful influences very well and thus mindful of making due adjustment of the effect of situational forces as long as these forces are salient enough.

One crucial basis for the anchoring and adjustment theory of the correspondence bias comes from the phenomenon of spontaneous trait inferences. It has been repeatedly shown at least in European American samples that when behaviors are presented within a memory paradigm (so that there is no explicit demand to infer any attitudes from the behaviors), people automatically infer attitudes corresponding to the observed behaviors. If the anchoring-and-adjustment theory of the correspondence bias should apply to East Asians, the phenomenon of spontaneous trait inference ought to be as strong among East Asians as among European Americans.

Na and Kitayama (2011) tested this prediction. They ran a memory task first, in which participants were to memorize many pairs of both a face and a behavior. Later, under the guise of an intervening task before the memory test, participants were asked to perform a lexical judgment

task. In this task, a number of words and non-words were shown one at a time. The participants judged whether each sequence of letters was an English word or not. The words used in the lexical traits were either the traits corresponding to the behaviors included in the memory test or their antonyms. Importantly, as a fixation, one of the faces used in the memory test was used. Thus, on some trials, one of the faces was shown, followed by a trait that corresponded to the behavior that had been paired to the face during the memory test. On some other trials, the face was followed by an antonym of the corresponding trait. On yet other trials, the face was followed by nonwords.

Imagine that during the memory test, people automatically infer a trait from a behavior shown and associate the trait to the face that is paired with the behavior. Then, during the lexical judgment task, the face should activate this trait, which may facilitate the speed of the lexical judgment. This is exactly what Na and Kitayama found for European Americans. This demonstrates that the spontaneous trait inference is quite robust. Moreover, the trait that is spontaneously inferred is also spontaneously bound to the face of the person who performed the behavior. The facilitation of lexical judgment by paired faces, however, was negligible for East Asians, indicating that spontaneous trait inference is very fragile at best among them. This study shows that the assumption that trait inference is automatic and obligatory regardless of culture is likely to be invalid. The cultural variation in the correspondence bias seems to go more deeply than the anchoring-and-adjustment theory would suggest. It may be the case that initial inferences of attitudes or traits that correspond to observed behaviors are automatic among those engaging in European American cultures, but they are not among those engaging in East Asian cultures.

We should hasten to add that East Asians will, and surely can, infer attitudes when they intend to. Moreover, they may adjust their inferred attitudes more fully by attending to situational constraints than European Americans do. However, the assumption that the initial inference of corresponding attitudes or traits is automatic and obligatory is likely to be incorrect, contrary to the

anchoring-and-adjustment theory of correspondence bias. Moreover, it is important to underscore another important point. That is, the correspondence bias is often weak or negligible, especially when situational constraints are made salient for East Asians. This conclusion, however, does not mean that East Asians are not thinking about anything. On the contrary, East Asians are likely to infer situational constraints as experienced by the target, thereby drawing inferences about their beliefs and perceptions about the impinging social situation from the target's point of view. It is these inferences about the target person's mental state that make it hard for them to draw dispositional inferences that correspond directly to the observed behaviors.

Agency Detection Is a Crucial Factor for the Emergence of Religious Intuitions

The great majority of people worldwide believe in some kind of supernatural being or god, despite the lack of any objective evidence for it. Many cognitive theorists (e.g., Norenzayan et al. 2016) have argued that the belief in supernatural beings arose as a nonadaptive by-product of ordinary and adaptive cognitive functions, including mentalization (in concert with teleological thinking and mind-body dualism). Mentalization (as the second step involved in agency detection) does not only allow individuals to infer the minds of others, but it also supplies the cognitive foundation for assuming the existence of supernatural agents, such as gods or spirits. Believers tend to treat gods as humanlike others and ascribe certain traits to them (e.g., "God is a good father"), or mental states such as intentions (e.g., "God wants us to treat each other as brothers and sisters"), or feelings (e.g., "God is angry if we do not follow his rules"), etc. They may also believe that they actually interact with God who is thought to respond to their prayers. In fact, consistent with the account of religious intuitions as by-product, studies with Christian participants have shown that during prayers the same brain regions are active that are also associated with theory of mind. In addition, reduced mentalization capacity

has been shown to coincide with reduced belief in God. In sum, there is strong supportive evidence for the proposition that religious intuitions arose as a by-product of adaptive mental capacities which partly relate to agency detection.

The tendency to see intentional beings may also provide a default explanation for many otherwise inexplicable natural incidents. For instance, it is easy to see thunderstorms to have been caused by a furious god. All cultures seem to have developed similar ideas independently of each other and given different names to the god they invented. It is called Thor in Germanic mythology, for example. It has been suggested that, by inventing an intentional explanation for otherwise random, and uncontrollable, natural events, people take solace in an illusory sense of being able to control the events by, for example, begging their god for his mercy. Accordingly, this tendency should be particularly strong when natural explanations are lacking and when the motivation to explain unfolding events is strong.

There is evidence for this proposition. First, the belief in God may be more strongly held by people who are deprived of control. Evidence is consistent. When the sense of personal control is lowered experimentally, there is a boost in the belief of religious deities. Second, the emotion of awe is based on a recognition of something overwhelmingly bigger than life. It therefore makes one feel much smaller, lacking in personal control, in the presence of the awe-inducing events. This induced sense of uncertainty in personal control may be linked to increases in religiosity. Building on this reasoning, Vandesolo and Graham (2014) tested whether the feeling of awe induced by overwhelming natural sceneries may increase religiosity. The researchers presented their participants with either (i) awe-inducing video clips taken from BBC's *Planet Earth* to their experimental participants or (ii) positive or neutral videos that were not awe inducing. In comparison to those in the control condition, participants in the awe condition reported increased intolerance of uncertainty, as well as increased belief that the universe is controlled by supernatural agency and increased religiosity.

Furthermore, the impact of awe on the belief in supernatural agency was statistically mediated by uncertainty tolerance.

The mechanisms that we reported so far may also explain the emergence of religious intuitions. Norenzayan et al. (2016), however, moved beyond the religion as cognitive by-product account, arguing that religion (in particular the belief in a punitive, monitoring God) played an important role in the cultural evolution of modern large-scale societies. Once supernatural beings are perceived, they may have an additional function of inducing an uncanny sense of "being watched," which in turn may increase norm-congruous behaviors, including prosocial behaviors to ingroup members. Evidence is strong that incidental exposure to eyes of others or even stimulus configuration that can be interpreted as such (e.g., three dots arranged in a reversed triangular shape) is sufficient to increase prosocial behavior. Evidence for the link between the sense of being watched by a supernatural agent and norm compliance can be found very early in socialization. Piazza et al. (2011) had young children between the age of 5 and 9 perform a challenging task: They had to throw a ball several times at a target from some distance, with their nondominant hand, while looking away from the target. The task was difficult. But it was possible to cheat. For example, they may come closer to the target, they may look back and see the target, or they may even use their dominant hand. Moreover, the children were tempted for cheating since they anticipated a little gift when one of the balls stuck at the target. Unbeknownst to the children, however, they were videotaped. Within this setting, the researchers introduced an invisible person named "Princess Alice," who was alleged to be sitting on a chair in the room watching the children perform the throwing task. Half of the children received this instruction and the remaining half did not. As may be expected, the children in the Princess Alice condition cheated less than those in the control condition. Furthermore, children's expressed belief in the existence of Princess Alice significantly predicted the reduction in their cheating behavior.

Conclusion

Agency detection refers to the inference that observed events in the environment are being caused by intentionally acting others. First, an action tendency is recognized, and then second, mental states such as beliefs, feelings, and intentions are ascribed to the agent that is detected. These mental processes are supposedly adaptive in an evolutionary sense, and moreover, especially in the case of humans, they provided a basis for the perception of supernatural agency in natural, supposedly completely random events. Evidence shows that this perception is motivated in part by a desire to find control over natural, otherwise, random events. Of importance, the perception of supernatural agency, and religion, may have been instrumental in promoting norm-abiding behaviors, including prosocial behaviors to ingroup members, thereby contributing to increased efficiency in social coordination and cooperation. The putative evolutionary force operating to make the inference possible over the course of primate evolution is consistent with the social brain hypothesis, which holds that primate brains evolved in order to facilitate social life in larger groups.

While the process of agency detection is likely universal, it does take culturally variable forms. For a long time, it is commonly assumed in the case of humans that agency detection necessarily entails the perception of dispositions such as personality traits and attitudes when another person's behavior is observed. At the first glance, this psychological bias, variously called the fundamental attribution error and the correspondence bias, may appear a direct consequence of agency detection. Indeed, this bias is both pervasive and robust among Westerners. However, it is elusive among non-Westerners. Evidence suggests that people in Asia, Arab regions, and Latin regions tend to see mental states of another person from the person's perspective. Thus, the mental states that are inferred relate to the person's perception of social expectations and norms, rather than his or her intentions, goals, or attitudes. Thus, the fundamental attribution error appears to be a

culture-specific manifestation of the universal tendency of agency detection.

Altogether, agency detection is an evolutionarily prepared psychological capacity that likely increased the chances of survival and reproduction in the ancestral past. This capacity is enbrained, with its manifestations heavily dependent on cultures. Over the last 10,000 years of human evolution, it likely provided a crucial basis for religion and religious movements, which in turn played key roles in promoting increasingly large modern societies. As a feature of the social brain, agency detection is an important piece of completing a full understanding of human evolution, culture, and socio-cultural and biological adaptation.

Cross-References

► Social Brain Hypothesis

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Age-Related Reproductive Potential

- Children Have Greater Reproductive Value than Sibs
-

Aggregation

- Grouping and Predation
-

Aggression

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Synonyms

Assault; Attack; Hostility; Violence; War

Definition

Aggression generally refers to the intended harming or targeted injury of one organism by another.

Introduction

Among humans and other animals, there exists a variety of behaviors by which individuals try to impose costs on other individuals. Male walruses fight for dominance, lions hunt for prey, a man smashes a mosquito, a woman poisons her abusive husband, etc. Given this variety of aggressive behaviors, aggression is sometimes defined in broad, abstract terms (e.g., the targeted infliction of disorder on one organism by another; Tooby and Cosmides 2010). Sometimes aggression is defined in more specific terms to demarcate a subset of aggressive behaviors (e.g., using the

term indirect aggression for inflicting harm via the manipulation of other people or gossip). Researchers in biology, psychology, anthropology, sociology, public health, psychiatry, and political science have worked to document and understand aggressive behavior. Below is an overview of some of this research with a focus on human aggression. The overview follows Tinbergen's four questions and thus discusses why aggression might have evolved, how aggression might have evolved in humans, how aggression develops over the human life course, and how the psychological mechanisms that regulate aggression work.

Why Has Aggression Evolved?

The short answer to why aggressive behaviors have evolved is that aggression sometimes pays off; sometimes the benefits of violence are greater than the costs. Survival machines that would be more likely to aggress in those circumstances, in which it is likely to yield resources relevant for survival and reproduction, would reproduce more than those that would not aggress in those situations. Over successive generations, such aggressive survival machines would become more numerous because of natural selection (Dawkins 2006). Of course, there are different resources that allow organisms to reproduce, such as food, safe places to sleep, safety of offspring, high social status, or mating opportunities. In general, organisms might use aggression for two distinct goals: organisms can use aggression to remove obstacles to their fitness (e.g., humans might remove snakes from their homes), and they can use aggression as bargaining power (e.g., a stronger man might bargain with a weaker man for a larger than equal share of some resource; Tooby and Cosmides 2010). The costs and benefits of aggressive behavior depend on the resource at stake and the features of the organisms involved. The aggressive hunting behavior of lions (in which a lion and its prey are in a contest over the use of the prey's meat) has probably evolved for slightly different reasons than the aggressive intrasexual competition among male walruses (in which two male

walruses are in a contest over opportunities to mate with certain female walruses).

Some of the adaptive problems relevant to human aggression have been illuminated by theorizing about rational agents. The logic of the costs and benefits of violence is rather complex when aggression occurs between rational agents (Pinker 2002, 2011). In the seventeenth century, Thomas Hobbes described three incentives for violence: competition, diffidence (fear or distrust), and glory (honor or credibility). When there is competition over some resource, the agents will invade (aggress) for gain. When there is distrust among the agents, they will invade for safety. Because of the incentive for credibility, the agents will invade for reputation. Hobbes noted that these three incentives explained why humans might fight over resources like wives and cattle, why they might fight to defend these resources, and why they might fight over insults and other signs of undervalue.

To understand why agents might aggress for reputation, consider how the three incentives are connected: survival machines that obtain more reproductively relevant resources outcompete others. Therefore, survival machines have reason to suspect that others will want to take their resources (e.g., by theft or murder). This sets of a vicious circle. Because each agent has reasons to distrust the other, they both have a reason to attack first, to strike preemptively. This vicious circle is called the Hobbesian trap of the security dilemma. There is a solution to this security dilemma: deterrence or having a credible policy of retaliation. Such a policy can consist of (1) refraining from preemptive attacks, (2) being strong enough to survive an attack by the other, and (3) being strong enough to retaliate in kind. Because this policy involves retaliation, it imposes costs on the attacker and so removes the incentive for the other (the attacker) to invade for gain. Furthermore, because this policy involves being strong enough to survive an attack and retaliate, it removes the incentive for the other to invade because of distrust (because the other no longer has to fear being the target of a preemptive attack). Note that deterrence only works when the policy of retaliation is credible.

If one agent doubts that the other is able to retaliate, the agent has reason to suspect a preemptive attack, which sets off the vicious circle. To remove any doubt that one is able to retaliate, the agent could strive to respond to each sign of undervalue – however slight – with retaliation. Hobbes also described another solution to the security dilemma: the Leviathan, a bystander that punishes any use of aggression. Because the agent can expect to be punished when using aggression, there is no longer an incentive to invade for gain. This removes the incentive to invade for safety, which in turn removes the incentive to invade for reputation.

This theorizing about rational agents suggests that humans might have evolved aggressive traits to manage distinct adaptive problems (gaining resources, defense, and reputation). Possible additional adaptive problems for which humans might have evolved aggressive traits are inflicting costs on intrasexual rivals, negotiating dominance hierarchies, deterring mates from sexual infidelity, reducing resource expenditure on unrelated children, and gaining otherwise inaccessible mating opportunities (Buss and Shackelford 1997). Furthermore, recent research has argued that certain aggressive traits may have evolved by sexual selection, meaning that certain aggressive behaviors might have evolved specifically because individuals of the opposite sex perceive these behaviors as attractive (Archer 2009a).

How Has Human Aggression Evolved?

Aggression is ubiquitous among animals, but it also comes in many varieties. This precludes a simple account of the phylogeny of aggression in humans or how aggression has evolved in humans. Many aggressive behaviors (predation, intrasexual competition) are present in many mammal species and might be traced to aggressive behaviors in common ancestors of these species. Other aggressive behaviors that are prevalent among humans, such as war (aggression between two or more multi-individual coalitions), are not common among mammals (Tooby and Cosmides 1988).

A key question regarding the phylogeny of aggression in humans is whether a particular aggressive trait is a homologue of a similar trait in another species (the traits in the two species evolved from a single trait in a common ancestor) or is an analogue of a similar trait in another species (the traits in the two species evolved independently). There have been multiple studies with animals showing that aggressive behaviors (e.g., hunting, defense of territory) are based on some cost-benefit analysis. In species that are phylogenetically distant, such resemblances in the aggressive traits are likely analogous structures (Archer 2009b).

Some violent traits in humans might be homologues of traits observed in other primate species. For example, a particular aggressive trait observed in both humans and chimpanzees might have evolved from a trait present in the common ancestor of both species. However, there is considerable debate about what kind of aggressive behaviors were the characteristic for the common ancestor of humans, chimps, and bonobos (e.g., Boehm 2012).

Although it might appear that humans have evolved few specifically aggressive features – in contrast to deer with antlers and lions with sharp canines, the human body has few features that appear to be exclusively for harming others – this does not mean that ancestral humans were peaceful. A gruesome form of aggression – cannibalism – seems to have been practiced by ancestral humans (Fernández-Jalvo et al. 1999). Substantial research in archeology and anthropology has explored to what extent warfare has occurred over human evolution. Given that uncertainties are greater when interpreting older archeological findings and when extrapolating from current hunter-gatherer tribes to increasingly ancient times, exactly how much warfare there was among ancestral humans remains a topic of debate.

How Does Human Aggression Develop Over the Life Course?

As humans appear to have evolved few or no conspicuous aggressive organs such as antlers,

the development of aggression in humans is not linked to the growth of particular organs. However, humans do seem to reliably develop motivations for aggression.

Recent research suggests the following developmental trajectory of physical aggression in humans: infants develop physically aggressive behaviors such as hitting and biting before the age of two. The frequency of such aggression increases till about the age of three. After that, the frequency of physical aggression decreases (Alink et al. 2006). In addition, it seems that men and women develop to be violent in different ways. Various forms of physical aggression (e.g., fist fights) are more common among men than among women, whereas indirect forms of aggression (gossip, social exclusion) seem more common among women than among men (Archer 2004). Notwithstanding the general pattern that humans of both sexes seem to become less violent as they get older, there is evidence that certain forms of high-risk violence such as homicide are most prevalent among young adult men (e.g., Wilson and Daly 1985).

As alluded to in the discussion of why aggression evolved, it is unlikely that natural selection has evolved indiscriminate aggressive behaviors. That is, over the course of human evolution, there has likely been a selection for being aggressive in those situations where it yields benefits. This implies that humans likely have evolved to develop contingent aggressive behaviors and to regulate their aggression based on some cost-benefit analysis. (Even very aggressive individuals are not aggressive all the time toward all others.) Hence, the development of aggressive behaviors might be influenced by factors that affect the development of psychological mechanisms involved in the cost-benefit analysis or in behavioral inhibition. This reasoning might help explain why certain individual difference variables (e.g., psychopathy, self-control) or environmental variables (e.g., having a mother who smoked during pregnancy) are associated with increased aggression.

Clearly, aggression varies across human societies. So it seems that in some cultures, people grow up to be more aggressive (or differently

aggressive) than in other cultures. Evolutionary-minded researchers have studied cross-cultural variation in aggression. Some research suggest that variables related to mating strategies influence the development of aggression. For example, data from foraging societies in the standard cross-cultural sample shows that warfare within societies correlates positively with the proportion of polygyny (Marlowe 2003). Another finding is that homicide rates across the states of the USA correlate positively with teenage birth rates, a variable indicative of a fast reproductive strategy (Hackman and Hruschka 2013).

Of course, various forms of learning are involved in the development of aggressive behaviors. But it makes little sense to talk about human aggression in general being either innate or learned (Pinker 2002). Humans evolved capacities to learn certain things more quickly than others, and some forms of aggression (e.g., smashing a mosquito biting your arm) require less or different learning than other forms of aggression (e.g., bullying, armed combat).

How Do the Psychological Mechanisms That Regulate Aggression Work?

Several commonsense explanations or folk-psychological theories of “how aggression works” have intuitive appeal. It might feel as if a series of insults creates some kind of aggressive pressure that will reduce when you retaliate. This implies a hydraulic or pneumatic model of aggression (i.e., describing aggression regulation mechanisms as resembling pumps, communicating vessels, or other devices involving a liquid or gas-like substance under pressure). A prediction of such a hydraulic model is that expressing aggression (catharsis, “letting the anger out”) should reduce aggression. However, there is not much evidence that catharsis reduces aggression (Bushman 2002). Another commonsense notion is that perceiving violence makes people violent. Although learning certainly influences aggression, researchers have argued that it is time to discard general learning models that assume that aggression is an automatic and maladaptive

response to perceiving violence (Ferguson and Dyck 2012).

There are different ways to describe how aggression regulation mechanisms work. An information-processing perspective suggests that aggression regulation mechanisms work like other cognitive systems, using fast and frugal “if-then” heuristics (e.g., Todd and Gigerenzer 2007). As humans can engage in aggression for various reasons (e.g., predation, dominance, revenge, jealousy, sadism), there are probably multiple information-processing mechanisms involved in regulating aggressive behavior, each involving specific heuristics and each implemented in particular neurological pathways. Thus, in terms of information processing, each of the aggression regulation mechanisms consists of if-then rules that convert specific inputs into outputs. As alluded to above, the inputs might consist of specific cues about the costs and benefits of aggression.

Other ways to describe aggression regulation mechanisms involve identifying the common physiological or psychological antecedents, for example, the hormones, neural activity, emotions, or beliefs that are associated with aggression. For example, aggression has been associated with low serotonin (Duke et al. 2013), high testosterone (Dabbs and Morris 1990), and consumption of certain psychoactive substances (e.g., alcohol, cocaine; Boles and Miotto 2003). However, aggression is not produced by a single hormone or neurotransmitter. Research in neuroscience has yielded diverse descriptions of the brain systems underlying aggressive behaviors. Such research typically distinguishes two or more complex neural systems, e.g., systems for affective aggression, predatory aggression, and defensive aggression (Adams 2006; Blair 2004).

Several emotions have been related to aggressive behaviors: anger (Sell et al. 2009), hate (Sell 2013), revenge (McCullough et al. 2013), and jealousy (Harris 2003). Although research of non-human animals suggests that fear (or fear-like affective states) is involved in defensive aggression, there has been little research of fear-motivated aggression in humans. The recalibration theory of anger proposed by Sell

et al. illustrates that current research aims to explain aggressive behaviors as being the product of regulatory mechanisms. In short, this theory proposes that anger is a negotiation tactic to bargain for better treatment. For anger to be successful as a negotiation tactic, it should correlate with having a better bargaining position. The research by Sell et al. suggests that some of the mechanisms that regulate aggression are influenced by cues of having a good bargaining position: their data showed that among men, physical strength was a predictor of anger and aggression, whereas among women physical attractiveness was a predictor of anger and aggression.

Aggression has also been related to the phenomena of dehumanization and anthropomorphizing. Humans seem to be able to decrease and increase their attributions of humanlike traits such as intentions and suffering to animals (including humans) and nonanimals (Brandt and Reyna 2011). In general, humans might be less prone to aggress toward entities that are perceived as relatively humanlike (e.g., your pet cat or dog) and more prone to aggress toward entities that are perceived as less humanlike (e.g., a fish, a human who committed a heinous crime; Bastian et al. 2013).

Conclusion

Aggression is part of human life: conflict, rape, violence, and weapons are human universals. As all behaviors, aggressive behaviors are amenable to the four kinds of explanations outlined by Tinbergen (ultimate function, phylogeny, development, proximate mechanism). Human aggression has been studied in various disciplines, with each discipline focusing on particular kinds of aggression. There is no unified or general psychological model of human aggression. One way to organize various forms of human aggression is to distinguish aggressive behaviors based on the identities of the victim and the perpetrator (e.g., parent-child, male–female; Campbell 2005). The challenge for evolutionary psychologists is to continue to use insights of related disciplines to build better explanations of the various forms of human aggression.

Cross-References

- Attractiveness and Anger-Proneness
- Boys Physical Bullying
- Bullying
- Contexts for Men's Aggression Against Men
- Culture of Honor
- Culture of Honor and Individual Differences
- Decline of Violence
- Derogation of Promiscuity
- Dominant Acts Expressed (Buss 1981)
- Employment Status
- Girls Psychological Bullying
- Humans: Within-Group Conflicts
- Individuals that Impose Costs
- Living in Groups
- Marital Status
- Nonhuman Primates: Within-Group Conflicts
- Procedures for Dealing with Bullies
- Same-Sex School Bullying
- Self-Assessment of Fighting Ability
- Sex Differences in Anger Proneness
- Sex Differences in Death by Homicide
- Sexual Coercion and Violence
- Sexual Jealousy
- Strength and Anger-Proneness
- Verbal Derogation

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A

Aggression for Sexual Access

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Synonyms

[Sexual aggression](#); [Sexual coercion](#); [Rape](#)

Definition

Aggression that is used to gain access to sexual activity to which one of the participants does not consent.

Introduction

This article describes evolutionary psychological (EP) perspectives on aggression that is used to gain access to sexual activity to which one of the participants does not consent. Rape is one of the extreme forms of sexual aggression, and it will be focused on primarily in the discussion here.

EP perspectives seek to identify ultimate causes of behavior, complementing the focus on proximate causes characteristic of other psychological theorizing. In addressing ultimate causation, evolutionary psychologists have often asked whether the ability to inflict sexual aggression, and/or to avoid being a victim of it, contributed to reproductive success in our species' ancestral history, possibly giving rise to dedicated psychological mechanisms pertaining to coercive sex. Although addressing such questions is standard in EP theorizing, some critics have raised concerns that this might imply that sexual aggression is "natural" in the sense of inevitable or morally neutral, an implication the authors clearly wish to avoid (i.e., the naturalistic fallacy).

Sexual Aggression in Other Species

Relevant to EP theories of aggression for sexual access is evidence of sexual aggression in other species. In fact, physical force, harassment, and other intimidation to obtain sex have been reported in many species. Based on a review of the literature on forced copulation among non-humans, Lalumière et al. (2005) identified specific characteristics in those species that exhibit sexual coercion. Across all nonhuman species in which forced copulation has been observed, it is always perpetrated by males on females. Despite the tendency of females in some species to be assertive in the mating process, these authors could not find one instance of a female forcing sex on a male. Further, males are more likely to target fertile than infertile females for forced copulation. Relatedly, forced copulation does occasionally result in insemination, fertilization, and offspring. Also, males of most species tend not to engage solely in coercive sexual behaviors. In fact, most males who engage in forced copulation sometimes, at other times, court females. Finally, Lalumière et al. (2005) recognized the role of individual differences in sexual aggression. Certain males are more likely than others to engage in forced copulation. Some males are more successful at sexual aggression than others. Lalumière et al. conclude that sexual aggression (particularly in

the form of forced copulation) "...is a tactic used by some males under some conditions to increase reproduction" (p. 59).

A particularly interesting species is the orangutan, one of the few nonhuman primates for which sexual coercion is common. There is evidence for two distinct classes of orangutan males: large males and small males. Small males are relatively unsuccessful in obtaining sex with females via courtship. Although both types resort to forced copulations, they are more often perpetrated by small males, who force more than 80% of their total copulations at some orangutan sites, although only about half or fewer of their copulations are forced at other sites, suggesting the role of environmental contingencies such as population density and sex ratio (Knott 2009).

The evidence from orangutans can be contrasted with other similar species in which forced copulation has not been reported, such as bonobos and common chimpanzees. This suggests the importance of factors such as the isolated social system unique to orangutans among the apes (see Smuts 1995, for analyses emphasizing the importance of female coalitions as a deterrent for male sexual aggression across various primate species and potential implications for humans). Chimpanzee males have been found to harass and intimidate females, however, which can increase future sexual access to the target. For example, long-term data from a study of wild chimpanzees showed that a female's willingness to initiate copulation with a male is positively correlated with how frequently the male has been aggressive toward her, suggesting that female mate preferences are constrained by sexual coercion (Muller et al. 2011). A related study (Muller et al. 2007) found that male chimpanzees achieved more matings with females toward whom they were more aggressive and directed more aggression toward more fecund females.

Frequency of Sexual Aggression in Humans

Another issue relevant to an evolutionary-based model of aggression for sexual access is its

frequency in human history, because regularly occurring events are more likely to have a “...logic embedded in the dynamics of natural selection for reproductive success” (Wrangham and Peterson 1996, p. 138). Sexual coercion does appear to have occurred throughout human history (e.g., Chagnon 1994), and as discussed below, as with other species it is the case that among humans, males are much more likely than females to use aggression for sexual access. Cross-cultural surveys reveal that male sexual aggression occurs in most societies today. Moreover, even relatively rape-free societies described in such surveys (e.g., Sanday 1981) have social rules intended to counter male sexual aggression, suggesting that there is universal risk for such behavior.

Data suggest that particularly when fear of punishment is reduced, signaling conditions in which the costs of sexual coercion are low or the perpetrator has anonymity, many men do rape, such as in times of war. At least one-third of men admit some likelihood of sexual coercion if they could be assured that they would not suffer negative consequences (e.g., Malamuth 1989). In addition, sexually coercive fantasies are common among men. In one study 54% of college men “fantasized about forcing a woman to have sex” (Greendlinger and Byrne 1987). Similarly, 33% of a community sample of men sometimes or frequently fantasized a scene “where you rape a woman” (Crèpault and Couture 1980). Imagined sexual aggression is a key predictor of actual sexual aggression (e.g., Knight and Sims-Knight 2003). Imagined aggression may reveal important information about evolved mental mechanisms.

Sex Differences

The EP paradigm considers clues to motivational differences between men and women that may have a bearing on the potential occurrence of aggression for sexual access. Differences in minimal parental investment contribute to a greater likelihood that a man will be motivated to have sex with certain women than vice versa and that, for men, sex may be more easily separated from

emotions associated with long-term mating. Such differences create conflicts that can result in some men using coercion to overcome female reluctance and resistance. Consistent with the predictions derived from parental investment theory, as well as with the evidence from non-human species, is the finding that across various societies and recorded human history there are large sex differences in the use of sexual coercion. Males are typically the perpetrators, and females are disproportionately the victims. For example, an estimated 19.3% of American women have been raped during their lifetime versus an estimated 1.7% of men (Breiding et al. 2014). For female rape victims, an estimated 99% had only male perpetrators; 79% of male victims also had only male perpetrators. If one examines criminal statistics, the sex differences are huge. The US Bureau of Justice Statistics has reported that 99% of those imprisoned for rape were men (Greenfeld 1997). Although there are cultural differences in the frequency of sexual aggression, large sex differences are found even in the most egalitarian and low general violence nations (e.g., Krähe et al. 2014).

Overview of EP Models

Symons (1979) first discussed extensively whether rape is produced by adaptations or by-products of adaptations. Adaptations are naturally selected (i.e., they resulted in increased ancestral reproductive success). Criteria for establishing adaptation within evolutionary science include attributes of economy, efficiency, complexity, precision, reliability of development, and functionality in solving a specific problem. By-products are incidental characteristics that did not evolve because they solved adaptive problems. For example, male nipples, which have no design functionality, are by-products of the adaptive value of nipples (Symons 1979).

Symons (1979) concluded that the available data are insufficient to presume that rape is a facultative adaptation in humans. Rather, rape may be a by-product of male adaptations that produce sexual arousal and adaptations that

motivate coercion to secure desired goods. This model, in that it places the propensity to sexually aggress within a larger framework of aggressive tendencies that describes a propensity for antisocial behavior in general, is an example of what has been somewhat similarly referred to in the criminology literature as a “generalist model” (see amplification below). Later EP models of rape have extended Symons’s proposal to include rape as a by-product of both sexual desire and a generalized possessiveness or desire to control others or as a manifestation of an alternative strategy, for example, psychopathy, whereby rape is a by-product of the use of coercion in other areas (Mealey 1995). All of these essentially argue that those individuals who are relatively prone to use aggressive tactics in many circumstances will also use them to gain sexual access but that there are not specialized mechanisms that evolved for using coercive tactics to gain sexual access.

The contrasting model is one that suggests that there are specialized evolved mechanisms pertaining to rape. This type of model corresponds to some degree to the “specialist model” in the criminological literature. In EP theorizing, Thornhill and Palmer (2000) have advanced this model in proposing that there may be various specialized adaptive mechanisms designed to address fundamental problems of sexual access, including decision rules designed to (a) evaluate female vulnerability to rape, essentially by identifying scenarios in which potential reproductive benefits of aggression for sexual access would have exceeded potential costs (e.g., injury or social ostracism); (b) identify cues associated with fertility (e.g., age, ovulation status), so that the most fertile women could be preferentially targeted; (c) optimize sperm counts produced during rape; (d) motivate rape under conditions of sperm competition; (e) motivate rape in men who lack sexual access to females (the “mate deprivation” hypothesis); and (f) produce sexual arousal specific to opportunities of rape. These theories of adaptation as they relate to sexual aggression have been further elaborated and expanded upon elsewhere (e.g., Camilleri and Stiver 2014). This article will evaluate theory and data specially pertaining to sexual arousal specific to forced

sex, explaining how such an adaptive decision rule might be selectively constituted.

The adaptation hypothesis suggests that, in ancestral environments, being sexually coercive under some circumstances (and, particularly for women, having the capacity to avoid being sexual coerced) contributed to reproductive success sufficiently frequently to have resulted in some change in the evolved psychological architecture that would not have occurred without the recurring fitness consequences of sexual coercion. Therefore, this hypothesis posits specific psychological mechanisms pertaining to sexual aggression. Such specialized mechanisms might include reactions such as emotions or arousal patterns that, in the proximate environment, mediate between relevant environmental cues and behaviors.

Although the topic of this article is aggression for sexual access, it is important to note that it is actually more likely that specialized mechanisms for avoiding sexual aggression evolved in women than that specialized mechanisms for engaging in aggression for sexual access evolved in men. Underlying this assertion is the idea that the reproductive costs to ancestral women of losing the ability to choose among mating partners due to sexual aggression would have been greater than the reproductive increase to men of, at times, using coercive sex. In the past few years, this topic of female counter-adaptation to the risk of male sexual aggression has been an area of emphasis of EP rape research. The authors have explored this research in more detail elsewhere (Huppin and Malamuth 2016).

Data Pertaining to the Generalist Versus Specialist Models

As outlined above, two schools of thought have developed: “generalist” and “specialist” theories of sexual offending. Generalist models suggest that the propensity of offenders to sexually aggress can be explained by a broad-spectrum tendency toward unwarranted aggression. Research on convicted rapists has to some degree been supportive of this perspective. Most

convicted rapists are generalists vis-à-vis antisocial behavior. They have a history of nonsexual offenses, their criminal records often resemble those of other offenders, and on most measures of antisocial traits and behaviors, convicted rapists are comparable to other types of violent criminals (Lalumière et al. 2005). These men engage in various antisocial acts because they differ from other men not necessarily on some specific mechanism for sexual aggression but on mechanisms underlying general antisocial behaviors. They may be more likely to steal or to use coercion for obtaining any desired goal.

Although similarities between sexual and nonsexual offenders are substantial (e.g., Fanniff et al. 2016; juvenile sexual and nonsexual offenders show equivalent general recidivism rates over a 7-year follow-up), generalist explanations of male sexual aggression still paint an incomplete picture. A meta-analysis of 59 studies comparing male adolescent sex and non-sex offenders, for instance, did not support the notion that adolescent sexual offending can be parsimoniously explained by generalist theories of sexual aggression (Seto et al. 2012; see also Fanniff et al. 2016; juvenile sex offenders show higher sexual recidivism rates than other offenders, although this rate was low). Findings such as this suggest the need to consider “specialist” models of sexual aggression or at least to supplement contributors to general delinquency (e.g., lack of inhibitory self-control, high impulsivity, low empathy, and/or callousness) with risk factors specific to sexual aggression (e.g., sexual arousal to violence, hostile masculinity, impersonal sexual attitudes) in a combined model (Lussier and Cale 2016). From an EP “specialized mechanism” perspective, the question is not whether sexual coercion is a better strategy for males than engaging in consensual sex but whether for some ancestral males, under some circumstances, it may have been reproductively effective to use aggression for sexual access as compared to not using it. In other words, did recurrent ancestral conditions exist under which for some men, some of the time, an overall fitness increase resulted from sexual aggression? Although the hypothesis that sexual aggression contributed to reproductive success has been

criticized on grounds that rape rarely leads to conception, Gottschall and Gottschall (2003) estimated pregnancy rates resulting from penile-vaginal rape among women of reproductive age to be twice that of consensual per-incident rates (6.4% to 3.1%). Controlling for age, rape pregnancy rates per incident remained 2% higher than consensual rates (see also Holmes et al. 1996, indicating a rape-related pregnancy rate of 5.0% per rape or 6.0% per victim in a national sample of reproductive age women; for indirect corroboration, see Beirne et al. 2011, in a sample of 105 normally ovulating sexual assault victims, identifying “a trend and a distinct rise in the number of assaults when the victims were in the middle of their cycle” [p. 315], that is to say at peak fertility).

Another factor to think about when considering the potential fitness outcomes of sexual coercion is the fact that a substantial minority of women continue to have sex with the men who sexually assault them (Koss 1988). This is particularly true of completed sexual assault, pointing to the use of sexual coercion as a tactic to secure subsequent copulations. Illustratively, Ellis et al. (2009) identified more than two thousand North American undergraduate women who reported having been sexually assaulted, dividing victims into two groups: assault blocked (59.4%) and assault completed (40.6%; i.e., sexual intercourse occurred). A sizable number of women in both groups indicated future intercourse at least one time with the assailter, with more women in the assault-completed group (27.2%) than in the assault-blocked group (19.4%) reporting this outcome. Overall, these results indicate that “at least a minority of men may have evolved tendencies to use assaultive tactics to secure mating opportunities beyond those obtained by men who only employ ‘voluntary’ tactics” (p. 461) (see also Wilson and Durrenberger 1982; 39% of rape victims had another date with their assailters, compared to 12% of victims of attempted rape).

Relatedly, in Holmes et al.’s (1996) study, 41.2% of rape-related pregnancy cases involved repeated assaults, one of which was assumed to have resulted in the pregnancy. Although the data are unclear about what percentage of these women

endured multiple assaults from a single perpetrator (indicating only that for these victims, rape-related pregnancy occurred in a context of ongoing abuse), it does point to the possibility that sexual coercion may have increased the likelihood of future copulations with the victim.

Sexual Arousal to Force

One hypothesized candidate for a specialized psychological mechanism motivating aggression for sexual access that has received focused attention is sexual arousal specific to forced sex, referred to here as *sexual arousal to force* (SAF). Such arousal may be a manifestation of a broader category of sexual arousal generated by controlling or dominating women, which can be accomplished by the use of force.

Using an adaptation model, R. Thornhill and Thornhill (1992) discussed SAF and argued that higher sexual arousal to coercive sex among men should be associated with greater success with coercive sexual tactics, thereby contributing to ancestral reproductive fitness under some circumstances. They noted that given the costs of forced mating in ancestral environments, including possible loss of status or life, men might be expected *not* to have evolved preferences for forced sex and, therefore, *not* to evidence SAF. If, however, under some recurrent ancestral environments, the reproductive benefits of forced mating outweighed the costs, psychological mechanisms enabling sexual arousal despite a woman's lack of consent may have evolved. Harris, Rice, Hilton, Lalumière, and Quinsey's (2007) selectionist hypothesis of psychopathy provides an example of a model suggesting that SAF could reflect a design feature of a rape adaptation. This hypothesis asks: "Do psychopaths respond more to sexual stimuli depicting violence, coercion, and rape simply because they are indifferent to the suffering of others, or does psychopathy entail a mechanism promoting coercive sex?" (p. 20). Harris et al. (2007) suggest that sexual aggression could be a fundamental feature of psychopathy.

Hagen (2004) argues that specialized mechanisms pertaining to rape would not be expected

unless the problems involved in "successfully" committing such an act in ancestral environments were not the same problems as with the use of aggression in other contexts. The occurrence of sexual arousal in the context of coercive acts may be an important distinguishing characteristic. For most aggressive acts, sexual arousal would be irrelevant or even detrimental. Because the preferred sexual strategy for most men in most circumstances is to pursue consensual sex, the most common calibration of sexual arousal mechanisms should be to become sexually inhibited by indications of lack of sexual receptivity by women. However, if an individual were to effectively sexually aggress in ancestral environments, such behavior may have required reversing of the default arousal pattern. This may be hypothesized as a unique adaptive problem associated with sexual coercion as contrasted with the use of coercion in nonsexual contexts.

In evaluating empirical data, the next section relies on studies that measure SAF (often by direct genital measures), and it suggests that studies using related measures, such as reported dominance as a motive for sex and rape fantasies, assess closely related constructs that are also relevant to the present analysis.

Proposed Evolved Function of Sexual Arousal to Force

Within some ancestral circumstances, the inhibition or activation of sexual arousal in response to cues associated with using force might have affected the likelihood of successfully dominating and exerting sexual control over an unwilling woman. Some emotions motivate avoidance of particular stimuli, whereas others motivate approaching or pursuing particular stimuli. Just as fear of spiders motivates avoidance of specific threats, sexual arousal cued to the use of force may motivate sexual aggression. This hypothesis is supported by the meta-analysis of Allen et al. (2000), which documented that sexual arousal is associated with positive psychological affect, a precursor of approach or pursuit.

This hypothesis that sexual arousal cued to the use of force may serve as an approach emotion designed to increase the likelihood of engaging in sexually coercive behavior may be contrasted with non-evolutionary hypotheses of SAF. For example, Marshall and Fernandez (2000) hypothesized that SAF is not designed to facilitate sexual coercion but instead that the causal connection is in the opposite direction. Marshall and Fernandez argue that SAF and other forms of “deviant” sexual arousal are the result of repeated sexual offending. This model suggests that, because the offender lacks the requisite social skills and confidence to engage in consensual sex, he uses coercive tactics repeatedly, eventually resulting in the conditioning of SAF. Other hypotheses have also conceptualized such arousal as an abnormality that is likely to be evidenced by a small percentage of men.

An evolutionary-based model uniquely suggests that, due to calibrating mechanisms grounded in the consequences in ancestral environments, a substantial percentage of “normal” men evidence the sexual arousal pattern that facilitates sexual coercion. How might such calibration occur? In keeping with the proposition that humans share a common evolved psychology that enables relevant developmental experiences to “set” mechanisms at different levels, the model we outline here (labeled the *evolutionary functional* [EF] model) emphasizes some relevant perceived negative experiences with women that may set the sexual arousal versus sexual inhibition to force mechanism more in one direction or the other. Although full testing of such a process would require a longitudinal study that would be difficult to conduct, it may be possible to prime similar processes to create a *state condition* related to the *trait condition*. Yates et al. (1984) found that college men who were insulted by a woman were more sexually aroused by rape portrayals as compared to portrayals of consensual sex. Creating general arousal by physiological exercise instead of an insult by a woman did not result in a similar increase.

Other relevant findings pertain to the trait rather than the state of anger and hostility toward women. These studies indicate that men who are

hostile to women, typically on measures that include items referring to perceived rejection from women, show relatively high SAF as contrasted with men who are relatively low on such measures of hostility toward women. For example, many studies focusing on the *confluence model of sexual aggression* (Malamuth and Hald 2017) have found a strong connection between measures of individual differences in men’s hostility toward women and their SAF or similar constructs such as dominance as a motive for sex and men’s rape fantasies. Other studies examining differences between behaviorally sexually non-aggressive men and sexual aggressors (some of whom are likely to have the relevant calibration of increased SAF) have found similar results (e.g., Murnen et al. 2002). Several priming studies have revealed that sexually aggressive men may be more prone to automatically associate women with hostility, sex, and power (e.g., Leibold and McConnell 2004). Barbaree (1990) reported a study with a rapist who was asked to imagine raping women for whom he held different emotional feelings. He found that the greater the hostility to the woman, the greater the sexual arousal to rape cues. Forbes et al. (2004) found that the key component linking various measures of male dominance ideology (e.g., attitudes supporting aggression or sexism) to aggression against women is hostility toward women. Baumeister et al. (2002) have summarized many studies indicating that experiencing rejection by women, particularly by men who are relatively narcissistic, contributes to sexually aggressive behavior. Taken together, these findings provide some support for the hypothesis that perceived blocked access to desired women and associated hostility toward women may affect the calibration of men’s sexual arousal patterns in ways that could affect the likelihood of committing sexually coercive acts.

How might a mechanism of SAF operate to affect the likelihood of committing sexually coercive acts? Consider a simple distinction between two types of men: one for whom the best prospects involve mating only with a consenting partner and the other a man whose prospects could be augmented by using sexual aggression.

(A more dimensional conceptualization would be preferable here but a simple dichotomy is used to facilitate explication.) If one were to design a psychological mechanism that provided the best decision rule (for total ancestral fitness) for each of these men, what might be its properties? For the first man, there would be sensitivity to cues when a sexually desired female indicated disinterest, disgust, or other negative responses. This would be an effective mechanism for inhibiting approach tendencies where persisting in sex with an unwilling female would have high costs compared to pursuing consensual sex with alternative mating prospects. However, for the second type of individual, it could have been ancestrally adaptive to have this inhibiting mechanism disengaged. Potentially, for this latter type, there may even have been fitness benefits to increased SAF relative to consenting sex because engaging in coercion may require relatively greater persistence and energy to overcome the resistance of an unwilling partner. Consistent with this hypothesis, Bernat et al. (1999) found that the penile tumescence of self-identified sexually aggressive men who also held callous sexual beliefs increased when force was introduced into a sexual scenario (see also Lawing et al. 2010; finding that adolescent sexual offenders high in callous/unemotional traits showed more sexualized aggression and had a greater number of victims than other adolescents with a sex offense).

This analysis suggests that type 1 men should show inhibited SAF, whereas type 2 men should show at least equal sexual arousal to consensual and coercive sex (i.e., the shutting off of the inhibiting mechanism) or even greater arousal to some types of coercive sex (the activation of a mechanism creating greater sexual arousal). The distinction between two types of men bears some similarity to the distinction between large and small orangutans insofar as that distinction may serve as a useful illustration of how differently situated individuals may respond based on their unique developmental and current circumstances. In summary, if there were ancestral conditions in which, for some men, some of the time, there was an overall fitness increase resulting from sexual coercion, then for these men it may

have been important not to be inhibited by cues of a woman's unwillingness and to potentially be sexually aroused by dominating and controlling the victim.

Specialization and Coercive Potential

How might one select two groups of men for comparison purposes to correspond to the hypothesized two types? Previous researchers have compared convicted rapists to other men. Because most convicted rapists seem to be relatively more generalists, this is not the ideal comparison, however. The data indicate that it is among non-criminals, particularly those drawn from college populations, that specialization may be most evident. In such general community samples, men who self-identify as having committed sexual coercion show more evidence for "specialization" rather than relatively generalized antisocial characteristics. Ronis et al. (2010) found that self-identified sexually coercive community men exceeded incarcerated rapists on diverse measures of sexual and paraphilic fantasies, including sadism, sexual preoccupation, and bondage. Self-identified sexual coercers among criminals who had not been convicted of sexual crimes also showed higher scores on such sexual and paraphilic fantasy than convicted rapists, suggesting that, even among criminals, self-identification might be a better way to identify specialists for sexual aggression than only considering the crime for which the person was convicted. Overall, these data support the conclusion that most of those currently identified by the judicial system and convicted of acts of sexual aggression display less evidence of specialized psychological mechanisms than other self-identified sexually coercive men. However, caution is necessary in interpreting the data provided by convicted rapists, who might seek to portray a positive image because of the belief that this will increase their likelihood of being paroled.

Researchers focusing on noncriminal samples have seldom addressed whether sexually aggressive men engage in other forms of antisocial behavior. The authors conducted analyses

focusing on this issue in our longitudinal database of close to 150 men (for a discussion see Huppin and Malamuth 2016). Several measures were administered to the same men at about 20 years old (Time 1) and then again 10 years later (Time 2). Measures assessing SAF and other characteristics and behaviors showed a pattern supporting specialization. Other findings provide corroboration for such a specialized mechanism (for a discussion see Huppin and Malamuth 2016). Malamuth and Impett (1999) conducted a series of mediational analyses to directly test the hypothesis that high SAF is a specific mediator of forced sex. They found evidence supporting SAF as a specific mediator of coercive sexual behavior.

Malamuth and Hald (2017) recently reviewed a large number of studies, primarily with non-criminal samples pertaining to the “Confluence Mediational Model” (CMM) of sexual aggression. This model incorporates both “generalist” mechanisms and “specialized” mechanisms. The research provided a great deal of support for this model.

Conclusion

EP theory and research seek to better understand the ultimate causes and the design of evolved psychological mechanisms underlying manifest behavior. In addressing aggression for sexual access, there has been considerable focus on whether there may have been, on average, fitness consequences in recurring ancestral environments of the ability to successfully inflict sexual aggression.

The discussion in this article focusing primarily on perpetrators suggests three competing models:

1. There were no recurring fitness consequences of using sexual aggression; therefore, the mind does not include mechanisms relevant to aggression for sexual access.
2. Fitness consequences were a function of the ability to selectively use aggression in various arenas, with sexual conflict being one of many, but no specific adaptive problems existed

unique to using coercion in the sexual arena. The mind, therefore, includes mechanisms designed specifically to motivate coercion in various arenas, including but not limited to sexual aggression.

3. Because there were unique adaptive problems associated with the use of coercion in the sexual context (e.g., how to maintain an erection and subdue a victim who is fighting back), specialized mechanisms evolved that enabled the effective use of aggression for sexual access. Such specialized modules evolved because there were fitness benefits in ancestral environments specific to the selective use of sexual aggression that differed from the use of coercion in nonsexual contexts.

In seeking to identify potential candidates for specialized mechanisms, it is useful to reiterate that sexual aggression may be produced by differing motivations and antecedents. The data support the conclusions that rapists identified by the legal system are frequently generalists who commit various types of antisocial behavior and often may not reveal the activation of specialized mechanisms motivating sexual aggression. However, among convicted rapists there has also been considerable evidence of sexual arousal to force that differs from that of non-rapists. In contrast, in the general population, sexual aggressors as compared to non-aggressors, have both higher levels of general antisocial mechanisms as well as specialized mechanisms particularly relevant to gaining sexual access via aggression.

Cross-References

- [Evolution of Female Resistance](#)
- [Forced Copulation](#)
- [Rape and Dating](#)
- [Sexual Assault and Intimate Partner Violence](#)
- [Sexual Coercion as a Mechanism of Sexual Selection](#)
- [Sexual Conflict and Sex Differences in Parental Investment](#)
- [Sexual Conflict Theory](#)

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Aggressive Behavior

- Costs of Aggression
- Development of Aggression

Aggressive Behaviors

- Men Riskier, More Aggressive

Aggressive Fantasies

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Synonyms

Fantasy aggression; Fantasy violence; Violent fantasy

Definition

The imagination of actions which have the goal of causing injury to another organism

Introduction

Aggressive fantasy refers to the imagination of an act which has the goal of injuring another organism. Functionally, aggressive fantasy may serve to increase the availability of aggressive actions in response to real-world situations and to normalize such aggressive behaviors (Guerra et al. 2003;

Huesmann and Eron 1984). Furthermore, in extreme circumstances, aggressive fantasies could also serve as precursors to homicide, through homicidal ideation. If acted upon, homicide has the potential to lead to benefits such as preventing premature death, removing rivals, and gaining resources, among others (Duntley and Buss 2011).

Research on the relationship between aggressive fantasy and real-world aggression dates back more than 60 years. Initially, such research aimed to determine whether aggressive fantasy functioned as a cathartic influence, allowing an individual to displace real-world aggression, and harmlessly release any hostile impulses they may have (Mussen and Rutherford 1961). However, most subsequent research has examined aggressive fantasy as a negative influence, suggesting that fantasizing about aggression stimulates hostile impulses and increases aggressive behaviors. This shift occurred as data increasingly demonstrated that aggressive fantasy had a positive correlation with aggressive behavior. As a result, aggressive fantasy is generally conceptualized as a form of social information processing, where additional factors, such as sex, empathy, psychopathy, violence exposure, and fantasy absorption, may influence the relationship between aggressive fantasy and aggressive behavior (Dean and Malamuth 1997; Smith et al. 2009; Williams et al. 2009).

The Catharsis Hypothesis

The catharsis hypothesis states that engaging in aggressive fantasy allows an individual to harmlessly release their aggressive impulses, and effectively displace their aggression, leading to a reduction of overt aggression (Dollard et al. 1939). Some early research supported this hypothesis; a study by Feshbach (1955) found that participants displayed less aggression toward an experimenter who was rude to them if they were given the opportunity for fantasy than if they were given no opportunity for fantasy. Additionally, research also showed that, in boys who were aged 9–10, aggressive movements decreased

aggressive fantasy relative to nonaggressive movements, which suggested that enacting an aggressive goal response results in a cathartic effect, reducing future aggression and aggressive fantasy (Murray and Feshbach 1978).

Evidence Contrary to the Catharsis Hypothesis

In spite of the limited amount of support for the catharsis hypothesis, however, a preponderance of evidence suggests that aggressive fantasy does not have a cathartic effect and even leads to increases in aggression rather than a decrease. For instance, one study showed that lower-class boys were more likely to display overtly aggressive behaviors when they described an aggressive story than when they described a nonaggressive story (Mussen and Naylor 1954). Additionally, children who were assigned to watch an aggressive cartoon subsequently expressed more aggression than those who either observed a nonaggressive cartoon or did not observe a cartoon at all (Mussen and Rutherford 1961). In another experiment, frustration was induced in groups of kindergarten students, and then spontaneous fantasy behavior was either elicited or suppressed. Results showed that children who engaged in fantasy behavior behaved in a significantly more aggressive manner than kindergarteners who did not engage in fantasy play (Lockwood and Roll 1980). Finally, in another study, subjects who hit a punching bag while ruminating about someone who made them angry behaved more aggressively in a subsequent task than subjects who hit a punching bag while thinking about exercise (Bushman 2002). Thus, although the catharsis hypothesis had some limited support among early studies, the majority of research on the subject suggests that such fantasies increase, rather than decrease, real-world aggression.

Aggressive Fantasy as Social Cognition

Current research tends to conceptualize aggressive fantasy as social cognition, which functions

to normalize violent and aggressive actions, as well as further aggressive fantasies (Guerra et al. 2003). Simultaneously, aggressive fantasies are cognitively rehearsed, and over time, the availability of aggressive actions is increased in response to real-world situations (Huesmann and Eron 1984). Research supports this hypothesis; a study by Guerra and colleagues examined longitudinal data in children from first to sixth grade and found that increased exposure to violence predicted increased aggressive fantasies, normative beliefs about aggression, and aggressive behaviors. Furthermore, the strength of these relationships increased over time, suggesting that exposure to violence leads to the development of aggressive social cognitions and the imitation of violence as children get older (Guerra et al. 2003). Similarly, a study examining preschool children found that those who tended to engage in higher rates of aggressive fantasies were more likely to display antisocial and aggressive behavior, less likely to help a friend and less likely to display empathic moral sensibilities than children who did not typically engage in aggressive fantasies (Dunn and Hughes 2001). Finally, research on media exposure, including television shows, movies, and video games, shows that exposure to violent media causes increases in aggressive cognitions, aggressive behaviors, and violence (Carnagey and Anderson 2004; Huesmann and Taylor 2006).

Other Factors Affecting Aggressive Fantasy

Research has also examined potential third variables, which may influence the relationship between aggressive fantasy and aggressive behaviors. For instance, research has shown that, among young boys, having a mother who is supportive of aggression leads to a positive correlation between aggressive fantasy and aggressive behavior, while boys whose mothers disapproved of aggressive behavior had a negative correlation between aggressive fantasy and aggressive behavior (Lesser 1957). Additionally, children who are highly prone to fantasy display reduced

aggression after they watch a fantasy film, but children who are not fantasy prone display increased aggressive behavior after watching the same fantasy film. While this finding may seem counterintuitive, it is likely due to the fact that children who fantasize more often are more accustomed to fantasy than the others are, resulting in a reduced effect of the fantasy on their subsequent behaviors relative to children who do not fantasize frequently (Biblow 1973). Also, research examining deviant and aggressive sexual fantasies has found that psychopathy moderates this relationship, such that in those with high psychopathy, such fantasies are strongly associated with behaviors enacting these fantasies, but in those with low psychopathy, there is no such correlation between the fantasies and the behaviors enacting them (Williams et al. 2009). Finally, aggressive fantasy and aggressive behavior may be moderated by violence exposure, such that these variables have a strong, positive correlation at high levels of violence exposure, but no relation at low levels of violence exposure (Smith et al. 2009).

Conclusion

Research on aggressive fantasy suggests that such fantasies do not have a cathartic effect on aggression. On the contrary, current research suggests that such fantasies function as social cognitions, which serves to normalize aggressive or violent behavior, and increase aggressive cognitions and behaviors over time. However, research also suggests that several additional variables may be involved in this relationship, including parental approval, proneness to fantasy, psychopathy, media exposure, and violence exposure. Future research should continue to examine the influence of other variables on the relationship between aggressive fantasies and aggressive behaviors.

Cross-References

- [Homicide](#)
- [Imitative Aggression](#)
- [Physical Aggression](#)

- Sexual Aggression
- Social Cognition

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Aggressive Imitation

- Imitative Aggression

Aggressiveness

- Facial Width to Height Ratio and Dominance

Aging

- Life Expectancy and Reproduction
- Senescence
- Theory of Senescence

Agonistic Interactions

- Primate Dominance Hierarchies

Agonistic Support

- Feelings of Excitement and Brotherhood

Agreeableness

- ▶ Five-Factor Model

Agropastoral Cultures of Violence

- ▶ Culture of Honor and Nepotism

Agropastoral Honor Cultures

- ▶ Culture of Honor and Nepotism

Aid

- ▶ Charity

Alarm Call

- ▶ Predator Confusion Hypothesis

Alarm Call Confuses Predator

- ▶ Predator Confusion Hypothesis

Alarm Call Creates Confusion

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Synonyms

Confusion effect

Definitions

Alarm calls may signal the presence of a predator, creating confusion and reducing the threat of predation.

Introduction

Group living increases the likelihood that predators will be detected through cooperative vigilance. This social structure is particularly beneficial if individuals can alert others to potential threats as soon as these are detected. Hence, alarm calls are evident in a numerous group living species across a range of taxa including fish, birds, and mammals (e.g., Bessey and Heithaus 2013). These alarm calls may convey a range of important information such as predator type or location through varying the number or rate of calls, amending the intensity or volume of call, or generating calls that are qualitatively different (Zuberbuhler 2000). It has been suggested that those signaling the presence of a predator may be at increased risk of detection by predators. The present entry outlines the manner in which alarm calling may impact on group behavior, create confusion, and hence reduce the likelihood of predation.

Alarm Calling

A range of theories have been proposed to explain the tendency to produce alarm calls which may draw attention to the caller, delay escape, and increase the personal risk of detection and capture for the caller. In particular, these calls may deter predators, startle predators leading to the release of captured prey, encourage others to seek cover, or attract individuals to the vicinity in order to defend vulnerable group members (Goedert et al. 2014). It has been suggested that producing an alarm call may not increase the individual risk of predation. For example, calls providing an honest signal of caller quality may reduce the likelihood that the individual is targeted by predators or alarm calls may signal to the predator that it has

been detected, encouraging the predator to abandon the attack (Bergstrom and Lachmann 2001; Laiolo et al. 2007). Similarly, alarm calls may contain a range of features which reduce the conspicuousness of the signaler. Hence, calls may be difficult for predators to localize or ventriloquial (Wood et al. 2000).

Confusion

Alarm calls may also create a confusion effect which reduces the likelihood of successful attack (Cresswell 1994). This confusion may result from the number of individuals seeking cover and vocalizing or from the presence of additional predators and heterospecifics attracted by the alarm calls and increased activity (Chu 2001). Solitary prey may be quickly captured though many unsuccessful attempts are often required for predators to capture a member of a group living species. Hence, the confusion effect makes it difficult for predators to identify, track, and attack single members of a group and leads to a greater number of attacks required per kill (Curio 1976). It is of course important to consider the form and function of alarm calls separately for each prey and predator type.

For example, Belding's ground squirrels (*Spermophilus beldingi*) produce distinct alarm calls in the presence of mammalian terrestrial (multiple note trills) and avian aerial (single note whistles) predators. Squirrels producing trills are more vulnerable to terrestrial predation, and mammalian predators appear attracted to those producing these calls. Therefore, alarm calls (trills) produced in response to mammalian predators appear to be a form of kin focused protection. In contrast, aerial predators (raptors) rarely capture squirrels after an alarm call has been produced, and alarm callers are less likely than noncallers to be killed (Sherman 1985). Those most likely to produce the calls were close to the predator and further from cover. Hence, the production of single note whistles in response to aerial predators appears to reduce the likelihood of personal risk of predation.

Conclusions

In some circumstances, the increased activity among group members which follows alarm calling may confuse predators, leading to a *reduced* rather than increased threat of predation for alarm callers.

Cross-References

► Predator Confusion Hypothesis

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Alarm Callers Are Females with Greatest Genetic Representation

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Synonyms

Cooperation; Dispersal; Nepotism; Partial migration; Philopatry; Primate

Definition

Philopatry is the retention of individuals in the natal group or territory (Ekmann et al. 2001). *Kin selection* is a selective interaction between relatives that increases the fitness of the recipient at the expense of the fitness of the actor. Such behavior will be selected if the cost to the actor (c) is less than the benefit to the recipient (b) multiplied by the coefficient of relatedness (r). This can be summarized with Hamilton's law: $br > c$ (reviewed in Silk 2002). *Nepotism* is behavior between relatives through which the actor provides a benefit to the recipient regardless of any increase or decrease in the fitness of the actor (Silk 2002).

Introduction

Philopatry to and dispersal from a natal group is a critical element of any animal's life history and is driven by three primary selection pressures: kin selection, resource competition, and inbreeding avoidance (Moore 1992; Lawson Handley and Perrin 2007). Because these forces are frequently sex specific, philopatry often also follows a sex bias. In female philopatric species, females will be best represented genetically because maternal lineages continue across generations, unaffected by migration patterns.

While a combination of these selection pressures promotes a species-specific dispersal strategy, kin selection is the strongest predictor of dispersal given that relatives can only interact if neither has dispersed from a group (Moore 1992). Nepotistic behavior promotes kin selection and has been observed in a variety of mammal and bird species (reviewed in Lawson Handley and Perrin 2007). For example, in birds, offspring are offered exclusive access to food and defended from competitors (Ekmann et al. 2001).

This entry reviews the role of alarm vocalizations as nepotistic behavior in female philopatric species.

Kinship as a Determinant of Alarm Calling

Alarm calling is a prevalent antipredator behavior among many species. Males are typically better suited to defending a group against predators given their larger size and more capable adaptations (e.g., larger canines – Gould et al. 1997). Where the vocal repertoire in a species differs between male and females, males are therefore often assumed to provide the majority of protection from predators; however, the nepotistic nature of any such behavior, including selective alarm calling, has only been tested empirically in a small number of bird and mammal species (Ekmann et al. 2001).

In return, immigrant males in female philopatric groups that benefit females with anti-predator behavior are expected to be accepted and tolerated within the group. This was found not to be the case in vervet monkeys (*Chlorocebus pygerythrus*), where no sex differences in alarm calling rate were found (Baldellou and Peter Henzi 1992). Similarly, Bolt et al. (2015) found no significant difference in vocalization rates between dominant alpha males and subordinate immigrants in female philopatric ring-tailed lemurs (*Lemur catta*). Instead, male vocalization rates correlated with increased predation risk and temporal vocalization rates of other group

members, subsequently interpreted as attempts to confuse predators. This is consistent with Gould's previous study of *L. catta* at the same site in which no difference in vigilance behavior was found between sexes, nor was any relationship found between vigilance behavior and male ranking (reviewed in Gould et al. 1997).

Instead, in other female philopatric primate species, females exhibit higher rates of anti-predator behavior than males. For example, Verreaux's sifaka (*Propithecus verreauxi*) females emit alarm vocalizations in response to predators at a higher rate than males (Lewis 2005). In ring-tailed lemurs (*Lemur catta*), alpha females are the most vigilant member of the group, which is consistent with female dominance over typically immigrant males (Gould et al. 1997). Siberian jay (*Perisoreus infaustus* – Griesser and Ekman 2004) alpha females produce alarm calls at a significantly higher rate when in proximity to offspring compared to immigrant males. This behavior not only confers a nepotistic benefit but also suggests that the presence of immigrants is more costly to alpha females than alpha males, possibly because of increased competition.

Intrasexual differences also influence nepotistic alarm calling. In three female philopatric species (vervet monkeys; capuchin monkeys, *Cebus apella nigritus*; ground squirrels, *Spermophilus* spp.), females with more offspring issue alarm calls in response to predator encounters at greater rates than those with fewer offspring (reviewed in Wheeler 2008). This pattern has been attributed to variation in parental care, as females with more offspring stand to gain greater evolutionary benefit with increased offspring survival.

Conclusion

Where antipredator behavior is nepotistic, it can be considered a behavioral mechanism of kin selection and will select for a sex-biased strategy of dispersal. For example, nepotistic antipredator behavior only benefits the recipient as long as they remain in the natal group or until the actor and the recipient disperse together (parallel dispersal – Lawson Handley and Perrin 2007). Such a benefit

would be expected to delay dispersal for recipients of both sexes; however, in species with strong matrilineal hierarchies (e.g., vervet monkeys; baboons, *Papio* spp.; macaques, *Macaca* spp. – reviewed in Silk 2002), this will lead to female philopatry. For example, even where both male and female parents exhibit nepotistic behavior, only female offspring remain in the natal group. Numerous other selection pressures will drive male dispersal in addition to any altruistic trade-offs – for example, low social integration is the primary cause of male dispersal in blue monkeys (*C. mitis*). Similarly, in other taxa, certain costs will apply that lead to sex differences within parental nepotism.

While antipredator behavior is often both observable and empirically testable, nepotistic behavior is not restricted to protection from predation. Among others, selective infant care by parents (e.g., vervet monkeys) and nepotistic coalition formation to invade mixed-sex groups (e.g., gray langurs, *Presbytis entellus*) have all been identified as altruistic mechanisms of kin selection (Moore 1992). Advances in substantiating primate recognition highlight the role of reciprocal altruism outside of kin. Future behavioral research complemented by work at the genetic level will provide confirmation of the forces driving cooperative behavior and the evolution of female philopatry (Silk 2002).

Cross-References

- [Alarm Calling Predicted by Inclusive Fitness](#)
- [Females Remain with Natal Group](#)

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Alarm Calling

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Synonyms

Alert calling; Antipredator calling; Distress calling; Mobbing calling

Definition

Vocal behavior emitted in response to a threatening situation

Introduction

The term alarm calling is used to refer to an acoustically diverse group of animal vocalizations, emitted in response to some threatening event, usually a predator. Alarm calling is widespread among social animals, although most data are from primates, rodents, and birds.

Evolutionary Function

This behaviour is puzzling from an evolutionary perspective. The term is used to refer to an acoustically diverse group of animal vocalizations, emitted in response to some threatening event, usually a predator. Alarm calling is widespread among social animals, although most data are from primates, rodents, and birds. Why should an individual vocalize in the presence of a predator and hereby reveal its location and attract attention? How can such seemingly maladaptive behavior evolve?

Different non-exclusive hypotheses have been proposed to explain the evolution of this seemingly paradoxical behavior (Stephan and Zuberbühler 2016). They differ both in terms of the presumed beneficiary (selfish vs. altruistic alarm calling) and in terms of the targeted recipient (predator vs. conspecifics).

Selfish Alarm Calling

One group of hypotheses presumes that alarm calling is directly beneficial to the caller, either because it impacts on the predator or because it induces behavior in other prey that is beneficial to the caller. First, alarm calls can signal detection to a predator, the **perception advertisement hypothesis**. This strategy is particularly effective with predators that hunt by surprise and abandon hunting after detection. The hypothesis can also explain alarm calling by lone individuals and nonsocial species. Related to this is the **pursuit-deterrence hypothesis**, put forward to explain stotting behavior in ungulates, a visual alarm signal that showcases a prey's superior locomotor capacities and the futility of pursuit.

However, selfish alarm calling is not always aimed at the predator. Under the **prey manipulation hypothesis**, alarm calling functions to trigger escape behavior in other prey, which creates general pandemonium that distracts the predator and, as a consequence, increases the caller's own survival chances. Under the **cooperative defense hypothesis**, alarm calling is also aimed at other prey, but to trigger predator approaching and chasing ("mobbing"), which increases the likelihood of the caller's own survival.

Altruistic Alarm Calling

A second group of hypotheses presumes that alarm calling evolved to benefit the caller indirectly by favoring genetic relatives and other valuable group members. Under the **kin selection hypothesis**, alarm calling provides genetic advantages to a caller, which is the case if the caller is surrounded by own offspring or other closely related individuals. Following Hamilton's rule, alarm calling can evolve even if it is costly to the signaller, provided it sufficiently benefits genetic relatives. In some species, there is evidence that callers maximize their indirect fitness benefits by taking the audience into account, for instance, by alarm calling more in the presence of young and vulnerable offspring than other audiences (e.g., yellow-bellied marmots, Blumstein 2007).

Finally, costly alarm calling may also evolve if it favors a caller's reproductive success by preserving mating opportunities, the **sexual selection hypothesis**. This argument has been made for adult males in polygynous species. For example, in Diana monkeys males produce acoustically highly conspicuous alarm call that carry over long distances, much beyond what is predicted for communication to the predator or other group members, suggesting that male alarm calls operate in male-male competition and female choice. However, this is most likely a secondary evolutionary process, by which already existing alarm calls are subject to the forces of sexual selection to take on an additional function in reproduction.

Information Content

Call Production

What kind of information is encoded in animal alarm calls? Communication involves at least two partners, a signaller and a recipient, which may experience different processes. First, the **acoustic structure** of alarm calls is determined by the shape of the signaller's vocal tract, which provides recipients with reliable information about the caller's body size, age, sex, and identity (Bowling et al. 2017). In addition, psychologically relevant events often have physiological effects, such as changes in heart rate, skin temperature, or hormone levels, which create further variation in a signaller's vocal tract shape and, consequently, the acoustic quality of alarm calls, Morton's motivational-structural rules (Morton 1977). Since this process is determined by a caller's prior experience with an event, call production is also under cognitive control.

Call Comprehension

Recipients, on the other hand, may either be directly affected by the acoustic structure of alarm calls (Owren and Rendall 2001), or they have learned about the referential relations between alarm call types and events (Schlenker et al. 2016). One ongoing debate is about the nature of the mental representations, or memories, that mediate between alarm calls and events (Seyfarth et al. 2010). If an alarm call is only given to a narrow set of situations, listeners can directly infer the eliciting event, even in the absence of further cues, to the effect that the call obtains something akin to **lexical meaning**. However, most studies are unable to pin down more specifically what type of information is conveyed, such as the type, behavior, or distance of the predator, and many alarm calls are given to a range of situations that do not share clear similarities – at least from a human perspective (Dezecache and Berthet 2018). Here, listeners appear to rely on **pragmatics** to identify the event that has caused the call. A number of playback studies have tested this idea and produced

evidence that referentially broad alarm calls can obtain relatively specific meaning during a process by which listeners can associate the call to a range of possible events and then choose among the most probable one. Also, some species use social knowledge to react to others' alarm calls. For example, vervet monkeys react less strongly to alarm calls given by juveniles, possibly because they give alarm calls to wider range of disturbances than adult monkeys that only call in cases of real danger.

Call Sequences: Temporal and Morphological Structure

Alarm calls are often emitted in sequences, raising the possibility that information could be conveyed by resulting **structural** differences, such as due to variation in temporal structure. This is the case for titi monkeys that emit alarm calls more regularly in predator-related than non-predator-related sequences. In black-capped chickadees, call rate differences also exist, but here they have been linked to size differences of predators. Another relevant example is alarm call sequences in black-and-white colobus and guereza monkeys, which produce sequences of few roars when encountering leopards and many roars when encountering crowned eagles, a difference discriminated by listeners.

Second, alarm call sequences sometimes consist of different call types, which result in sequences that qualify as ordered **permutations** or unordered **combinations** (Zuberbühler [in press](#)). An example of call combinations is titi monkeys combining A and B alarm calls into sequences, whereby the proportion of B-call combinations reliably encodes predator type and location.

An example of a permutation is male Campbell's monkeys combining "krak" alarms (typically given to leopards) and "hok" alarms (typically given to eagles) with an acoustically invariable vocal unit ("oo") in cases of non-imminent danger. Recipients discriminate krak from krak-oo alarms, suggesting that -oo performs a semantic operation. The system thus resembles a common operation in human

language, **affixation**, whereby an utterance with lexical meaning is combined with a meaningless affix, to generate a derived meaning.

Another example of a permutation is male Campbell's monkey "boom" calls, produced prior to subsequent krak-oos, whenever the disturbance is non-predatory (e.g., falling tree). In playback experiments, Diana monkeys discriminated alarm sequences with and without preceding booms, suggesting that the booms altered the meaning of the sequence.

Permutations have also been found in putty-nosed monkeys. Here, males produce series of pyows to terrestrial disturbances and series of hacks to crowned eagles. In addition, males sometimes add brief combinations of several pyows, followed by several hacks. The pyow-hack transition appears to carry its own meaning, unrelated to the meaning of the constituent parts, by announcing forthcoming group movement. The pyow-hack transition hence resembles an **idiomatic** expression, i.e., the meaning of the call combination cannot be derived from the meaning of its parts, similar to English expressions such as "raining cats and dogs," i.e., raining heavily.

Compositionality

An important discussion is whether any animal call sequence qualifies as truly **compositionality** (Townsend et al. [2018](#)). Compositionality is a defining feature of human language whereby the meaning of an expression is determined by the meaning of its parts and the rule that combines them. Some of the best current examples of animal compositionality come from studies on bird alarm calls. For instance, Japanese tits possess "alert" calls that warn conspecifics about the presence of predators and "recruitment" calls that attract conspecifics in non-dangerous situations, for example, to food. When mobbing a predator, however, tits combine the two calls to "alert-recruitment" sequences, which engage nearby conspecifics into cooperative antipredator behavior. Interestingly, reversed sequences do not elicit mobbing behavior, suggesting that the system is both permutational and compositional (Zuberbühler [in press](#)).

Ontogeny and Learning

Comprehension

How do animals acquire their alarm calls? Most ontogenetic studies of alarm calls have focused on recipients, i.e., how animal learn to comprehend the meaning of alarm calls. In many species, infants appear to be born with partly innate knowledge of alarm calls. For example, newborn ground squirrels react to conspecific alarm calls by freezing or increasing vigilance. Similarly, cross-fostered dunnocks cease to beg for food when hearing conspecific, but not foster parent alarm calls. Nevertheless, their response is weaker compared to normally raised chicks, suggesting that learning plays a moderating role (Hollen and Radford 2009). In many species, however, alarm call comprehension is subject to social learning. Social learning is highly adaptive, especially in acquiring antipredator behavior, as it protects infants from committing fatal errors. For example, infant meerkats that have stayed close to adults are more likely to respond appropriately to alarm calls than other infants.

Production

Research on the ontogeny of alarm call production is more limited. Generally, learning appears to have only minor effects on the acoustic structure of alarm calls. For example, in species such as yellow-bellied marmots, great gerbils, and meerkats, juvenile and adult alarm calls are nearly identical. Partly, this may be because the acoustic structure of animal alarm calls itself has been under strong selection pressure. For example, bird raptor alarms are often difficult to localize (presumably to prevent detection), whereas monkey leopard alarms are highly conspicuous (presumably to promote dissuasion). A notable exception is the **fork-tailed drongo** that, in addition to its own species-specific alarm calls, is able to mimic other species' alarm calls, although this ability functions in deceptive foraging.

Usage

Call use, finally, appears to be more plastic, but again relatively little work has been carried out. As a basic principle, infants must learn to recognize the dangerous species, which can happen through a process of either elimination or addition. For example, young vervet monkeys begin by giving alarm calls to a broad range of stimuli, including non-predatory species (e.g., flying pigeons), albeit in a nonrandom manner: eagle alarms are produced to flying animals, leopard alarms to terrestrial species, and snake alarms to snake-like objects. This has also been demonstrated in monkeys experimentally exposed to unfamiliar threat. For example, green monkeys exposed to a drone will produce alarm calls that resemble vervet monkey eagle alarms. The inverse process has been described in infant chimpanzees that do not appear to have any pre-existing knowledge of alarm call use but learn by observing others interacting with unfamiliar threats.

Conclusion

Alarm calling is of importance to various scientific disciplines, including evolutionary theory, behavioral ecology, animal cognition, comparative linguistics, and philosophy of mind. They are relatively uncomplicated to work with and easily recognizable, due to their context specificity and unique acoustic structure. They have been essential in addressing a range of basic questions, such as the evolution of altruism, the behavioral ecology of predator-prey relations, and the evolution of animal cognition. Detailed behavioral analyses, based on naturalistic observations and experiments across a wide range of species, have produced much progress and provided a window into the animal mind and some of the basic forces that drive evolution.

Cross-References

- ▶ [Alarm Call Creates Confusion](#)
- ▶ [Alarm Callers Are Females with Greatest Genetic Representation](#)

- ▶ Alarm Calling and Kinship
- ▶ Alarm Calling Predicted by Inclusive Fitness
- ▶ Alarm Calling upon Predator Detection
- ▶ Alarm Calls
- ▶ Predator Confusion Hypothesis

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Alarm Calling and Kinship

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Synonyms

Alert call; Altruistic behavior; Kin selection; Warning call

Definition

Vocal behavior of prey animals to defend themselves and others from predation.

Introduction

Alarm calling is a widespread phenomenon in the animal kingdom, usually produced by individuals during predation attempts, a context with large fitness consequences, suggesting that the behavior has been under strong selection pressure. But there is something paradoxical about animal alarm calls. Why should an individual, faced with a potentially lethal predator, behave in conspicuous ways to warn others, rather than trying to escape or hide from the danger? This seemingly altruistic behavior has posed a major challenge for evolutionary theory and become the topic of countless studies. Two major research themes have been addressed with studies on animal alarm calls: the cognitive processes involved in call production and perception and the evolutionary forces that have shaped the behavior. The following sections review some of the current research trends in both areas.

The Cognition of Animal Alarm Calls

In many species, alarm calls seem to “stand for” something in the external world, which has raised questions about potential parallels to human language and the idea that alarm calls are useful to investigate cognitive processes underlying vocal communication. However, this line of research has remained controversial, mainly because of difficulties in describing the nature of the internal processes triggered by external events. Discussions often revolve around how “cognitive” these internal processes and psychological states are, for example, whether predatory events merely trigger specific emotions (e.g., fear) to which alarm calls are hardwired. Empirical support for this position comes from studies showing that animals sometimes give alarm calls to non-predatory situations, such as putty-nosed monkeys (*Cercopithecus nictitans*) and other primates producing “eagle” alarms to falling trees or baboon fights, as well as “terrestrial predator” alarms to a wide range of disturbing events, which include encounters with non-predators.

Also relevant is that, in many species, alarm calls show only limited acoustic flexibility. In birds, alarm call structure is often highly conserved across species, especially to aerial predators (Marler 1955). One hypothesis is that these aerial alarms have evolved to conceal the location of the signaler by limiting sound propagation and directional cues (for review, also see Marler 2004). For example, the “seet” alarms of many bird species appear to be a hardwired response to the limited auditory range of raptors, which limits the amount of information a signaler can encode in this call type.

Some other studies, however, have found more flexibility in alarm calling behavior with sometimes tight relationships between external events and corresponding signals, including event-specific differences in acoustic structure, call rates, or sequential organization of calls. For example, in several species it has been shown that not only predator type but also predator size, predator distance, and predator behavior can trigger distinct alarm call behavior, suggesting that some animals can represent external events in

complex ways and have means to communicate them to their nearby audiences. Here, a particularly interesting line of research has been to look at sequences of alarm calls. Although many primate and non-primate species have restricted vocal repertoires with rigid call structures, some species appear to have overcome this limitation by producing call sequences of different composition that are sometimes linked to specific external events. Differences in perceived urgency can also lead to different call combinations, with information about external events sometimes additionally included.

A second controversy concerning the internal states associated with animal alarm calling revolves around the question of whether animals give alarm calls with the intention to inform others. Human language appears to be built on this principle, insofar as speakers convey mental content that is directed at particular partners and largely for their benefit, after relevant judgments that can be rather complex (Sperber 1986). The alternative extreme position to this view is that callers do not understand what they communicate, but that selection has equipped them to produce specific signals in specific situations, with callers remaining oblivious to the social consequences of their behavior.

One way to address this second controversy is to study the impact of the audience on an individual’s alarm calling behavior. Although not fully clarified, results so far suggest that, in chimpanzees (*Pan troglodytes*), alarm vocalizations are not mere automatically triggered utterances but indeed represent a means to communicate the nature of a danger to others. However, there is also important negative evidence, such as female vervet monkeys (*Cercopithecus aethiops*) failing to use alarm calls to change the knowledge state of their offspring in dangerous situations. For the time being, the underpinning cognitive processes of animal alarm calling, especially its intentional nature, remain nebulous for many species, with no clear phylogenetic trends.

A third research theme centers on considerations about the other end of a communicative interaction, the cognition involved in processing alarm calls. One basic question here is whether

receivers react directly to the physical features of calls (e.g., Rendall et al. 2009) or whether this is mediated by a mental representation of the call-eliciting event, i.e., whether calls carry specific information for the recipient (Seyfarth et al. 2010). Although more research needs to be done, there is some evidence that predator alarm calls in primates elicit responses due to their referential links to external events, not because of their physical features. In primates, predator alarm calls can trigger specific anticipations in recipients, suggesting that they do more than just spreading a motivation within a group, but possibly activate a relatively specific mental representation of the predator normally associated with the alarm call.

If receivers are able to extract and encode information when hearing a call, then another question is whether they infer the same information that the signaler originally responded to and whether they take the identity of the caller into account. Here, more progress has been made, largely due to the relative ease with which receivers can be tested with field experiments. An emerging pattern is that animals typically take the identity of the caller into account, as well as the pragmatic circumstances of a call-eliciting event.

In sum, current evidence is in line with the more general hypothesis that signalers and receivers are driven by different internal states and that there is a cognitive disparity between them. Thus, unlike in human language, producing and comprehending alarm calls might be linked to different cognitive underpinnings that probably followed different evolutionary pathways but are, nonetheless, often taking place in the same individual. However, more research is needed here to address this problem more directly.

The Evolution of Animal Alarm Calling

The second major research topic with animal alarm calls concerns the question of why it is adaptive for an individual to produce conspicuous vocalizations that reveal its presence and location to a dangerous predator and, as a result, increase

predation risk. The prediction here is that alarm calling must have some beneficial effects for the caller that outweigh the obvious costs incurred; otherwise, selection would have acted against it.

Three levels of selection have been identified to explain the evolution of alarm calling, i.e., alarm calling to enhance the caller's own survival (individual selection), the survival of its relatives (kin selection), or its reproductive success (sexual selection). If a caller can accrue benefits due to one or several of these forces, then the costs of alarm calling might be outweighed, and selection will favor the behavior, according to "Hamilton's rule" (Hamilton 1963). It is important to consider that the three levels of selection are by no means mutually exclusive but represent three possible ways by which an individual can maximize its genetic contribution to future generations, as follows.

Individual Selection: Alarm Calling to Enhance Signaler Survival

Although alarm calls generally reveal a caller's location, they can have a number of secondary beneficial effects, namely, by impacting on the behavior of other animals, in ways that increase the probability to survive for the signaler. Two main mechanisms have been identified, a direct one by influencing the predator's hunting behavior ("perception advertisement" or "pursuit deterrent" hypotheses; Frankenberg 1981) and an indirect one by influencing other prey's anti-predator behavior ("prey manipulation" hypotheses; Charnov and Krebs 1975).

Perception Advertisement

Some predators rely on stealth and experience, and experience significantly reduced hunting success if prey animals are aware of their presence. Signaling perception to a predator can therefore be adaptive if the predator is likely to abandon a hunting attempt and move on to target other individuals. If alarm calls have a predator-deterring function, then the prediction is that a predator's hunting behavior must change in response to alarm calls. In one study, forest leopards, "*Panthera pardus*" were radio-tracked, and the resulting ranging data revealed that forest

leopards hunted by approaching monkey groups to hide in nearby vegetation, apparently to wait for unaware individuals to descend. Data also showed that leopards abandoned their hiding positions soon after detection by alarm calling monkeys, often additionally accompanied by approaching the predator directly.

However, most animals are hunted by a range of predator species that differ considerably in their hunting strategies, to the effect that alarm calls only work as a perception advertisement signals for some but not other predators.

The perception advertisement hypothesis therefore presupposes some relevant cognitive capacities on behalf of the prey, insofar as callers not only have to discriminate predator classes but also need knowledge about their respective hunting strategies, in order to adjust their alarm calling behavior accordingly. African forest monkeys, for example, readily produce loud alarm calls to two of their predators, leopards and crowned eagles, but remain silent to two other major predators, chimpanzees and humans, and there is evidence that the different antipredator strategies are learned. In a study on Diana monkeys, “*Cercopithecus diana*” in Taï National Park, Ivory Coast, it was shown that groups in the center of a chimpanzee territory behaved differently to the simulated presence of chimpanzees compared to groups living at the periphery of a territory (Zuberbühler 2000). Chimpanzees spend the majority of time in the core area of their territories and only occasionally venture into the peripheral parts. As a result, monkey groups in the center of a chimpanzee territory will have more experience with chimpanzee behavior than monkey groups living in the periphery. Chimpanzees also face predation pressure by leopards and, when encountering a leopard, respond with specific calls (“SOS” screams). In one experiment, chimpanzee SOS screams to leopards were broadcasted to different groups of Diana monkeys. As predicted, groups in the center of chimp territories responded more often with their own leopard alarms than groups in the periphery, who mostly responded cryptically with no signs that they could discriminate the chimpanzee SOS screams from screams given during fights with other group members.

The most likely interpretation is that peripheral Diana monkeys had fewer opportunities to observe chimpanzees responding to leopards compared to central groups and were thus mostly prevented from learning the meaning of the different chimpanzee calls.

Many animals are hunted by aerial predators and have evolved acoustically distinct alarm calls to defend themselves. For example, crowned eagles (*Stephanoaetus coronatus*) are specialized primate predators. Although they can sometimes be deterred by alarm calling monkeys, often in combination with physical attacks by adult males (KZ and CS, unpublished data), they remain extremely dangerous for monkeys, with attacks sometimes happening several times per day. Crowned eagles typically hunt by sitting and waiting in the upper forest canopy for an approaching group of monkeys. Their attacks are sudden and at short range by launching upon an individual from their perch. If unsuccessful they can engage in prolonged hunting efforts on a group of monkeys, sometimes by hunting in pairs, suggesting that callers must gain benefits other than perception advertisement when alarm calling to aerial predators.

In sum, although alarm calls can have dissuasive effects on some predators or in some situations, perception advertisement and predator deterrence cannot fully account for the evolution of animal alarm calls.

Prey “Manipulation”

A caller’s probability to survive a predation attempt can also increase if alarm calls trigger behavior in other prey animals that benefits the caller or that leads to more efficient antipredator responses. For example, if alarm calls trigger flight in others, a predator may find it more difficult to focus on the caller, who can benefit from “safety in numbers” (Bednekoff and Lima 1998) or “confusion” effects (Milinski and Heller 1978). While safety in numbers simply decreases the probability of being caught due to stochastic processes (a dilution effect), the confusion effect relates to increased capture time for a predator (and thus an increased probability to escape for prey), possibly due to a sensory overload of

chaotic movements during flights. If alarm calls trigger such movements, the caller will benefit not only from dilution but also from confusion effects.

However, alarm calls may also induce collective antipredator behavior, such as predator mobbing. This can occur if calling attracts others for a communal antipredator response, in line with the etymological origin of alarm as “all’arme” (= to arms). Alarm call-induced cooperative defense can be observed in many species (Curio 1978), but it can also occur in hetero-specific associations, for instance, between males of different guenon species living in polyspecific groups. Predators are often repelled by mobbing groups of prey animals, most likely because they are prevented from carrying out their preferred hunting strategy.

A third direct benefit of alarm calling arises if callers can provide essential learning opportunities for less experienced individuals during predator encounters, which will increase the number of reliable sentinels for future predatory events, a mechanism that has been proposed for meerkats. In one classic experiment, Curio et al. (1978) conditioned naïve blackbirds to alarm call to a harmless object by social cues alone. The main manipulation consisted of presenting a demonstrator bird with a raptor model (to elicit alarm calls) in the presence of a second naïve bird. The observer bird did not see the call-eliciting raptor but was allowed to see a novel, but harmless, model during the conspecific’s alarm response. When retested, observers responded with alarm calling to the harmless object, suggesting that blackbirds learn antipredator behavior from conspecifics by observational learning, without a need for direct predator experience.

To conclude, individuals can gain direct fitness benefits from producing alarm calls to predators in two major ways, either by directly interfering with the predator or by causing a change in the audience, which lowers the predator’s hunting success, and effects may occur simultaneously during natural hunting events.

Alarm Calling to Favor Kin

Another main explanation for the evolution of alarm calls is to interpret them as a form of

extended parental care, i.e., reproductive individuals alarm call to prevent predation on their offspring (Blumstein et al. 1997). A more general version of the same idea is that alarm calling is adaptive if this benefits other individuals with whom the caller shares a substantial proportion of its genome (Smith 1965). The kin selection hypothesis of alarm calls makes several testable predictions. Most importantly, the alarm calling behavior of an individual should be a function of the costliness of alarm calling, the benefits for listeners, and the (cumulative) relatedness between the caller and the nearby listeners, according to Hamilton’s rule. Moreover, solitary individuals should not vocalize (unless calls carry over long distances and benefit distant relatives).

Empirical support for these assumptions is surprisingly inconsistent. Female Siberian jays (*Perisoreus infaustus*) utter more alarm calls when with their own offspring compared to other conspecifics, but males give alarm calls regardless of their relatedness to other group members (Griesser and Ekman 2004). Alarm calls as form of parental care is sometimes also seen in males. For example, in blue monkeys (*Cercopithecus mitis*), the single males produced higher rates of alarm calls if their group members (including own offspring) were closer to a simulated danger than further away, regardless of the male’s own distance to the predator (Papworth et al. 2008). However, the effect was only observed for eagle not leopard-related dangers.

Evidence for an effect of non-descendant kin is generally rare. Exceptions are female Gunnison’s prairie dogs (*Cynomys gunnisoni*), calling more to terrestrial predators in the presence of non-descendent kin than other individuals, and similar effects have been reported for Belding’s ground squirrels (*Spermophilus beldingi*; Sherman 1985) in which anti-predation behavior toward terrestrial predators increased with the presence of non-descent kin, but no such effects were found to aerial predators. In contrast, Columbian ground squirrels (*Spermophilus columbianus*) showed increased anti-predation behavior in the presence of non-descent kin toward aerial predators and no effect of kinship toward terrestrial predators (Macwhirter 1992).

Inconsistent patterns for the impact of kinship on alarm calling were also found in vervet monkeys. While captive females alarm called more in the presence of kin, it was also found that higher-ranking females called more than lower-ranking females, with no correlation between rank and the presence of kin (Cheney and Seyfarth 1985).

Finally, male Thomas langurs (*Presbytis thomasi*) and yellow mongooses (*Cynictis penicillata*) do not alarm call when alone (Wich and Sterck 2003; Le Roux et al. 2008), but solitary Campbell's monkey, "Cercopithecus campbelli" males living in a polyspecific association with Diana monkeys have been observed to alarm call to predators (KZ, unpublished data).

However, kin selection may have favored other aspects of animal alarm calling, notably the evolution of individually distinct acoustic cues. In Belding's ground squirrels, alarm calls not only encode identity, but the acoustic similarity between alarms is a function of genetic similarity (McCowan and Hooper 2002). Acoustic cues of kinship may provide receivers with important information to decide whether a caller should be helped during a predation attempt.

In conclusion, genetic relatedness appears to have influenced the evolution of alarm calling, but the link between the kinship and alarm calling is often unclear, most likely due to additional factors having impacted on the evolution of alarm calling (see previous section).

Alarm Call Evolution in Relation to Sex

A third way for an individual to increase its inclusive fitness during costly alarm calling is if the behavior enhances future access to mating partners and opportunities to sire offspring. Several studies suggest that alarm calling may function in this way, but along different pathways. First, alarm calling may function in intersexual selection, such as mates (usually males) advertising their quality to choosy partners. Second, alarm calling may function in intra-sexual selection as a way to compete for access to sexual partners. Interestingly, in forest guenons, it is mainly the single adult males that engage in conspicuous alarm calling, which can be heard far beyond the group boundaries, suggesting an additional

function in male–male competition. If males differ in their ability to engage in predation defense, then females may choose group males accordingly, while their alarm calling behavior might serve as a cue for their genetic quality or physical condition. In primates, indirect evidence comes from gray-cheeked mangabeys (*Lophocebus albigena*) in which the highest-ranking males engage most actively in predator-mobbing behavior (Arlet and Isbell 2009), suggesting a link between antipredator behavior and reproductive success.

In various mammal taxa, vocal structures, such as call duration, fundamental frequency, or formant frequencies, are linked to body size and competitive strength, suggesting that female receivers should attend to these cues. For instance, female red deer hinds and female koalas attend to acoustic cues of vocalizations to infer and compare the males' physical characteristics and momentary condition (Reby et al. 2010; Charlton et al. 2012). Other evidence comes from birds (e.g., Beecher and Brenowitz 2005) and anurans (e.g., Ryan and Rand 1990). Here, differences in the variability of notes, call rate, call intensity, or call duration in calling males appear to form the basis for female mate choice.

Whether or not sexual selection has been equally at work in alarm call evolution, however, is less clear. Many species produce alarm calls in sexually dimorphic ways, both at the level of call structure and call use. For instance, male vervet monkeys and male domestic chicken are more likely to alarm call in the presence of (unrelated) adult females than other individuals, which is predicted neither by kin nor individual selection. In red jungle fowls (*Gallus gallus*), male alarm call rates and mating frequencies are correlated, although this may be the result of differences in previous mating success rather than a way to increase a male's attractiveness.

Some other relevant evidence in support of sexual selection comes from Diana monkeys, in which both sexes emit predator-specific alarms to leopards and eagles. Recent evidence has shown that males alarm call, not just to provide predator information to nearby group members and the presence to distant rivals but also to advertise to

their own females their willingness to defend the group. When confronted with contradicting predatory information (e.g., perceiving a leopard followed by own females' eagle alarm calls), males prioritize the information provided by the females and respond with eagle alarm calls, contrary to their own experience (Stephan and Zuberbühler 2016). In contrast, if females are presented with contradicting information, they ignore the male's alarm calls and only respond to the predator they have witnessed themselves. Another effect was that, as soon as a male produced alarm calls that referentially matched the females', the females stopped giving their own alarm calls. One interpretation of these findings is that, by referentially matching his alarm calls to the females', the male signaled his readiness to engage with the predator identified by the females. In this view, the females used the male's compliant behavior as kind of a "stopping rule" for own risky antipredator behavior. In sum, the study demonstrates an advanced coordination between the two sexes during predatory events, which goes beyond advertising mere physical condition and includes others' assessments of external events and signaling readiness to engage with them. One likely evolutionary scenario is that males have been under sexual selection pressure to act this way. What remains to be tested is whether this type of coordinated alarm call behavior in males indeed leads to more surviving offspring. One prediction is that compliant males are more preferred as group males, have longer tenure, and sire more offspring than males that produce alarm calls in response to their own assessment.

Overall, differences in alarm calling between females and males are a widespread and well-known phenomenon, and vocal signals have been shown to provide direct means to access mating partner quality. The Diana monkey study mentioned before suggests another way by which sexual selection could have acted on male callers, beyond providing cues linked to physical condition, in that males use alarm calls to advertise their antipredator commitment. But how exactly females choose males based on variation in their antipredator commitments is subject to further investigation. One possibility is that their tenure

as single group males is constantly at stake and that males who show decreased commitment over time will eventually be expelled and replaced by another male. Generally, polygynous systems are supposed to be especially susceptible to be targeted by sexual selection, and a sexual dimorphism in call structure and usage might give first hints on functional differences between male and female calls.

Conclusion

There is solid evidence that selection has acted in different ways on the evolution of alarm calls, contributing in various ways to the increase of an individual's inclusive fitness. What is more difficult to show is how exactly costly alarm calling enhances a caller's own survival, the survival of its kin, and its future reproducing success in different animal species. In all likelihood, selection has shaped alarm calling behavior in different ways and in a cumulative manner (Zuberbühler 2002). Predator deterrence benefits may have originally triggered the evolution of alarm calling behavior, but kin and sexual selection may have contributed additionally, in parallel with a species' social evolution. Also important is that, even within species, selection may have acted differently on different age/sex classes causing differences in alarm calling behavior, as illustrated by, e.g., sex-specific patterns of alarm calling in Diana monkeys.

In sum, studies on alarm calling behavior need to take into account how a species' ecology and social organization constrain individuals in how they can maximize their inclusive fitness. Predation is one of the most important evolutionary forces and continues to exert selection pressure on animal behavior. Across species, future studies should consider the relative potential contribution of individual, kin, and sexual selection on the evolution of alarm calling behavior.

Finally, alarm calling has long been thought as cognitively simple, the result of basic stimulus (predatory event)-response (alarm call) arithmetic. But new evidence across a range of species shows that behavioral decisions during

predation can be cognitively complex, with signalers taking contextual information into account and producing alarm calling flexibly to maximize their benefits. In primates, receivers can infer complex information from calls by integrating pragmatic cues and social variables, suggesting that alarm calling reflects a species' cognitive capacities as well as any other type of social behavior.

Cross-References

- ▶ [Alarm Call Creates Confusion](#)
- ▶ [Alarm Callers Are Females with Greatest Genetic Representation](#)
- ▶ [Alarm Calling](#)
- ▶ [Alarm Calling Predicted By Inclusive Fitness](#)
- ▶ [Alarm Calling Upon Predator Detection](#)
- ▶ [Alarm Calls](#)
- ▶ [Hamilton's Rule](#)
- ▶ [Hamilton's Rule and Kin Investment](#)
- ▶ [Hamilton's Rule and Genetic Relatedness](#)
- ▶ [Hamilton's Rule and Theoretical Implications](#)

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Alarm Calling Predicted by Inclusive Fitness

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Synonyms

[Altruistic nepotism](#); [Antipredatory behavior](#); [Kin selection](#); [Vocalization](#)

Definition

Alarm calling: vocalizations that alert other animals to immediate danger ([Sherman 1977](#)).

Inclusive fitness: a theory to explain cases when an animal behaves in such a way as to promote the advantages of other members of the species not its direct descendants at the expense of its own ([Hamilton 1963](#), p. 354).

Introduction

Alarm calling is an inherently dangerous behavior, and its adaptive function was poorly

understood for decades. Calling individuals suffer direct costs (e.g., predation), and so the ultimate function was initially described as a residual behavior thought to have evolved as a signal from parents to offspring ([Maynard-Smith 1965](#)). Subsequent theories described the behavior as individually selective. Trivers ([1971](#)) suggested that alarm calls reduce the caller's vulnerability, while calls may also reveal the predator's location ([Dawkins 1976](#)) or else promote antipredatory behavior in socially living primates. Finally, Hamilton ([1971](#)) hypothesized that announcing a predator's presence may promote aggregation by potential prey and reduce the likelihood that any one individual is killed (reviewed in [Cheney and Seyfarth 1981](#)).

A

Alarm Calling and Kinship

Across taxa, alarm call production is correlated with the probability that kin are within acoustic range ([Sherman 1977](#)); alarm callers derive inclusive fitness benefits by warning kin of danger ([Bergstrom and Lachmann 2001](#)). In female-philopatric species (where males disperse), adult females produce more calls than adult males, suggesting proximity to relatives drives alarm calling. But that may not be the most parsimonious explanation.

Subsequent investigation into Sherman's ([1977](#)) data on Belding's ground squirrels (*Urocitellus beldingi*) found that females with offspring produce more calls than males do, suggesting that rather than inclusive fitness, it was direct fitness benefits that drive the behavior.

Blumstein and colleagues ([1997](#)) later supported the idea of direct benefits as well, demonstrating that in yellow-bellied marmots (*Marmota flaviventris*), a primary predictor of female alarm calling was whether her pups had emerged from underground dens that year. The two hypotheses are not mutually exclusive. That is, as Cheney and Seyfarth ([1981](#)) noted, for a female to protect her offspring, she must also stay alive, and so alarm calling may target a broad audience to ensure the survival of multiple individuals. They found support for both

hypotheses in vervet monkeys (*Chlorocebus pygerythrus*), whereby adult females' alarm called more than adult males, but there was no relationship between calling and number of offspring or the proximity to offspring as might be expected.

A few studies have attempted to test the various hypotheses of alarm calling in primates, with similar findings. Forest guenon alarm call behavior in Tai Forest, Ivory Coast, for example, varies with predator-type (leopard vs. chimpanzee) and is thought to be evolved to deter (especially cryptic) predators that depend on surprise attacks. When the above hypotheses were tested against each other in the same species, new world tufted capuchins (*Cebus apella nigritus*) showed similar patterns. Like the guenons, the capuchins exhibited predator-specific responses as well. Thus, there is growing evidence that alarm calling to felid predators has evolved as a self-preservation behavior, while calling to predators that can be more readily mobbed (e.g., snakes) may be better explained as a kin-selected behavior.

Conclusion

Shelley and Blumstein (2005) conducted a phylogenetic analysis to investigate whether alarm calling had evolved initially as a selfish or else nepotistic (promoting inclusive fitness) behavior. Their results supported the idea that it initially evolved to communicate to predators, not to nearby kin, and thus while benefits to relatives likely contributed to the persistence of the trait in a population, it was less important than the benefits incurred by the callers themselves. In summary, results from investigations into the function of alarm calling in social animals converge on indirect benefit to group members, often kin, but also on direct benefit to the caller and their offspring.

Cross-References

- ▶ Alarm Callers Are Females with Greatest Genetic Representation
- ▶ Females Remain with Natal Group

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Alarm Calling upon Predator Detection

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Synonyms

Alarm calls warn relatives; Anti-predator vocalization; Co-efficient of genetic relatedness (r); Predator attraction; Predator deterrence hypothesis; Proximate behavior; Shared genetic material; Squirrel family *Sciuridae*; Ultimate behavior

Definition

When a predator is seen, animals from various taxa produce alarm vocalizations. In some cases,

alarm calling when a predator is nearby drives the predator away, but in other cases, the caller is pursued by the predator. Calling therefore often leads to greater risk to the vocalizer. Some rodents make anti-predator vocalizations despite this greater threat to themselves because doing so may warn their close relatives of a nearby predator. By warning relatives, they are preserving additional copies of their own genes.

Introduction

Animal species ranging from birds to mammals are well known to produce alarm calls in response to perceived threats, ranging from unknown and potentially harmful stimuli to known predators. Alarm calls vary in urgency, and some low-arousal calls are produced in response to potential dangers (e.g., an unfamiliar object or animal flying overhead), while others are produced in response to more direct dangers (e.g., a predatory bird swooping from the sky to catch prey species, then perching on a nearby branch) (Bradbury and Vehrencamp 1998). When a prey species produces an alarm call, it can be part of a mobbing response, which involves multiple conspecifics banding together to intimidate a predator and drive it away. Alarm calls can also be produced as part of an escape response, where callers vocalize while fleeing from predators (Zuberbühler et al. 1997). For both types of alarm calling situation, various hypotheses have been proposed to explain why vocalizing is an adaptive response for prey species and for individual callers within groups of prey species. Calling may drive the predator away, leading to direct benefits to the alarm caller. However, calling may also lead to the alarm caller being targeted by the predator, meaning that other explanations are useful for understanding why this behavior would persist over evolutionary time in prey species (Maynard 1965).

Alarm Caller Targeted by Predator

Animals ranging from birds to mammals make alarm calls when a predator is seen. Such alarm

calls are thought to put the vocalizer at risk by attracting the attention of predators. According to theoretical predictions (Hamilton 1964; Dawkins 1976), predators are alerted to a prey individual's presence and location by their alarm calls, which are often loud and recurrent. In the case of group-living prey animals, predators would more likely pursue a noisy individual over a silent one (Maynard 1965). Animals who vocalize in response to a threat are therefore more likely to be pursued by that predator, according to theoretical biologists (Hamilton 1964; Maynard 1965; Dawkins 1976). Although results are mixed (e.g., Cresswell 1994; Zuberbühler et al. 1997), evidence from several mammal and bird species supports the idea of callers being targeted by predators. For example, in the American pika (*Ochotona princeps*), predatory weasels were seen actively pursuing alarm callers immediately following their vocalizations (Ivins and Smith 1983). In Belding's ground squirrel (*Urocitellus beldingi*), predators including coyotes and weasels were seen chasing callers following their alarm vocalizations (Sherman 1977). For Gunnison's prairie dog (*Cynomys gunnisoni*), individuals did not alarm call if they were in very close proximity to a predator, suggesting increased risk from alarm calling (Hoogland 1996). For bell miner (*Manorina melanophrys*) bird nestlings, vocalizations of any kind increased risk of consumption by avian or rodent predators (McDonald et al. 2009). In each of these cases, vocalizing is thought to have put the prey individual at greater risk (Sherman 1977). Alarm calling is therefore not an adaptive behavior at proximate level for individuals of these species, meaning it does not enhance their personal survival. Evolutionary explanations are necessary to account for the development and persistence of anti-predator vocalizations in these animals.

Alarm calling is more obviously adaptive for species where vocalizing by an individual directly discourages predatory pursuit (Maynard 1965). Alarm calling in response to a predator's presence is advantageous if calling drives the predator away, thus decreasing the level of threat to and directly benefiting the individual who calls (Hamilton 1964). The pursuit deterrence

hypothesis (Sherman 1977) suggests that alarm calling is adaptive for the caller because it discourages predatory targeting and leads to increased survival for the caller. Vocalizations are therefore directed towards predators rather than nearby conspecifics (Wheeler 2008). Anti-predator vocalizations are the acoustic dimensions to multifaceted mobbing behaviors, which communicate to stealth predators that prey are aware of their presence (Sherman 1977; Bradbury and Vehrencamp 1998). Evidence that acoustic signaling deters an ambush predator from approaching or pursuing prey has been found in a number of taxa, ranging from birds to mammals such as ungulates and primates. For the Eurasian skylark (*Alauda arvensis*), individuals who sang when chased by predatory falcons were less likely to be caught than animals who remained silent (Cresswell 1994). For the klipspringer antelope (*Oreotragus oreotragus*), alarm calling was thought to signal predator awareness and to discourage pursuit (Tilson and Norton 1981). For primate species including Campbell's guenon (*Cercopithecus campbelli*), the sooty mangabey (*Cercocebus atys*), the Diana monkey (*Cercopithecus diana*), the lesser white-nosed monkey (*Cercopithecus petaurista*), the western black and white colobus (*Colobus polykomos*), and the western red colobus monkey (*Colobus badius*), stealth predators such as leopards stopped pursuing monkey groups that made alarm calls at high rates (Zuberbühler et al. 1997). In each of these cases, animals made alarm vocalizations in response to perceived threat, and these calls reduced their own risk of predation by driving predators away at increased rates.

Anti-predator vocalizations are highly variable in their utility to individuals (Bradbury and Vehrencamp 1998). For some species, alarm calls encourage predator pursuit and increase vulnerability to predation (e.g., Ivins and Smith 1983), while for other species, alarm calls drive predators away (e.g., Cresswell 1994). Anti-predator vocalizations are adaptive at proximate level if they directly discourage a predator from pursuing an individual but are not advantageous to the individual if calling encourages predatory pursuit (Maynard 1965; Sherman 1977). Other

hypotheses for the evolution of alarm calling should therefore be considered. If alarm calling does not lead to increased survival for the caller, evolutionary explanations involving inclusive fitness, altruism, group selection, and genetic representation in the animal's social group should also be investigated.

Alarm Callers and Genetic Representation

Prey animals from a broad range of taxa produce alarm calls in response to threats. While in some cases alarm calling has been found to discourage pursuit by stealth predators (e.g., Zuberbühler et al. 1997), for other species, alarm calling puts the individual who calls at greater risk of pursuit (Maynard 1965; Dawkins 1976; Sherman 1977). For prey species where the latter applies, theoretical models predict that alarm calling would be adaptive for individuals if calling improved the chances of survival for their relatives (Hamilton 1964; Dawkins 1976). How related an alarm caller is to a relative can be determined by the co-efficient of genetic relatedness (r), which quantifies the level of genetic relationship between any two individuals of the same species (Wright 1922; Hamilton 1964). The co-efficient reflects the probability that at any given genetic locus, genes passed down will be identical due to shared ancestry between individuals. Clones or identical twins would have a relatedness co-efficient of $r = 1$, while unrelated individuals would have a co-efficient close to $r = 0$. Clones or identical twins would therefore share 100 % of the genes found at specific loci due to inheritance from common ancestors, while unrelated individuals would share no genes found at specific loci due to shared inheritance. Amongst non-clone relatives, individuals are most closely related to their offspring, full siblings, and parents (all $r = 0.5$) and less closely related to grandparents, aunts/uncles, cousins, and half-siblings ($r = 0.25$ or less) (Wright 1922).

According to theoretical predictions by Hamilton (1964) and Maynard Smith (1965), individuals are more likely to alarm call, thus putting

themselves at greater risk of predation, in situations where doing so benefits their close relatives (i.e., offspring, siblings, and parents) by warning them of a nearby threat. Therefore, individuals would make alarm calls in dangerous situations and put themselves at increased risk because their signaling would lead to increased survival for kin, thus saving copies of the caller's own genes from predation (Dawkins 1976; Sherman 1977). Evidence supporting this idea has been found for numerous rodent species from the squirrel family (*Sciuridae*). For example, female Belding's ground squirrels (*Urocitellus beldingi*) who had relatives in their group made alarm calls at higher rates than other group members (Sherman 1977, 1981). Similarly, individual Richardson's ground squirrels (*Urocitellus richardsonii*) were most likely to alarm call when they had offspring or siblings nearby (Davis 1984). For the Eastern chipmunk (*Tamias striatus*), adult females called at higher rates when close to relatives, who were likely to live in neighboring burrows (da Silva et al. 2002). In the Alpine marmot (*Marmota marmota*), adult males who were related to most group members alarm called at higher rates than other individuals (Barash 1976). In the black-tailed prairie dog (*Cynomys ludovicianus*), individuals alarm called at higher rates when offspring, siblings, or parents lived nearby (Hoogland 1995), while in the Gunnison's prairie dog (*Cynomys gunnisoni*) females with nearby kin or offspring made anti-predator calls at the highest rates (Hoogland 1996). Despite these many examples of rodents from the squirrel family, strong evidence for the increased genetic relatedness of vocalizers to nearby conspecifics is lacking for species in other taxa, although other social mammals, such as the tufted capuchin (*Cebus apella*), have been tested (Wheeler 2008). There is clearly wide variation in how anti-predator alarm calls are functional and adaptive for each animal species. Consideration of the life history of many *Sciuridae* rodents, where close kin such as parents, offspring, and siblings (all $r = 0.5$) typically live or are located in close proximity to alarm callers, may help explain why genetic representation significantly affects alarm calling behavior in many species of this taxonomic group. For other

animal species, theoretical explanations other than genetic relatedness should be considered in addressing how alarm calling behavior is adaptive.

Conclusions

Although anti-predator vocalizations are used by prey animals across taxonomic groups, there is wide variation in how these vocalizations are employed. Alarm calls attract predator attention and put the vocalizer at increased risk in species including ground squirrels and birds but drive the predator away in prey species including antelope and monkeys (Sherman 1977; Tilson and Norton 1981; Zuberbühler et al. 1997; McDonald et al. 2009). Different explanations exist addressing why alarm calls are adaptive for each animal species. Alarm calls may function in predator deterrence or may lead to an alarm caller being targeted by a predator (Wheeler 2008). In situations where alarm calling brings additional risk, individuals may call if close kin such as offspring, siblings, or parents are nearby. By warning relatives, alarm callers from the squirrel family are thought to promote the survival of their genes as represented in their kin (Sherman 1977, 1981). However, for other animal taxa, other adaptive explanations should be considered for the persistence of risky alarm calls.

Cross-References

- [Alarm Call Creates Confusion](#)
- [Alarm Callers Are Females with Greatest Genetic Representation](#)
- [Alarm Calling](#)
- [Alarm Calling and Kinship](#)
- [Alarm Calling Predicted by Inclusive Fitness](#)
- [Alarm Calls](#)
- [Deceptive Alarm Calls](#)
- [Evolutionary Arms Race](#)
- [Genetic Relatedness Affects Aid to Kin](#)
- [Hamilton's Rule and Genetic Relatedness](#)
- [Hamilton's Rule and Kin Investment](#)
- [Prey Availability](#)

- Prey Choice
- R = Coefficient of Relatedness
- Vigilance, Sentinels, and Alarms

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Alarm Calls

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Synonyms

Alerting calls

Definition

Communication is ubiquitous in animals and involves one individual influencing the behavior of another individual through the use of signals or cues (see the ► “Communication, Cues, and Signals” entry for more information). Animals often communicate when they detect a potential predator by producing alarm signals. Although such signals can be produced via different modalities, many species rely on vocal signals – alarm calls (Bradbury and Vehrencamp 2011). Alarm calls function to alert others of the potential danger related to a perceived predator. In order for such communication to be adaptive, the benefits associated with alarm calling in the presence of a predator must be greater than the costs.

Introduction

Both the physical structures of alarm calls and the motivations behind their production are important to understanding signal function (Bradbury and Vehrencamp 2011). In birds and mammals, and possibly other groups, vocal signals that are

low-frequency and harsh are often produced by individuals behaving aggressively. Low-frequency sounds are easier to locate; animals often use calls with this structure to mob or indicate distress. Signals that are higher in frequency and that possess relatively little frequency modulation are often produced by fearful signalers. These signals are more difficult to localize and likely function as alarm calls meant primarily for receivers of the same species as the signaler. Receivers often freeze or flee when high-frequency alarm calls are produced.

When considering the adaptive functions of alarm calls, the costs and benefits of producing an alarm signal must be determined. For alarm calling to be adaptive, the benefits of signaling must outweigh the costs over time. There are several hypotheses to explain the adaptive benefits of alarm signaling (Caro 2005; Wheeler 2008). Under the *kin selection hypothesis*, an alarm signaler will risk making an alarm call and attracting the attention of the predator because the signal may increase the sender's indirect fitness by alerting and potentially saving related family members. Similarly, the *parental care hypothesis* proposes that the signaler will risk alarm calling because the signal may increase their direct fitness by alerting their own offspring. Under the *selfish herd hypothesis*, a sender produces an alarm call to attract other individuals, thus increasing the number of individuals present and thereby reducing the probability of predation for the signaler. Similarly, the *mobbing recruitment hypothesis* predicts that a signaler risks making an alarm call because it will attract others to the area to harass the predator and increase the chances that the predator leaves. The *predator confusion hypothesis* states that the signaler risks making an alarm call because it may cause a sudden burst of movement from others as they flee, which confuses the predator and reduces the threat. Lastly, with the *pursuit deterrence hypothesis*, a signaler risks sending an alarm call because the call may cause the predator to give up the hunt after it has been spotted by its prey. These hypotheses are not mutually exclusive; for example, when testing the adaptive function of alarm

calling in wild capuchins, *Cebus apella nigritus*, Wheeler (2008) found that in the presence of a predatory viper, the kin selection, parental care, and mobbing recruitment hypotheses were all supported. Capuchins, therefore, alarm call to recruit others to mob the predator but also to communicate to their offspring and related family members. The functions of alarm calls may thus differ depending on the composition of the group and the predator threat level.

Semantic Alarm Calling

Some individuals can encode specific information in their alarm calls about the type of predator, the predator threat level, or both (Gill and Bierema 2013). Semantic, or referential, alarm calls are signals that refer to specific predator types or predator behavior patterns (Seyfarth et al. 1980). In a seminal experiment, Seyfarth et al. (1980) used a playback method to test different alarm calls produced by vervet monkeys, *Cercopithecus aethiops*, in response to three different predators: leopards, eagles, and snakes. These varying alarm calls were considered referential because they were each produced by signalers in specific contexts (i.e., each was produced in relation to the specific predator detected), and the behavior of the receivers differed depending on the type of predator that elicited the alarm calls. For example, when vervet monkeys heard playbacks of leopard alarm calls, the monkeys more often ran high up into a tree, which is the adaptive behavioral response to this type of predator. Vervets produced different behavioral responses to playbacks of the eagle and snake alarm calls, revealing specificity in receiver response.

Other species may encode information into their alarm calls that indicates the threat level of the potential predator, rather than the predator type. For example, Siberian jays (*Perisoreus infaustus*) produce alarm calls when predatory hawks are detected, but the specific structure of the calls is related to whether the predator is perched (lower-risk) or attacking (high-risk; Griesser 2008). Chickadee, tit, and

titmouse species also vary the number of specific note types in their “chick-a-dee” calls in relation to the level of risk associated with different sizes of predators they have detected.

Deceptive Alarm Calling

Whereas it is typically adaptive for signalers to produce alarm calls when a predator has been detected, and for receivers to react to alarm calls appropriately, some individuals use alarm calls in non-predator contexts in deceptive ways. These false alarm calls are seen in several species. For example, great tits, *Parus major*, alarm call to deceive competitors of the same species as the signaler for food, even when there is no predator threat (Møller 1988). These deceptive calls cause surrounding individuals to be temporarily distracted and/or flee, thus allowing the deceptive signaler better access to limited food resources.

Deceptive alarm calling can occur between members of different species. For example, the fork-tailed drongo, *Dicrurus adsimilis*, is able to mimic the alarm calls of meerkats, *Suricata suricatta*, and can deceive meerkats by producing the meerkats’ own species-specific alarm call (Flower 2010). Meerkats eavesdrop on the alarm calls of drongos and thus benefit from their species-specific alarm calls. Meerkats that react to a drongo’s mimicked meerkat alarm incur the cost of abandoning found food. However, because drongos also regularly produce honest alarm calls, the meerkats benefit from using a “better safe than sorry” strategy when drongos alarm call (Flower 2010). A general view of deceptive alarm calling is that such calling persists in many systems because the costs of responding to false alarm calls (when a predator is not present) in a food context are much smaller than the costs of failing to respond appropriately to true alarm calls (when a predator is present).

Conclusion

Alarm calls are one class of vocal signaling related to anti-predator behavior (Caro 2005). Other

classes of signal used in anti-predator contexts include predator deterrence, mobbing, and distress signals. Predator deterrence signals function minimally to communicate to the predator that it has been detected, and may also provide information regarding the signaler’s condition or evasion ability. Mobbing calls function to attract members of the same and different species as the signaler to gather, harass, and deter the predator to drive it from the area. Individuals may also produce distress calls when they are physically captured or constrained by a predator, potentially to cause the predator to release the distressed individual.

Alarm calls represent an important class of animal signals in that they are strongly related to individual fitness and also because many of them seem to involve complicated cognitive processing on the part of signalers or receivers or both. For example, alarm calls falsely produced in contexts of contested resources (like food or mates) often represent cases of tactical deception and suggest signaler awareness of perceptions or knowledge of receivers. In some species, signalers vary production of alarm calls in sophisticated ways to communicate about not just predator presence but also predator behavior. Additionally, some of the most structurally complex signals in animal communication function in anti-predator behavior. One example is the already mentioned “chick-a-dee” call of black-capped chickadees and related species. Another example involves the syntax-like combination of different vocalizations in putty-nosed monkeys (*Cercopithecus nictitans*) to signal increased predator threat (Arnold and Zuberbühler 2004).

Taken together, alarm calls are an important type of vocal communication that signal about potential predator threats. While these vocalizations may draw the attention of a predator, species that utilize alarm calls do so in an adaptive way, with benefits generally outweighing the costs of signaling. There are several hypothesized functions of alarm calls, including to alert others, to recruit others, and to confuse or deter the predator. Further research can highlight the adaptive value of more nuanced aspects of alarm signaling, such

as distinctive alarm calls made by parents for their offspring compared to other adults in the immediate environment (e.g., Suzuki 2011).

Cross-References

- ▶ [Communication, Cues, and Signals](#)
- ▶ [Costly Signaling](#)
- ▶ [Deceptive Alarm Calls](#)
- ▶ [Manipulation and Dishonest Signals](#)
- ▶ [Predator Confusion Hypothesis](#)
- ▶ [Signal Reliability](#)
- ▶ [Vocal Communication](#)

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Alarm Calls Warn Relatives

- ▶ [Alarm Calling upon Predator Detection](#)

Alcohol

A

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Synonyms

Ethanol

Definition

Alcohol is a by-product of fermentation of sugar.

Introduction

When alcohol is discussed in the context of health, often it refers to consumable forms of alcohols. In this regard, ethanol is often taken up for discussion or debate. Less often methanol is also discussed in the context of health due to its toxic effects. Worldwide, ethanol is used as alcoholic beverages in social gatherings (World Health Organization 2018). When alcohol is used in harmful pattern, it results in significant health hazards. Harmful use of alcohol increases the vulnerability for many noncommunicable as well as infectious diseases. Alcohol has negative impact on maternal and child health. Alcohol attributes to many psychiatric disorders and accidents. Hence, it stands as an obstacle before the Sustainable Development Goals (World Health Organization 2018). This entry aims at giving a brief overview of alcohol with special emphasis on health and sociocultural aspects of ethanol.

Chemistry of Alcohol

Alcohol is a hydrocarbon formed by the process of hydroxylation. The first alcohol in the alcohol series is methanol (methyl alcohol), which contains single carbon atom and is denoted by the chemical formula “ CH_3OH ” (Henze and Blair

1931). Ethanol or ethyl alcohol (C_2H_5OH) is next in the series. Different names have been denoted to alcohols (propanol, butanol, pentanol, etc.) with different numbers of carbon atoms. Alcohol is a volatile, inflammable, and colorless liquid. It is a good organic solvent.

As per their structure, alcohol has been classified into primary, secondary, and tertiary alcohol (Henze and Blair 1931). There are various names used for different concentrations and mixtures of ethyl alcohol. Absolute alcohol is a concentrated form of alcohol that contains less than 1% of water and more than 99% of ethyl alcohol. A concentrated form of alcohol is prepared by the process of repeated fractional distillation, which is commonly known as “rectified spirit.” “Denatured spirit” is referred to the ethyl alcohol that is made undrinkable by adding methyl alcohol. Methanol is used in the preparation of wood paints. It is also used as fuel. There are many uses of ethanol, other than its use as alcoholic beverages; however, from the point of view of medicine, alcohol is used for preparation various medications and disinfectants. It is also used in the treatment of methanol poisoning.

Among different alcohols, ethanol is the form of alcohol that is consumable. Ethanol is commonly prepared by the process of fermentation of sugar (fructose or starch). The raw materials for production of alcohol are fruits, rice, wheat, rye, barley, and potato. The concentration of alcohol is regulated by certain chemical processes (distillation). Certain alcoholic preparations (e.g., beer) contain lower concentration of alcohol, whereas certain other preparations (e.g., rum, whisky) contain higher concentrations of alcohol.

Alcohol: Developmental Significance

From the developmental point, certain arguments were put forward by the researchers. The convincing ones are – alcohol as a component of diet (as source of calories) or alcohol as a substitute to water (Vallee 1994). Evidences support that alcohol use might be a maladaptive ancestral

strategy to meet the nutritional needs (Dudley 2000). However, certain vulnerability factors and the chemical and clinical properties of alcohol resulted in development of alcoholism as a pathological entity (Dudley 2000).

Across the life span, the onset of alcohol commonly occurs during the second to third decade of life. This period mostly refers to the phase of adolescence. Common psychological characteristic features of adolescence are novelty seeking, risk taking, and experimenting. These behaviors have attribution to initiation of alcohol use (Ellis et al. 2012). Exposure to alcohol during different developmental stages produces different anatomical and physiological changes in the brain (Klintsova et al. 2013).

History of Alcohol Use in the World

Alcoholic beverages are used worldwide. The pattern of use of alcohol across the globe depends upon several factors like availability, accessibility, affordability, and sociocultural-moral values. Use of alcohol in world history can be traced back to the ancient times irrespective of the country and culture. History of alcohol use is depicted in ancient mythological stories. The most ancient literature of the world, the *Vedas*, gives vivid description of use of alcohol and its impact on the individual vividly (Sharma et al. 2010). Description of alcohol is also mentioned in ancient civilizations India, China, Egypt, Babylon, Africa, Europe, Aztecs, and North America. Ancient literature mentions about use of alcohols during festivals, celebrations, social gatherings, as well as certain cultural rituals. In the ancient times, there was increased alcohol use in certain castes and among people of higher status. Similarly it was prohibited among certain cultures and caste (Keller 1979; Sharma et al. 2010; Unnithan 1985). In the recent times, modernization, globalization, and migration resulted in acculturation and deculturation. Also, there is easy access to alcohol. All these factors attribute to prevalence of alcohol use among socioeconomic strata and sociocultural groups.

Alcohol: Pharmacokinetics and Pharmacodynamics

Alcohol is commonly absorbed from the stomach and proximal part of small intestine. Absorption of alcohol is better in empty stomach, and peak concentration of alcohol in blood is often reached approximately after an hour of alcohol consumption. Various factors determine the rate of absorption and time taken to reach peak blood concentration. Alcohol is commonly metabolized in the liver, and a fraction of it is also metabolized in the lungs and kidney. The enzymes that metabolize alcohol are alcohol dehydrogenase and aldehyde dehydrogenase. The effect of alcohol in the central nervous system is exerted through GABA_A, serotonin, as well as cholinergic receptors (Sadock and Ruiz 2015). Alcohol in human body can be quantified by analyzing blood, breath, and urine. Estimating the blood alcohol concentration is of clinical as well as forensic significance (Jones 1996).

Alcohol: Effects on Physical Health

The alcohol use contributes to significant health hazards worldwide. Alcohol has been identified as an important cause of morbidity and mortality (Griswold et al. 2018). As per the global burden of diseases report, 3.8% of females and 12.2% of males of 15–49 years of age die due to alcohol-related health problems (Griswold et al. 2018). Evidences support the association of alcohol with more than 60 different medical disorders (Room et al. 2005). Alcohol affects all the organs of the body. Alcohol consumption in pathological pattern results in hepatic (fatty liver, alcoholic hepatitis, cirrhosis of liver, hepatic failure), pancreatic (pancreatitis), and renal damage (renal failure, hepatorenal syndrome). Alcohol has toxic effects on erythropoiesis (anemia, pancytopenia) and body immune system. Alcohol is a gastric irritant, which produces damage to gastric mucosa resulting in gastritis, nausea, vomiting, as well as acid peptic disease. Alcohol users are more likely to develop esophageal varices, portal hypertension, ascites, cerebellar degeneration,

myopathy, neuropathy, metabolic disturbances (hypoglycemia, electrolyte imbalance), testicular atrophy leading to sexual dysfunction, gynecomastia, as well as menstrual irregularities (in females using alcohol) (Association 2013; Sadock and Ruiz 2015). Alcohol can increase the risk of malignancies (hepatocellular, pancreatic, as well as gastrointestinal).

Alcohol can adversely affect the development of brain, when exposed in early life and produces neurodegeneration (Dalal and Kar 2014). Long-term exposure to alcohol results in neuroinflammation, activation of microglial system, and oxidative damage of neuronal cells (Dalal and Kar 2014). Alcohol is a central nervous system depressant. It acts through the GABAergic neurotransmitter system. During intoxication with alcohol, various neurocognitive side effects (slurring of speech, motor incoordination, ataxia, stupor, coma) are reported, which are often related to the blood alcohol concentration. Alcohol has significant cardiovascular effects. Alcohol can cause hypertension, cardiomyopathy, and cardiac failure. Alcohol produces nutritional deficiencies.

Alcohol is having fetotoxic effect. Mothers using alcohol during pregnancy expose the fetus to alcohol. Chronic fetal alcohol exposure results in fetal alcohol syndrome, which is characterized by intellectual disability, facial dysmorphism, retardation of growth, and behavioral abnormalities (Denny et al. 2017).

Ingestion of methyl alcohol (methanol) is having severe harmful effects. Methanol poisoning results in metabolic acidosis and impairment of cellular homeostasis (Kraut and Kurtz 2008). Methanol poisoning produces neurological damage and renal failure as well.

Alcohol: Effects on Mental Health

Chronic and unrestrained use of alcohol often results in development of alcohol use disorder. The term “alcohol use disorder” incorporates harmful use, abuse, and dependent pattern of alcohol use. Alcohol use disorder often results in physical as well as social dysfunction, other than psychological impairments (emotional, cognitive,

and behavioral). Genetic factors do play some role in development of alcohol use disorders (Tawa et al. 2016). Male gender, certain personality-related vulnerabilities, pre-existing psychiatric illness, family history of alcohol use disorder, and stress are common risk factors for development of alcohol use disorder (Gowin et al. 2017). The *Diagnostic and Statistical Manual*, fifth edition (DSM 5), mentions alcohol-related disorders as an umbrella term to incorporate alcohol use disorder, alcohol intoxication, withdrawal syndrome of alcohol, other alcohol-induced disorders, and unspecified alcohol-related disorder (Association 2013). Individuals using alcohol for a long time develop craving (an intense urge to consume alcohol), tolerance (over time increasing the amount of alcohol consumption to get same amount of pleasure), preoccupation with the thoughts of alcohol, significant interference in the familial and socio-occupational activities, and withdrawal symptoms (disturbed sleep, tremor, palpitation, anxiety, sweating) (Association 2013). Sometimes the individuals with chronic and heavy alcohol use develop more severe and life-threatening withdrawal symptoms like seizure and delirium (delirium tremens). The withdrawal symptoms often develop between 12 and 72 h of reduction in amount or stoppage of alcohol consumption.

Individuals, who are dependent on alcohol, often continue taking alcohol despite physical, socioeconomic, as well as legal complications. During alcohol intoxicated state, there occurs disinhibited behavior, slurring of speech, unsteadiness of gait, mood swings, and increased reaction time. The clinical manifestations depend upon the blood alcohol concentration and chronicity of alcohol use. At higher blood alcohol concentration, the individual may go to coma, and death may happen. Many individuals often consume large quantity of alcohol in a single occasion, which is often known as binge drinking. Alcohol use disorder often follows a relapsing remitting course. Presence of psychiatric comorbidities like schizophrenia, bipolar affective disorder, depression, attention deficit hyperactivity disorder, and antisocial personality disorder increases the risk of alcohol use disorder (Association 2013; Sadock and Ruiz 2015). Alcohol use increases the risk of dementia. Chronic use of alcohol causes

personality changes. Alcohol increases the risk of suicide. Alcohol use is associated with development of amnestic syndrome (Wernicke-Korsakoff syndrome). Chronic alcohol use may result in development of auditory hallucinations (alcoholic hallucinosis) and morbid jealousy (paranoid delusions).

Conclusion

Alcohol (ethanol) has enormous impact on health. Wide use of alcohol across the globe resulted in significant burden of care, disability, and socio-occupational impairment. Despite country-specific legislations to regulate its marketing, transportation, and use, it still stands as a major obstacle in attaining the Sustainable Development Goals.

Cross-References

- [Alcohol-Related Violence](#)
- [Ethanol](#)
- [Frugivory By-Product Hypothesis](#)

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Alcohol and Balance

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Synonyms

Effects of alcohol on balance

Definition

Alcohol intoxication has deleterious effects on balance. It is referred to as an ototoxic drug.

A

Introduction

Alcohol intoxication has negative effects on one's balance in many ways. The vestibular system is greatly affected even if ingested in small amounts. It is concluded that alcohol intoxication causes a series of multifaceted deterioration of body movement.

Effects of Alcohol on Balance

The effects of alcohol intoxication can be devastating to one's health in a number of ways. More specifically, ethanol intoxication causes impairment in postural sway (Woollacott 1983). Its effects are well investigated on other structures of the brain and body, i.e., the oculomotor system, but there have not been many reports on the acute effects of alcohol on the vestibular system (Nieschalk et al. 1999). Nieschalk et al. have demonstrated in their study that alcohol intoxication affects mainly the vestibulocerebellum, a finding that disputed previous findings of Diener et al. (1983) who supported the fact that intoxication by alcohol affects mainly the spinocerebellum. Nieschalk et al. is consistent with Ikeda et al.'s (1980) research who indicated that small doses of ethanol interfere more with the synaptic transmission in the lateral vestibular nucleus (LVN) monosynaptic and polysynaptic II neurons than synaptic transmission in the spinal trigeminal nucleus (STN) relay neurons and interneurons.

Modig et al. (2012b) have comprehensively investigated alcohol-related impairments on postural control at specific blood alcohol concentration (BAC). They have found that alcohol has deteriorating effects on postural control based on certain doses, time of alcohol ingestion, and the direction of movement. Specifically, the researchers have noted that between 0.06% and 0.10% BAC, any increase in alcohol

intoxication would result in a decrease in postural control. They further noted that ethanol consumption causes more destabilization in lateral motion than in anteroposterior motion and that intoxication decreases the adaptation mechanism, particularly for stability control in a lateral motion.

Further evidence on the relationship of alcohol and balance is supported by a research done by Tianwu et al. (1995) who concluded that a moderate quantity of alcohol affects both the oculomotor system as well as the vestibular system. They suggested that one of the reasons that postural instability takes places after alcohol consumption is reduced vestibular function. Consistent with this view, Bellé et al. (2007) suggested that alcohol interferes with hearing and balance, causing deleterious effects on the organisms referring alcohol as an ototoxic drug.

How Alcohol Affects Balance

When alcohol is digested in high amounts, the cupula in the semicircular canals becomes lighter than the endolymph, making it sensitive to gravity, a process referred to as the buoyancy hypothesis (Fetter et al. 1999). Consequently, this process lead to positional alcohol nystagmus (PAN) and rotatory vertigo. Fetter et al. (1999) concluded that alcohol intoxication causes a vertical velocity offset, which may represent a toxic effect on the central vestibular pathways, producing a tone imbalance of the vertical vestibuloocular reflex.

Furthermore, when under alcohol intoxication, there is an inability to use gravitational cues when there is an attempt to determine distance. Therefore, the person relies in visual information instead (Hafstrom et al. 2007). Hafstrom et al. further concluded that alcohol intoxication in high levels initiates a decompensation of small subclinical vestibular asymmetries and a dysfunction of the otolithic organs. In essence, alcohol intoxication causes a series of complex and multifaceted deterioration of body movement (Modig et al. 2012a).

Conclusion

The devastating and deleterious effects of alcohol intoxication on balance were briefly reviewed. When the vestibular system is affected, the person is lead to rely on other cues to determine distance—such as vision; a process that has potentially dangerous effects in one's health.

Cross-References

► Vestibular System

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Alcohol and Rape on College Campuses

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Definition

The association, on and about college campuses, between ethyl alcohol consumption and the use of force or threat of force to achieve penetration of an individual without their consent.

Introduction

Incidence of aggression, risky sexual behavior, and rape peaks during adolescence and young adulthood. On college campuses, rape has been occasioned by heightened alcohol use, including binge drinking. Consequently, alcohol abuse has been advanced as a possible cause of rape and also a possible instrument with which males are able to more successfully rape females. This brief entry presents an evolutionary perspective on the possible role of alcohol in rape on and about college campuses, attending to potential interactions between the psychoactive effects of alcohol and hypothesized rape and rape avoidance adaptations. Throughout, tentative language is used to describe the nature of the association between alcohol use and rape because no causal effect of the former on the latter has been established (Lovett and Horvath 2009).

Alcohol Consumption on College Campuses

Most college students (appx. 60%) report recent alcohol use, and they are more likely to report binge and heavy alcohol use than their noncollege peers (Center for Behavioral Health Statistics and

Quality [CBHSQ] 2015). It is well recognized that alcohol impairs activity in the prefrontal areas of the brain that support executive functions including planning, working memory, and inhibition (George and Koob 2010; George and Stoner 2000). This impairment engenders decreases in capacity for integration of information stored in memory, contextual cues, and future goals, resulting in greater discounting of the future and impulsiveness or more present-oriented and risk-prone behavioral responding. The effects of alcohol on behavior are not only due to its impairment of prefrontal activity but also to its direct influence on dopamine transmission and thereby incentive salience (i.e., experienced utility). Through its effects on brain function, alcohol decreases attention to potential future consequences and also amplifies the experienced value of cues to immediate reward in the local environment. Consonantly, alcohol consumption has been linked to risky sexual behavior, delinquency, accidents and injuries, and also legal consequences among college students.

Rape on College Campuses

Surveys of college students suggest that among the types of sexual assault, unwanted sexual contact and coercion are most common, followed by incapacitated rape (i.e., completed rape while the victim was intoxicated), and then forcible rape (Fedina et al. 2016). Estimates of the prevalence of sexual assault, including rape, vary widely. According to Fedina, Holmes, and Backes (2016), this is partly due to measurement and definitional differences. For incapacitated rape, prevalence estimates have ranged from 1.8 to 14.2% for females and been observed at 1.9% for males, while forcible rape estimates have ranged from 0.5 to 8.4% for females and from 0.6 to 0.7% for males (Fedina et al. 2016). Notably, these estimates rest largely on samples of White, heterosexual, female students in traditional colleges. The prevalence of sexual assault among minority females may be higher, and rape incidence is likely underestimated generally due to underreporting.

Evolution, Alcohol, and Rape

Rape has been observed across all human cultures, and males in many nonhuman species have evolved strategies to sexually coerce and rape females (McKibbin and Shackelford 2011). As in nonhuman species, human perpetrators of sexual assault are nearly always male, and victims are most often female (Testa and Livingston 2009). The data have not rejected either of the possible evolutionary explanations for human male rape of females: (a) rape reflects a specialized psychological adaptation in males or (b) rape is a spandrel (i.e., a characteristic that is a by-product of the evolution of some other trait) reflecting adaptations that solve other, perhaps more general, problems (e.g., adaptations for acquiring resources that cannot be obtained except by force; McKibbin and Shackelford 2011).

Strikingly, at least half of all sexual assaults are occasioned by alcohol consumption (Testa and Livingston 2009). One possible explanation of the linkage between alcohol consumption and rape perpetration is that, through its modulation of brain activity, alcohol amplifies cues to the execution of adaptations contributing to rape via effects on the perceived biological value of potential victims, diminished ability to shift attention away from perceived sexual opportunities, reduced capacity for inhibiting sexual arousal, and reduced awareness of costs that could stem from rape. Indeed, male college students report that alcohol increases their sexual desire and disinhibition, risk taking, and aggression (Abbey et al. 2014; Cooper 2002). Alcohol also decreases control of penile reactions and has disinhibiting effects, among males, on responses to sexually aggressive depictions (George and Stoner 2000). The possibility that sexually aggressive males experience the effects of alcohol in unique ways has received little attention, though some evidence suggests convicted rapists may not display the typical alcohol-induced genital suppression effects shown by non-rapists (Wormith et al. 1988). Finally, it is important to note that studies have shown that alcohol beliefs or

expectancies interact with consumption to influence sexual experience. For instance, research indicates that alcohol amplifies *pre-drinking* intention to have sex and increases sexual arousal primarily among males who expect this effect (George and Stoner 2000).

Another possibility is that males identify females who are vulnerable or exploitable by attending to their alcohol consumption. Rape exacts a severe toll on females in terms of injury or death, circumvention of mate choice, disruption of parental care, and partner abandonment and has occurred throughout recorded history (Thornhill and Palmer 2000). Thus, some researchers have theorized that females may have evolved tactics to avoid rape and the associated harms. Stemming from this, research suggests that women execute a suite of rape avoidance behaviors (McKibbin and Shackelford 2011). These behaviors include avoiding strange men, avoiding appearing sexually receptive, avoiding being alone, and awareness of surrounding/defensive preparedness. From an evolutionary perspective, then, alcohol consumption might be seen as facilitating male rape of females through interference with female rape avoidance adaptations.

Consistent with the above, research suggests that alcohol increases vulnerability to sexual assault by making victims less likely to attend to cues to danger and less able to resist forcible rape (Lovett and Horvath 2009). Indeed, the victim was too intoxicated to resist in the majority of rapes of female college students (Testa and Livingston 2009), and drinking within risky contexts has been identified as *the* risk factor for sexual victimization (Testa and Livingston 2009). Alcohol may also make victims less able to remember the details of an assault, which could facilitate serial offending by making them less likely to report their victimization and by decreasing the likelihood that the offender is convicted. In general, then, alcohol consumption might make some females ideal targets for would-be male rapists.

Research indicates that in the majority of reported sexual assaults involving psychoactive substances, male perpetrators targeted females

self-intoxicated through alcohol consumption and exploited their alcohol-induced vulnerability (Lovett and Horvath 2009). Male perpetrators were often older than their victims, met them in the hours before the assault, and offended in bars and clubs, homes, or vehicles. In some contexts, they were also less likely to have also consumed alcohol themselves (e.g., when assaults occurred in vehicles). In contrast with rape and sexual assault generally, alcohol was more commonly involved when parties did not know each other well and in the context of bars and parties. Thus, males generally did not use alcohol as a “date rape” drug but rather selected victims they recently met on the basis of their alcohol consumption. Taken together, these findings suggest that alcohol consumption makes some females less (a) likely to avoid strange men, (b) avoidant of being alone, (c) aware of their surroundings, and (d) able to resist forcible rape. Alcohol consumption in females also appears to serve as a cue to sexual exploitability for male rapists. This targeting behavior on the part of perpetrators appears to be under-recognized and should be considered as a part of rape prevention efforts (Lovett and Horvath 2009).

Finally, it is important to attend to how perceptions of responsibility for rape are affected by alcohol involvement. People attribute more blame to victims and less to perpetrators when alcohol is involved (George and Stoner 2000; Lovett and Horvath 2009). Rapists may also attach less responsibility to perpetration when alcohol is involved, consistent with evidence that when listening to a date rape analogue, male college students took longer to stop a rapist from further advances when they consumed or expected alcohol (George and Stoner 2000). Similarly, sexually aggressive males who did not consume or expect alcohol themselves took longer to stop a date rape when the perpetrator and victim were depicted as drinking (Bernat et al. 1998). This pattern in attribution of responsibility suggests that alcohol may serve to minimize the blame and legal consequences rapists experience, and perhaps expect to experience, as a result of perpetration.

Conclusion

Rape on college campuses has been linked to alcohol consumption. This brief entry presented an evolutionary perspective on the possible role of alcohol in rape on and about college campuses, reviewing evidence suggesting that alcohol may contribute to rape through its effects on the brains of would-be male rapists, as well as by interfering with the functioning of rape avoidance adaptations employed by potential female victims.

Cross-References

- ▶ [Drugs and Rape on College Campuses](#)
- ▶ [Male-Male Competition or Male Provisioning?](#)
- ▶ [Rape](#)
- ▶ [Rape Avoidance](#)
- ▶ [Rape and Dating](#)
- ▶ [Rape in Warfare](#)
- ▶ [Sexual Coercion and Rape](#)
- ▶ [Sex-Specific Link Between Self-Esteem and Mate Value](#)
- ▶ [Victims of Violence](#)

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Alcohol Violence

► Alcohol-Related Violence

Alcohol-Related Violence

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Synonyms

[Alcohol violence](#)

Definition

Alcohol-related violence is defined as “violence associated with use of alcohol.”

Introduction

Alcohol use disorder is the most common form of substance use disorder worldwide (Degenhardt et al. 2018). In 2010, alcohol use disorder alone accounted for 9.6% of the disability-associated life years (DALYs) caused by mental and substance use disorders, worldwide (Whiteford et al. 2013), whereas in 2016, it became 4.2% (Degenhardt et al. 2018). Violence associated with alcohol use includes both intentional and unintentional injuries. Evidences support that the risk of both of these increases with alcohol use (Degenhardt et al. 2018). Evidences support that in nearly one third of firearm violence, the person who used firearm was found to be in a state of acute alcohol intoxication. Worldwide, nearly 50% of the violent crimes are associated with alcohol use (Gutwinski et al. 2018). One in every four perpetrators, who committed sexual crimes, was found to be under the influence of alcohol, as reported by the victims of the sexual crime (Gutwinski et al. 2018).

Alcohol also attributes to violent behavior directed toward self (suicidal behavior) by use of serious means like firearms (Branas et al. 2016). The aggressive and violent behavior associated with alcohol is highest among all substances (Miczek et al. 2004). Alcohol use increases the risk of domestic violence including intimate partner violence (Wilson et al. 2017). Many violent crimes are committed under the influence of alcohol (Murdoch and Ross 1990). The risk of violence after consumption of alcohol is five times the risk of violence in a sober state (Gutwinski et al. 2018). Alcohol disrupts social inhibition; hence individuals under influence of alcohol behave in a disinhibited manner, due to which alcohol is also commonly known as “liquid courage” (Gutwinski et al. 2018).

Attributes of Violence Associated with Alcohol Use

Violent behavior is often associated with alcohol use. Violence associated with alcohol use is attributable to several biological, psychological, as well

as sociocultural (environmental) factors. The biological factors explain how specific effects of alcohol on brain result in aggression, whereas the psychological factors explain the relevance of personality characteristics responsible for aggression associated with alcohol use. Sociocultural factors explain the importance of environmental influence on alcohol-related violence.

There are evidences of definite neurobiological association with alcohol-related violence. Alcohol-related violence is modulated through neurotransmitters like serotonin, glutamate, and gamma-aminobutyric acid (GABA) in the metabotropic and ionotropic receptors of dorsal raphe nucleus (Miczek et al. 2015). The aggressive behavior associated with alcohol use is aggravated through the complex interaction of neuropeptide Y, vasopressin, endogenous opioids, and corticotrophin-releasing factor with the above neurotransmitters (Miczek et al. 2015). Some evidences support that the gene coding for different subunits of GABA-A receptor predicts the occurrence of aggressive behavior after consumption of alcohol (Miczek et al. 2004). Alcohol produces neurodegeneration and structural alteration in the brain. These changes are more evident in the frontal cortex, limbic system, and hippocampus. The neurodegenerative process is more intense if alcohol had been consumed during the adolescence (Crews and Vetreno 2014). As limbic system is involved in regulation of emotions and prefrontal cortex is involved in cognitive appraisal of events/context, decision-making, and impulse control, their dysfunction due to alcohol may result in the aggressive and violent behavior (Crews and Vetreno 2014). Long-term repetitive use of alcohol and binge drinking causes alteration in the neurobiology and may contribute to violent behavior. During acute intoxication with alcohol, there occurs an impairment in the impulse control ability of the prefrontal cortex leading to impulsive and disruptive behavior (Potenza and de Wit 2010).

Heavy drinking often leads to violence. The individual under influence of alcohol often initiates the altercation, which leads to verbal argument, physical fights, and assault (Murdoch and Ross 1990). Alcohol-aggression expectancy also

predicts alcohol-related violence. Aggression expectancy after consumption of alcohol is more among males than females. In accordance with this, among the genders, alcohol-related violence is more common in males (Tedor et al. 2018).

Deficits in executive control and social learning also attribute to alcohol-related violence. People who display violent behavior, under influence of alcohol, often have history of learning such behavior through multiple similar social contexts (Gutwinski et al. 2018).

The social cognitive model explains the relevance of social cognition in alcohol-related violence. As per this model, alcohol use increases the expectation of aggressive behavior in the individual consuming alcohol. Alcohol activates various networks of alcohol-related memory (Gutwinski et al. 2018). The alcohol myopia hypothesis explains that alcohol narrows down the attention in perceptual field resulting in missing certain cues in different social contexts, which often lead to misinterpretation of events and information. This misinterpretation may result in conflict and violence (Gutwinski et al. 2018).

Alcohol-related violence also depends on the amount of alcohol consumed in a single setting. Those who are non-dependent users and are prone to heavy drinking are more likely to experience sedative effect acutely, whereas those with moderate level of drinking are likely to display disinhibited behavior and aggression (Gutwinski et al. 2018).

Evidence supports the persistence and increase in antisocial behavior with increased alcohol use in adolescence and early adulthood (Hammerton et al. 2017). People with antisocial personality often show violent behavior and have increased propensity for alcohol abuse. Hence, among persons with antisocial personality, alcohol-related violence is common.

Chronic and dependent users of alcohol are more likely to display aggressive behavior. Various mechanisms are responsible for the aggressive and violent behavior associated with acute and chronic use of alcohol. Alcohol impairs the executive control, which is responsible for increased amount of alcohol intake and violent behavior (Heinz et al. 2011).

Availability and accessibility to alcohol may increase the risk of alcohol consumption and alcohol-related violence (Speer et al. 1998). Peer pressure may also result in consumption of alcohol and binging, which may attribute to alcohol-related violence. Many other environmental factors like permissive environment, crowding, and availability of alcohol at an affordable price can be a determining factor of alcohol-related harm (Hughes et al. 2011). In night parties, many people often binge on alcohol. Usually, violence is expected, when people binge on alcohol (Pedersen et al. 2016). Alcohol induces violent behavior by means of developing personal affronts and jealousy as well as by sharpening the emotions. Binge drinkers often attribute alcohol to violent behavior, and they also expect conflict and violence to occur when they consume alcohol (Pedersen et al. 2016).

Prevention of Alcohol-Related Violence

Alcohol-related violence is preventable. Alcohol-related violence can be reduced or prevented by reducing the intake of alcohol, predicting the possibility of violence (by analyzing the context, mood state, and past experiences), responding cautiously to people who are under the influence of alcohol, and taking appropriate safety measures (by keeping vulnerable population like children and self away from the individual, who is in an intoxicated state) (Wilson et al. 2017).

For effective prevention of alcohol-related violence, the following factors need to be addressed (Pernanen 1998):

1. Personal or individual factors (personality, mood state, psychiatric illness)
2. Alcohol-related/specific factors (availability, accessibility, affordability, type of alcoholic preparation)
3. Contextual or situational factors (peer pressure, context of alcohol use, setting of alcohol use)
4. Cultural factors (permissiveness)

Systematic addressing of the above factors may facilitate effective prevention of alcohol-related violence.

Strategies that work on supply reduction by restricting the selling of alcohol are also found to be successful in effectively reducing alcohol-related violence (Duailibi et al. 2007). Some early evidences support that having a national policy on alcohol control and its effective implementation may be beneficial in preventing alcohol-related violence (Kearns et al. 2015). Many developing countries don't have a robust policy; and if at all it exists, either it is not fully followed or not properly monitored, which might be responsible for higher alcohol-related violence.

Conclusion

Violence associated with alcohol use is a biopsychosocial phenomenon. Alcohol-related violence ranges from intimate partner violence to heinous violent crimes. Alcohol-related violence is preventable to a larger extent. Understanding the predictors of alcohol-related violence and effectively treating individuals, who behave violently under the influence of alcohol, may be an effective prevention strategy of violence associated with alcohol use.

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Alert Call

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Alfred Russel Wallace (1858)

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Synonyms

Charles Darwin; Darwinism; Evolution of psychological faculties; Human evolution; Natural selection; Sexual selection

Definition

Alfred Russel Wallace (January 8, 1823–November 7, 1913) was a British naturalist, geographer, and theoretician in biology. Mostly known as the co-author of the *Theory of Evolution by Natural Selection* along with Charles Darwin, Wallace was also the founder of biogeography.

Introduction

Human evolution, particularly the evolution of high psychological faculties, was a controversial topic on the rising of evolutionary theory in the mid-nineteenth century. A comprehensive reading of *The Origin of Species* (Darwin 1859) reveals the discomfort generated by the inclusion of human beings in the evolutionary process. Sooner or later, Darwin would be pressured to solve this matter. An important part of this pressure came from the coauthor of the theory of evolution by natural selection, Alfred Russel Wallace, who had his own arguments to solve the matter of how human beings are part of the evolutionary process.

This entry focuses on the development of Alfred Wallace as a naturalist, as well as the context in which he developed his version of the theory of evolution by natural selection. The debate between Darwin and Wallace about the role of human psychological faculties in the evolutionary process is introduced, and the contributions of Wallace as a naturalist, collector, theoretician in biology, and social thinker are presented.

The Birth of a Naturalist

The story of Alfred Russel Wallace is frequently shadowed by Charles Darwin's. Wallace's role in history has often been limited to the episode of the co-discovery of natural selection as the mechanism for the evolution of species, suggested as a non-relevant contribution to Darwin's theory, or used to call into question Darwin's originality and ethical behavior during the process of publication of the theory.

Although Wallace's contributions to science are mostly associated to the co-discovery of natural selection, his story is that of a passionate naturalist and collector, an independent theoretician, a scientist with wide interests, sometimes controversial, and a thinker concerned with contributing to social progress.

Alfred Russel Wallace was born on January 8, 1823, near Usk, England, in the context of a socially disadvantaged family, due to his father's unfortunate decisions and the characteristic difficulties of the Victorian era. These difficulties lead to frequent housing changes, between London and Hertford, that promoted in him a sense of uncertainty as well as a capacity to adapt to new contexts, which would be of great value during his life (Raby 2001).

Despite financial shortcomings, the Wallace family had a good appreciation for education, so great efforts were made to send the male children to school. At home, Alfred found a good library, where he learned to read and write at an early age and acquired a taste for books and intellectual joys.

Alfred's religious formation was conventional, associated with the "Church of England." According to Wallace himself, he only experienced a moment of intense religious interest during his childhood, but this interest ceased when he questioned the nature of God and evil, not finding a satisfactory answer (Wallace 1905). Despite his skepticism, Wallace would keep a certain predisposition to believe in supernatural phenomena, which was the source of some discredit between his scientific colleagues, later in his career.

After his 14th birthday, Wallace travelled to London, where he lived with his brother John, and later, he started to work with his brother William as an assistant topographer. During the long journeys at this job, and despite the hard work involved in land surveying, Alfred developed an interest in the collection of specimens and a great interest for taxonomy (Wallace 1905).

In 1843, year in which his father died, Alfred published an article titled "The South-Wales Farmer," an anthropological work and the first of many papers published in scientific and non-scientific sources. Shortly after, when he became

an adult, Alfred obtained a job as a teacher in a private school in Leicester; this post was an opportunity to read some books that made an influence in his future work as a naturalist: *The History of the Conquest of Mexico* and *A History of the Conquest of Peru* by William Prescott; *The History of America* by William Robertson; and *Personal Narrative of a Journey to the Equinoctial Regions of the New Continent* by Alexander von Humboldt; they all made an impression on him and motivated his interest to visit the tropics. He also read *An Essay on the Principle of Population* by Thomas Malthus (Raby 2001). Some of these books were also documented by Darwin as an important motivation and background on the development of his own way of thinking about nature (Darwin 1887).

Amazon Basin

In Leicester, Wallace met Henry Walter Bates, with whom he shared a short but meaningful time in the Amazon and who became a good friend for life. Both Wallace and Bates started an academic interchange, mainly focused on the problem of the origin of man, either as creation or as the result of an evolutionary process. In this intellectual context, Wallace read, again and again, some crucial books for the development of his own thought. Among them are *Vestiges of the Natural History of Creation* by Robert Chambers, *The Voyage of the Beagle* by Charles Darwin, *Principles of Geology* by Charles Lyell, the work of Jean-Baptiste Lamarck, and *A Voyage up the River Amazon* by William Edwards.

The readings, the relationship with Bates, and his love for species collection altogether convinced him to follow a professional career as a collector. Wallace and Bates planned a voyage to the northern Brazilian state of Pará. On April 26, 1848, they departed from Liverpool onboard the *Mischief*. A month later, they arrived in Salinas, on the Brazilian coast, and then, after two additional days along the river Tocantins, they arrived in Pará (Wallace 1905).

During the following months, they travelled along the rivers Tocantins and Amazon, and a

series of channels that connect them, while collecting animal and plant species and developing their skills as professional collectors. The next year, Herbert Wallace came to the Amazon to join his older brother, and they visited several towns along the Amazon river. Wallace and Bates distanced themselves, but periodically met each other in the region, planned expeditions together, and remained as mutually esteemed colleagues for the rest of their lives. Herbert came to the Amazon along with Richard Spruce, a naturalist specialized in Botany. Like Wallace, Spruce had a humble origin, an irreducible interest in nature, and a strong sense of will and resigned his career as a professor to dedicate himself to specimen collection (Von Hagen 1945).

During the journey along the Amazon, Wallace visited Monte Alegre, Santarem, Obydos, Vila Nova, and the mouth of the Negro river (Guainía). From there, Wallace decided to go to Barra (now Manaus). The following months were dedicated to excursions along the Negro river, looking for specimens, especially the umbrella bird, an exotic species that Wallace captured and sent to England. Nevertheless, being disappointed with the limited success achieved in the region, Wallace went up the river, leaving his brother in Barra, not knowing that this was the last time he was to see him. When he was ready to return to England, Herbert fell ill with yellow fever and died. Alfred only knew that his brother had died months after, which caused him great emotional pain.

During his stay in the Amazon region, Wallace turned from collector to observer. His first manuscript was a series of observations of the umbrella bird (Raby 2001, p. 300, note 46). His observations encouraged him to ask questions about the distribution of species, a crucial matter for his later scientific contributions. At the same time, the way of life of the inhabitants on those places fed his social and political ideas, which were aligned with a socialist, egalitarian ideal of human society (Raby 2001).

On July 12, 1852, Wallace sailed back to England aboard the *Helen* with a vast collection of insects and invertebrates; a living collection of animals, especially birds and mammals; and his

personal drawing collection. After 3 weeks, the *Helen* caught fire, and all Wallace's collection was lost. It was a tragedy for him, not only from a scientific viewpoint but from a financial one. After travelling 500 miles on boats, Wallace and the rest of the *Helen*'s passengers were picked up and taken to England by the *Jordeson* (Wallace 1905). The return trip had taken 80 days; Wallace had returned to England, empty-handed.

The Malay Archipelago

During the next year, Alfred received invitations to scientific societies, collaborated with museums, and met other naturalists. Nevertheless, Wallace felt out of place. His relationships with other scientists did not go beyond occasional meetings, and the abovementioned activities led to little or no economic retribution (Browne 2002). Wallace started to think in another expedition, and after many considerations, he set off on a journey to Singapore in March 1854, starting an 8-year expedition in the Malay Archipelago, which was determinant for his career and later contributions to knowledge.

The exuberance of the archipelago was very similar to that of the Amazon and a dream for a collector. Hundreds of new species, mainly insects, constituted the basis of Wallace's work. During his stay in Borneo, he had the opportunity to observe, capture, and prepare specimens of many species, including orangutans (Wallace 1890).

Early in 1855, Wallace worked in a manuscript titled "On the Law Which Has Regulated the Introduction of New Species," published in the *Annals and Magazine of Natural History*. In this, later called the *Sarawak Law paper*, he stated: "Every species has come into existence coincident both in time and space with a pre-existing closely allied species." Since then, Wallace suggested that evolution occurs in a gradual way and that his law explained the organization of species, their geographical and geological distribution, and some of their anatomical features (Wallace 1855). Wallace's arguments pointed out some principles that fitted both his observations and

Darwin's similar ideas presented in *The Voyage of the Beagle* (1845), but Wallace's ideas did not suggest yet a mechanism that explained those principles.

Although the theoretical exercise had been pleasant for Wallace, this did not produce any income. On the other side of the world, his agent and clients did not find his theoretical task to be productive. Some of them openly indicated that his best options to contribute to science were found in his great capability for collecting; consequently, he should not be distracted by other activities which did not correspond to a man like Wallace (Raby 2001). Additionally, the Sarawak manuscript apparently did not produce any reaction among naturalists. Wallace sent the manuscript to Darwin (October 10, 1856), with whom he had corresponded in relation to requests by Darwin for information and specimens (Browne 2002). Initially, Darwin considered the manuscript unoriginal and dismissed it – perhaps due to a poorly detailed reading– based on the use of certain terms that differed from his own or the accepted scientific language. However, other academics saw something in it. Edward Blyth and Charles Lyell read the manuscript with a very different look and adverted Darwin that Wallace had a clue about the matter he was interested the most (Raby 2001).

During the 8 years he remained in the Malay Archipelago, Wallace systematically visited the main isles, Borneo, Sumatra, Bangka, Java, Bali, Lombok, Flores, Celebes (now Sulawesi), Timor, Maluku Islands, and New Guinea, as well as other smaller islands. Along with species collection, Wallace developed the ideas of the *Sarawak Law paper* about the distribution of the species and made observations about the inhabitants of the Malay islands who, as well as the species, exhibited important differences in their appearance and behavior. His anthropological and political interests were not to be open until his arriving in England; this would be one of his favorite discussion topics during his maturity and old age (Raby 2001).

Wallace found that the distribution of species suggested a divisor biological line between the regions of Asia and Australia, which he initially

(1863–1880) located at the east of Borneo, but it was later modified (1910) to put it at the east of Celebes. The line was built on the basis of the distribution of populations and species, according to Wallace's postulates showed with detail in *Island Life* (Wallace 1881/1998). The outline corresponded to important differences in fauna which can be noticed despite the relative closeness between the isles. The distribution of the original and modified lines responded to the particularities of the Celebes isle which was remarked by Wallace as peculiar, and he called Celebes an “ancient continental” island, the same category in which he put the Greater Antilles (Cuba, Haiti, Jamaica, and Puerto Rico) and Iceland.

During the time Wallace was developing his collection, his reflections about the influence of humans over nature were manifested in some of his writings. There is no doubt that Wallace was capable to overtake the utilitarian vision of his time and foresee the destiny of nature in the hands of human beings. His experience as a naturalist had an effect on his perception about nature and the human inhabitants of those regions, getting rid of the common prejudices from both his time and culture.

The Ternate Essay

Darwin's response to the Sarawak manuscript was initially unfavorable, but when Lyell and Blyth drew attention about the real value of the paper, Darwin read it more carefully. In his response letter (May 1857), Darwin expressed his agreement with some of Wallace's ideas, also expressing very clearly that he had been working on a very related problem for the past 20 years; finally, he encouraged Wallace to collect more data (Darwin 1887). Once again, it seemed that few people regarded Wallace as a theoretician; instead, he was expected to collect and send evidence to be used by other “thinkers.” Nevertheless, Wallace interpreted Darwin's letter as an encouragement. He had already received Bates' opinion whom, in a letter dated November 19, 1856, reminded Alfred that the origins of the

ideas put on the Sarawak manuscript could be traced to conversations they had in South America (circa 1845) about the geographical distribution of species. Bates praised Wallace's simplicity, maturity, and originality. Although Wallace was not giving credit to Bates in the manuscript, it was clear that the ideas presented in it had been originated from conversations with him and Spruce, during the long isolation periods in the Amazon (Von Hagen 1945).

Early in 1858, Wallace stopped at the island of Ternate. From there, he started several expeditions to the neighboring isles. In one of these, Gilolo (now Halmahera), Wallace fell sick, as many other times in the past, due to tropical fevers. During the feverish moments of his illness, Wallace came up with key ideas for a new theory. In the *Sarawak Law paper*, he had established that species transform in sequence, but some of them change more rapidly than others. But the hard question behind it was *how*. The answer came to Wallace in a very similar way as Darwin's: from Malthus' essay. When Wallace was recovering from a fever, he remembered Malthus' book which he read 11 years before; he was particularly interested in Malthus' idea that in every population, some individuals survive and some die, due to disease, accidents, famine, or wars. But why? What is the reason some individuals can survive those events and others cannot? The answer, Wallace said (1905), came in an unexpected way. Those who survive can do it because they are better prepared to cope with environmental challenges. The healthiest can survive to disease; the strongest, fastest, or smartest can survive to its enemies; the best hunter can survive to scarcity. Then, Wallace concluded that this process, repeated again and again, would lead to an improvement of the race, to changes of the species. A change, derived from a “special requirement from the environment,” could act over a particular feature, producing the characteristic isolation of the species over time. Unlike Darwin, Wallace stated his arguments highlighting the relationship between the individual and his environment, ignoring the competition between individuals of the same species. This difference in views was perhaps due to Darwin's interest on artificial

selection and its use as an analogy for natural selection, which suggested him a competition between individuals. In contrast, Wallace's interest on the geographical distribution of populations seemed to reveal a more relevant and fixed relation between individual and environment, in which the latter imposes an adaptive standard for each population (Bowler 1983). In any case, the idea emerged, twice!

During the following days, Wallace sketched the main elements of the theory and sent a paper to Darwin. Wallace had dated the letter on February 1858, and, although it was not conceived entirely on Ternate, he reported that island as the place where the idea originated because that was his place of residence. The document is widely known as the *Ternate Essay*.

Co-Discovery of Natural Selection

The events related to the presentation of Darwin and Wallace manuscripts to the Linnean Society have been extensively documented and interpreted in multiple ways, to reiterate the value of Darwin as discoverer of the mechanism of natural selection in some cases, to highlight Wallace's co-discovery and his role as a catalyst for the publication of *The Origin of Species*, or even to question the ethics on the resolution of the problem about the precedence of ideas between Darwin and Wallace (e.g., Browne 2002; Darwin 1887; Raby 2001; Wallace 1905). This is one of the most commented and well-documented episodes in the history of science.

Darwin was in the midst of a personal tragedy because of the serious illness, and subsequent death, of his little son, Charles. In the middle of this situation, and visibly affected by the impact of receiving the same solution that he gave to the most important problem of his work, Darwin left the moral dilemma he was facing to his closest friends, Charles Lyell and Joseph Hooker. They decided to present the *Ternate Essay*, along with some fragments of the draft of *The Origin of Species*, and a copy of the letter to Asa Gray – dated a year before and containing descriptive elements of the theory – at a meeting of the

Linnean Society. The great effort of Darwin's friends to give a satisfactory solution to the dilemma was made to preserve Darwin's precedence in the presentation of the theory. It seems, however, that there was also some solidarity with someone who represented a social class and an academic lodge, trying to deal with the untimely and disruptive arrival of someone from “other means” (Browne 2002).

Darwin and his circle accepted that the unexpected letter from Wallace had been the stimulus that forced the presentation of the theory in a short version. Wallace served as a catalyst for Darwin's work and served as a social catalyst to facilitate its acceptance, at least among a circle of colleagues who, while listening to Darwin with interest, were not yet ready to accept his theory; in fact, Lyell and Hooker only became enthusiastic Darwinists since this episode in which their participation was so crucial.

The way in which Wallace handled and interpreted this episode is, however, everything but a claim of precedence or reproach to the actions of Darwin or his colleagues. It is not possible to interpret with certainty if this was the result of Wallace's modest personality, or certainty about the sequence and nature of events, or both.

Once Darwin's manuscript was sent, it seems that Wallace only received a message about what happened in Down and London in late September or early October, when he received letters from Hooker and Darwin himself, dated at mid-July (Darwin 1887), in which they explained what occurred in the Linnean Society. Wallace had vital occupations to think about it. At that time, he was busy searching for birds-of-paradise, exotic, and beautiful specimens that would be highly appreciated by collectors and produce important profits. But, once he received the information, he considered that the solution was not just acceptable, but made honor to his work (Wallace 1905). In a letter sent to his mother on October 6, he mentioned the episode and manifested his joy with the outcome as well as with the chance to have an interaction with Darwin, Hooker, and Lyell upon his return to England (Raby 2001).

On the other hand, despite some difficulties, things started to go well. The collections Wallace sent to his agent in England sold well, and he had discovered a number of new species, including several species of birds-of-paradise and many species of butterflies, and even received recognition from taxonomists, who named new species with his name.

The following year, he received an advance of *The Origin of Species*, and there he found the mature work of a first-class researcher who, according to Wallace's own story, thwarted the development of his own book about the theory. Wallace expressed admiration for Darwin's work to Henry Bates, highlighting the extensive evidence presented, the clarity of Darwin's arguments, and the scope of his ideas (Wallace 1905).

Back to England

On February 1862, after 8 years out of his homeland, Wallace returned with alive animals (2 birds-of-paradise for the zoo), with a collection of stuffed animals (about 3000 pieces corresponding to a thousand species of birds, 20,000 specimens of beetles and butterflies of around 7000 species, including those sent by mail to his representative), with a name as a naturalist, and with a network of important naturalists whom he could now call "colleagues."

Finally, he began to receive some recognition. As a member of the Zoological Society and the British Ornithologists' Union, he frequented the meetings and was often invited to the Linnean Society (to which he was only accepted as a full member in 1871) and to the Ethnological Society of London. As foreseen, he was introduced by Darwin to the group of scientists who supported the theory of natural selection, which at that time did not exceed ten people. Wallace answered the call writing several articles in support of the theory and adding new data. He also published several articles on butterflies, parrots, and other species, in journals of prestigious societies.

However, all these achievements did not materialize in a stable job. It is not clear if his social status, his scientific ideas, or his personal style

were the reason why he was rejected from various positions in museums and scientific societies. Those difficulties were alleviated in part by his relation and subsequent marriage with Annie Mitten in 1866.

Around 1865, Wallace began to frequent spiritualism sessions. Contrary to his solid attitude as a scientist to deal with nature problems, he was willing to accept with little skepticism the tricks that all kinds of charlatans used to fool the naïve population who sought a connection with the "other world." Wallace had a weak point because of the emotional effect of his brother's death in Pará, and he was not only willing to believe, but he became an advocate of these practices.

In the following years, Alfred Wallace published two of his most important works, *The Malay Archipelago*, which he dedicated to Charles Darwin (1890), and *Contributions to the Theory of Natural Selection* (1870). Darwin read the first one with pleasure, but when he read the *Contributions*, he was surprised that his vision about the evolution of man differed in important ways to that of Wallace. At the end of the book, Wallace presented an idea about a supposed state of perfection, a final goal, to which the superior races (humans) were destined. Certainly, this idea was not shared by Darwin.

Mental Processes: Evolutionary Continuity or a Superior Force?

The development of Darwin and Wallace's evolutionary theory was stimulated by their desire to understand the origin of human beings. Although Darwin refused to talk about it in *The Origin of Species* (Darwin 1859), the extension of his ideas to humans was of great interest for him. In *The Descent of Man* (1889), Darwin developed the basis of his vision of evolution by natural and sexual selection and how they applied to the emergence of high psychological functions. From the second chapter of *The Descent of Man*, Darwin explicitly pointed out that the "mental qualities" are transmitted between species and within the human species. Thus, he suggested that there is an evolutionary continuity between man and

other animal species, which is evident by the transmission and preservation of certain psychological faculties that, although more complex in humans, are governed by similar mechanisms.

Darwin sustained the idea of evolutionary continuity of mental faculties by means of the comparison of anatomical characteristics between humans and primates – like the relative size of the skull regarding body size, related with some complex behaviors that suggest the presence of high psychological faculties, thus showing the affinity between humans and higher primates. The continuity that humans have with respect to other closely related primate species – which is evident at the moment of pointing out the similarities between them at anatomical, functional, and, especially, psychological level – led Darwin to conclude that the evolutionary principles also apply to the human species in all aspects, including the development of high cognitive faculties. These faculties, therefore, emerged by natural selection (Darwin 1889).

It is well known that the statements made by Darwin in *The Origin of Species* and in *The Descent of Man* provoked the most diverse reactions, for and against Darwinian ideas. Some of those objections about the emergence and development of psychological processes and mechanisms came from Alfred Wallace, who, despite being coauthor of the theory of evolution by natural selection, also had profound differences in terms of the applicability of the theory to the psychological abilities of humans.

Wallace made a series of observations to show the plausibility of evolutionary theory. In *Darwinism* (1889), he showed the main arguments of the theory of natural selection, including some contributions coming from several critics during the 30 years after the publication of *The Origin*. His ideas remained almost unchanged, supported by the law of multiplication of organisms, the law of limited population, the law of heredity, the law of variation, the law of unceasing change of physical conditions upon the surface of the Earth, and the law of equilibrium of nature (Wallace 1867). Nevertheless, Wallace himself clarified from the beginning that his

understanding of Darwinian theory offered very personal views about some specific topics.

On the emergence of high psychological functions, Wallace proposed very different ideas from Darwin's. In chap. XV of *Darwinism* – dedicated to the application of evolutionary theory to humans, Wallace supported the relevance of natural selection when talking about the morphological modifications suffered by humans, thanks to the similarities with some primate species. However, Wallace put more emphasis in some notorious anatomical differences: the erect posture of humans, absent in the other primate species; differences in the size of the skull which are evident between human and the other primates, but minimal or absent between the “civilized man” and the “savage man”; the presence of large canine teeth in primates, in contrast to humans whose canines are as large as the other teeth; and the absence of body hair in humans, among other differences. Based on these differences, Wallace concluded that the human speciation process began a long time before the speciation of the other primates, and then he started to show his particular reasoning about the emergence of the defining characteristics of human species, that is, psychological faculties. Before showing his own ideas, Wallace highlighted the inadmissibility of Darwin's argument about the applicability of natural selection to the emergence of high psychological faculties (Wallace 1889).

To illustrate his particular viewpoint, Wallace alluded to some intellectual manifestations only seen in humans – mathematics, music, arts, and philosophy – which also are manifested in an exceptional way in a reduced group of persons from the entire population. Wallace added that these complex manifestations cannot be the result of the mere process of natural selection because they are not useful nor necessary behavior for the survival of the species (it should be noted that, for both, Wallace and Darwin, the mechanism of natural selection is intimately attached to the idea of “struggle for existence” or “survival of the fittest”). This justifies the fact that those complex manifestations are not uniformly distributed across the whole population, but just observed in a

reduced number of persons. Thus, Wallace pointed out the incapacity of natural selection theory to explain the emergence of high-intellect manifestations:

The point to which I wish specially to call attention is, that to prove continuity and the progressive development of the intellectual and moral faculties from animals to man, is not the same as proving that these faculties have been developed by natural selection; and this last is what Mr. Darwin has hardly attempted, although to support his theory it was absolutely essential to prove it. Because man's physical structure has been developed from an animal form by natural selection, it does not necessarily follow that his mental nature, even though developed *pari passu* with it, has been developed by the same causes only. (Wallace 1889, p. 463)

From that point, he concluded that the psychological faculties owned by the human species emerged as a consequence of the action of a certain superior force: a force argued to be present in nature, but remained far beyond the scientific knowledge of his time.

The fact that Wallace presented such a daring hypothesis is something shocking, mostly after showing a well-developed scientific thinking along his life. Wallace himself knew beforehand that the addition of a spiritualist argument in his discourse would be taken as scientific heresy among his colleagues.

Before the publication of *Darwinism*, Wallace had already made manifest his spiritualist argument in some manuscripts and meetings. What began as simple, naïve comments about the difficulties of the theory of natural selection to give account of human faculties became a structured discourse, attached to his way of thinking. In a review of the tenth edition of *Principles of Geology* and the sixth edition of *Elements of Geology* by Sir Charles Lyell, published in the *Quarterly Review*, Wallace (1869) mentioned the “Overruling Intelligences” for the first time, showed as entities that supposedly molded the development of the human intellect. According to Wallace, some morphological traits of humans cannot be explained by natural selection, like the brain, the speech organs, the hand, and the external shape of the human body. Wallace concluded that it was necessary to admit that the human mind

must be the product of a supreme mind which controls the action of evolution laws, in order to make such a perfect organization of the moral and mental capabilities of the human being.

The following year, 1870, Wallace wrote a first essay dedicated completely to question the evolutionary theory applied to man. In fact, the title of his essay was clear enough: *The Limits of Natural Selection as Applied to Man*. In this essay, Wallace extensively argued about the impossibility of natural selection theory to explain the emergence and development of the intellectual and moral capabilities of humans, proposing as alternative the action of Supreme or Overruling Intelligences, arguing that these intelligences are ruled by the same physical laws that rule the universe and, therefore, can be scientifically studied.

As it was expected, Darwin's response was quick, and then a very interesting discussion about the role of the human psychological faculties in the evolutionary process ensued. In a letter sent in March 1869 (Marchant 1916), Darwin anticipated the “heresy” Wallace was about to commit with his review of Lyell's books:

I shall be intensely curious to read the *Quarterly*: I hope you have not murdered too completely your own and my child [the theory of natural selection]. (Marchant 1916, p. 241)

Then, after having read the review, Darwin manifested his disagreement with Wallace with another letter dated on April of the same year:

As you expected, I differ grievously from you, and I am very sorry for it. I can see no necessity for calling in an additional and proximate cause in regard to Man. But the subject is too long for a letter. I have been particularly glad to read your discussion, because I am now writing and thinking much about Man. (p. 243)

Nevertheless, in a letter dated January 1870, Darwin showed his rejection about the inclusion of additional causes to explain the emergence of human faculties (Marchant 1916). In fact, his tone reveals his altered mood when reading Wallace's essay about the *Limits* of natural selection:

[. . .] But I groan over Man—you write like a metamorphosed (in retrograde direction) naturalist, and you the author of the best paper that ever appeared in the *Anthropological Review*! Eheu! Eheu! Eheu!

Your miserable friend, C. Darwin (p. 251)

Darwin's Response

Darwin's answer about Wallace's spiritualist argument has its basis on a briefly developed idea on *The Origin of Species*: Sexual selection. A detailed reading of Darwin's work shows that in *The Origin of Species*, the argument about sexual selection is referred only in some fragments of chap. IV. But in *The Descent of Man*, this topic is the basis for the whole book (Darwin 1889). There is a question about why Darwin made such a broad discussion about sexual selection. And the answer is very simple: because this is the full explanation of the response Darwin did to Wallace in relation to the evolution of human psychological faculties (Ruse 2009).

Darwin partially agreed with Wallace on the fact that natural selection cannot fully explain some characteristics of humans such as the intellectual and moral ones, but Darwin also thought that it is completely unnecessary to invoke spiritual forces to answer the question. The simplest answer could arise by adjusting to the laws that had already been established with respect to the evolution of the species. So, Darwin thought that sexual selection could be the answer: the effects of the struggle with conspecifics can lead to great differences on reproduction and breeding (Ruse 2009). Some individuals with certain characteristics like an enhanced intelligence to make good decisions (e.g., mate choice) would have a better chance to reproduce. The idea behind sexual selection as the determinant mechanism on the emergence of high psychological faculties is that intraspecific struggle (whether by ritualized male combat or by female mate choice) allows the selection of the most appropriate characteristics to make possible the reproduction of offspring tending toward variability. As it was already stated in Darwinian arguments, variation is required to ensure adaptive adjustment to changing environmental conditions. Likewise, constant variation is necessary to ensure that the species do not fully specialize (Cartwright 2008). All of it, along with an accelerated process of development of the brain, made possible the selection of certain traits which, if not determinant in the struggle for existence, eventually

constituted very attractive elements for mate selection. Therefore, high intellectual qualities emerge because of their great value for reproduction. Darwin made it clear on *The Descent of Man*:

He who admits the principle of sexual selection will be led to the remarkable conclusion that the nervous system not only regulates most of the existing functions of the body but has indirectly influenced the progressive development of various bodily structures and of certain mental qualities. Courage, pugnacity, perseverance, strength and size of body, weapons of all kinds, musical organs, both vocal and instrumental, bright colours and ornamental appendages, have all been indirectly gained by the one sex or the other, through the exertion of choice, the influence of love and jealousy, and the appreciation of the beautiful in sound, colour or form; and these powers of the mind manifestly depend on the development of the brain. (Darwin 1889, p. 617)

Immediately after the publication of *The Descent of Man*, Wallace returned the favor, and, in a letter dated January 20, 1871 (Marchant 1916), he manifested his disagreement supported on his spiritualist argument, even though he agreed with the application of the laws of natural selection on human evolution from some related species:

Your chapters on Man are of intense interest, but as touching my special heresy not as yet altogether convincing, though of course I fully agree with every word and every argument, which goes to prove the "evolution" or "development" of man out of a lower form. My only difficulties are as to whether you have accounted for every step of the development by ascertained laws. (Marchant 1916, p. 256)

From that moment, the positions of both authors regarding the evolution of the human psychological faculties remained practically unchanged; their arguments were refined and evidenced their deep differences in understanding human nature. The discussion between Darwin and Wallace continued over the years, even after their deaths; the relationship between evolutionary theory and cognitive faculties continued to be a subject of discussion for the behavioral sciences during the following century and continues to be central to the explanation in psychological theory.

Conclusion

The interest of Alfred Wallace in humanity led him to try to understand not only his origin but his future. His idealism, manifested in a spiritual vision of the origin of human nature, was also expressed in his way of seeing the social organization of our species. Influenced by his social origin, his early experiences as a surveyor, his encounter with native populations from two very distant places of the world, and his experience with the colonialist systems in America and Asia led him toward a socialist vision of the distribution of the land. For Wallace, it was not enough to believe in an idea; there was an obligation to become a promoter of such idea. In 1881, he was elected as the president of the *Land Nationalisation Society* and published several books about land distribution, one of them published just weeks before he passed away.

In his mature years, Wallace was frequently invited to present his ideas in societies, events, and public meetings. One of his most important tours was in North America, where he was able to return to his most beloved and habitual activity, that of a naturalist. He visited multiple cities and natural parks, enjoying the immense natural wealth of that continent.

Alfred and Annie had three children: Herbert – who died at the age of 7, Violet, and William. It is well known that one of the most frequent preoccupations of Alfred and his family was their economic situation. Due to the fact that he was not able to obtain a permanent job position, he had to write paid articles for several publishers. In 1881, a year before his death, Darwin assumed a defense of Wallace and successfully managed a request to the English Government for a pension for his outstanding civil services to the Crown. This episode was an indicator of Darwin's character, who, despite his differences with Wallace in the development of the evolutionary theory, highly appreciated the value of a man dedicated to exploring and understanding nature, always trying to discover their secrets in an honest manner and, above all, a man whose ideas catalyzed his greatest achievements as a scientist.

Alfred Russel Wallace died on November 7, 1913, at the age of 90. His wishes for a modest fate were respected, and he was buried in Broadstone, Dorset. Two years later, a medallion in his honor was installed near the grave of Charles Darwin in Westminster Abbey. This represents the seal of destiny of two men who discovered the essential mechanism of the origin of species and the way we understand the nature of life. For Wallace, the thread of his life was the desire to understand the role of human beings in the universe, their origin, their relationship with nature and with their own kind, and his commitment with the more sublime ideals of justice and equality.

Cross-References

- [Charles Darwin: Theory of Natural Selection](#)
- [Controversies in Evolutionary Psychology](#)
- [Early Perspectives on Evolutionary Change](#)
- [Evolution of Intelligence, The](#)

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Alfred Russel Wallace and Charles Darwin

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Definition

Alfred Russel Wallace (8 January 1823–7 November 1913) and Charles Darwin

(12 February 1809–19 April 1882) are jointly credited with contributing the doctrine of natural selection to the scientific literature. There can be no doubt that they independently conceived of the same theory; the priority question was settled amicably by a joint publication in 1858.

Introduction

Darwin has become, with considerable justification, the flag-bearer of evolution, but many of his (near-)contemporaries poured over the same questions. The obverse side of hero worship is indignation over those who were overlooked: the perniciousness of Darwinists allegedly shown by the manner in which Wallace, a formidable biogeographical scientist in his own right, was robbed of the priority credit. However, history and human relationships can be, and thankfully often are, more subtle than squabbles over priority. In reality, Darwin's response was admirably honorable, and the real interest resides in appreciating both men's contributions against the backdrop of contemporary views on varieties in nature.

Affinity and mutability: the origins of an idea

Evolution, as *phenomenon*, is the corpus of observations attesting to the fact that life on earth has not always been the same. Over the course of mega-anni, ecosystems and the species that inhabit them have changed, often and dramatically. Evolution, as *theory*, is any account seeking to explain these facts, including contrarian accounts that attempt to explain the facts *away*, that is, to repudiate the measurement of the deep time scale, or the sweeping nature of the changes, or both. Or, spurred by an urge to reconcile respect for scientific observation with religious piety, one might countenance a theory of intelligent redesign, in which the creator continually revises and recreates.

The philosophical landscape was quite different in the time of Darwin and Wallace. The nature

and media of the changes observed took center stage. Mendelian genetics was being developed at the time, but would not be widely recognized until the turn of the century (Fisher 1936) – and molecular genetics lay even further in the future. Even if such gaps in contemporary knowledge seem all but fatal handicaps to us, we should examine without prejudice the development of evolutionary thought against the intellectual backdrop of the time.

The similarity or “affinity” that exists between parent and child, raven and crow, perhaps even shark and tiger, or octopus and jellyfish, must always have been evident to naturalists. But what were they to make of this affinity, and how could it allow one life form to pass into the other?

The idea of inheritance of acquired characteristics, previously widely accepted, had begun to fall by the wayside. This doctrine, traditionally associated with Jean-Baptiste Lamarck (1744–1829), who certainly gave it a crisp wording (Lamarck 1809), presupposes that the next generation may somehow be imprinted with the striving of the parents. We observe adaptive changes through the course of an individual’s lifetime, e.g., hypertrophy of muscles under strain, or learning – and we also observe adaptive changes over the course of generations. It is natural to suppose that similar mechanisms are at work and that, consequently, adaptive changes can be passed on through gamete or spore. In Lamarck’s thought this was wedded to the concept of an inherent force striving toward greater complexity; whereas Darwin imagined a neat mechanism for the inheritance of acquired characteristics, whereby each organ or tissue brings forth a microscopic representative “avatar” that contributes to the gamete (stretching this idea perhaps beyond its limit, we may here vaguely discern the outlines of modern epigenetics), Wallace roundly considered the experiments refuting Lamarckism to have settled the question, which, in any case, he felt was rendered moot by the operation of natural selection.

The ineffable affinity that ties living beings together finds a striking expression in Genesis 1:26: “God said, Let us make man in our image,

after our likeness: and let them have dominion over the fish of the sea, and over the fowl of the air, and over the cattle, and over all the earth, and over every creeping thing.” If man is made in God’s likeness, then the stuff that life is made of (muscles, sinews, blood, etc.) must be present in the human body in perfect proportion and harmony. Moreover, such perfection must be lacking in all other live forms, in increasing degree as we descend a hierarchy known as the *great chain of being*. One could view all nonhuman beings as lacking in reason, for instance, or regard the Mollusca as being out of proportion, relative to the divine formula of man, in being mostly composed of muscle. Thus we account for both the affinity and diversity of life and even have a rudimentary form of genetics in which species are defined by a divinely ordained “formula of (dis)harmony/(dis)proportion.”

This point of view severely constrains the definition and malleability of species and forbids *transmutation*, the ability of species to evolve into one another. We concur with Darwin that it is “absurd to talk of one animal being higher than another,” but if we momentarily allow that life is ordered hierarchically, we should applaud Lamarck for his boldness in proposing that life strives to move *up* this ladder. Going against such radical ideas, *prima facie* evidence for an immutable, ingrained (and Divinely ordained) “formula” was seen in the tendency for domestic animals, when released into the wild, to “revert to type,” that is, while breeding in captivity may have stretched the makeup of the beasts away from the divine formula, when left to its own devices, the species springs back, or regresses, to its true inborn form. Varieties may temporarily depart from the original type, but not forever, nor without bound.

It is precisely this doctrine that Wallace seeks to refute in his essay “On the Tendency of Varieties to Depart Indefinitely From the Original Type” where he argues that the apparent “regression” of domesticated animals gone feral can be explained precisely because the harsh conditions of the natural environment that produced “the original type” must again give rise to something quite like it. But as these challenges

change, so will the way the species respond to them, free to wander away arbitrarily far in morphogenetic space.

It seems uncanny to modern eyes that Wallace is talking so eloquently about natural selection without ever using these words; but that is just the terminology that was introduced with Darwin. Wallace's thinking is clearly along the familiar lines of linking the lifetime reproductive success of an individual to its ability to, first, survive through to these reproductive events and, second, amass the resources that are to be invested in offspring. He cites the stock examples of characteristics such as camouflage, strong thigh muscles, and sharp claws as the sort of traits that aid the organism in achieving this success. He observes that, were nature to provide for every zygote to grow into an adult, the biomass of every species would grow exponentially – a manifest absurdity on a finite planet, which explains why selective pressure is huge.

One may well imagine Darwin's consternation when Wallace sent him his essay in March of 1858: "If Wallace had my MS. sketch written out in 1842, he could not have made a better short abstract." Darwin offered to help Wallace publishing his views. Moreover, Darwin had previously communicated writings on his ideas, which would allow him to "prove that I take nothing from Wallace. I should be extremely glad now to publish a sketch of my general views in about a dozen pages or so. But I cannot persuade myself that I can do so honourably... I would far rather burn my whole book than that he or any man should think that I had behaved in a paltry spirit" (Darwin 1958).

A compromise was found, and Wallace's essay was published along with an extract from Darwin's essay of 1844 (Darwin and Wallace 1858). Darwin's "Origin of Species," on which he had been working since the mid-1850s, was published a year later (Darwin 1858). Darwin's ideas on evolution had first crystallized during his voyage on the Beagle in the 1830s and had been maturing ever since (Darwin 1958).

The wealth of case studies, the breadth of knowledge of natural history and biogeography,

as well as its thoughtful style of argumentation made "Origin" the standard-bearer for evolution. The primary obstacle it overcame during its day was the doctrine of immutability, which was abandoned in favor of ongoing speciation and common descent.

Conclusion

Against a background of pre-Mendelian genetics, rejection of the transmutation of species for traditionalist-religious reasons, and expeditions yielding a wealth of biogeographical data, Wallace formulated the mechanism of natural selection independently of Darwin, who recognized Wallace's insights as essentially identical to his own and shared the credit, in what effectively amounted to a preview publication of his "Origin of Species."

Cross-References

- [Adaptation and Natural Selection](#)
- [Charles Darwin: Theory of Sexual Selection](#)
- [Evolution of Adaptations](#)
- [Genetic Determinism](#)

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Alienation

- ▶ [Loneliness in Modern Life](#)

All Psychology Is Evolutionary Psychology

- ▶ [Evolutionary Perspective, The](#)

Allergic Reactions

- ▶ [Allergies](#)

Allergies

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Synonyms

[Allergic reactions](#)

Definition

An excessive pathological reaction of the immune system towards environmental substances, such as foods and pollens, that are tolerated by the immune system of nonallergic individuals.

Introduction

Allergies have become increasingly prevalent over recent decades, particularly in the West. As a consequence, interest has grown regarding why such a phenomenon exists in the first place, especially given the risk of experiencing a potentially fatal allergic reaction called anaphylaxis (Gross 2015). Early explanations typically viewed

allergies as merely immunological errors. However, the evolutionary persistence of allergic capability suggests that it has an adaptive value for the host, of which exerted a strong enough positive selection pressure to outweigh the physiological costs and risk of fatality. Margie Profet became a notable theorist for why allergies evolved with her controversial hypothesis regarding what this benefit of allergies may have been.

The Toxin Hypothesis

In her paper published in 1991, Profet proposed the “toxin hypothesis” which argues that allergies evolved as a defense mechanism against toxins. Toxins are unfortunately ubiquitous in the natural world and cause acute bodily damage to a host. Many are also secondarily mutagenic or carcinogenic, resulting in cumulative damage by inducing mutations or cancer, respectively. While the body has other defenses against toxins, Profet suggested that allergies provide an adaptive last line of defense against those which have previously proven able to bypass the host’s primary antitoxin defense mechanisms. Given the high prevalence and danger of toxins, if allergic capability does indeed provide protection then the phenomenon may have conferred a net advantage across mammalian history, thus explaining its evolutionary retention.

To support her hypothesis, Profet described how substances which tend to trigger allergic reactions (allergens) are commonly toxic, despite this characteristic being previously overlooked and underappreciated. It appeared to her that it was no coincidence that allergenic potential is often in line with toxicity, whether in terms of acute toxicity, mutagenicity, or carcinogenicity. As she pointed out, the four most strongly allergenic metals from the natural environment (arsenic, beryllium, chromium, and nickel) are known to be unambiguously carcinogenic. She also acknowledged that some allergens do not actually appear toxic themselves but noted that in these cases they commonly act as carrier proteins for low-molecular-weight toxins, thus ultimately aiding in toxin-induced damage.

Profet argued that the manifestation of allergies shows adaptive design for protecting the body from toxins before they, and any contained or adhering mutagens, can cause damage. She reasoned that symptoms like sneezing, coughing, vomiting, and diarrhea are consistent with serving a purpose of aiding the physical expulsion of toxic allergens from the nasal passages, lungs, stomach, and intestines, respectively. Meanwhile, she suggested that other symptoms like bronchial constriction, swollen sinuses, and a drop in blood pressure are suited to help block or slow the dissemination of toxins around the body. Interestingly, the benefit of these allergy symptoms may be twofold in that they might facilitate the conditioning of avoidance behavior which reduces future toxin exposure.

Profet also described how less salient features of allergies show good design for the toxin hypothesis but contrastingly poor design for an alternative idea known as the helminth hypothesis. This hypothesis purports that allergies evolved to protect against helminths (parasitic worms) rather than toxins and consequently views allergies towards the diverse range of non-helminth allergens as a by-product of pathogen defense. One example feature suggested by Profet as consistent with the toxin, but not helminth, hypothesis is the urgent and risky nature of allergies. Allergic reactions operate with a rapidity and severity that seems to imply design for countering threats that are able to cause serious harm within minutes or hours. Unlike toxins though, helminths do not impose serious harm in such a short time frame upon parasitizing a host. Profet reasoned that, in addition to other features, it would appear dysfunctional for allergies to have evolved this way if serving a purpose of protecting against helminths.

The toxin hypothesis received great interest from media and the general public with its novel and relatively radical view on the evolution of allergies. However, the hypothesis faced skepticism from the scientific community. Some criticism focused on Profet's educational background, but the predominant concern was the limited evidence demonstrating that allergic capability actually helps to protect against toxins. As interest in

allergies has grown within the last decade, an increasing amount of evidence for the hypothesis has emerged. Support largely comes from two major sources, including research on the association between allergies and risk of cancer and research on the protective effect of allergic capability towards venom.

Allergies and Cancer

One line of evidence commonly used for the toxin hypothesis is the observation that individuals with a history of allergies tend to have a lower risk of developing cancer. Since the early research described by Profet (1991), various meta-analyses and literature reviews have suggested that evidence for this inverse allergy-cancer correlation is substantial, most notably for the risk of glioma (e.g., Amirian et al. 2016). It is reasoned that the lower risk of cancer in allergic individuals reflects the fact that allergies protect the body from toxins, of which many are carcinogenic. However, many researchers consider that this relationship may have arisen rather fortuitously. The immunosurveillance hypothesis, for example, suggests that it occurs simply because allergies are a side effect of a hyperactive immune system that is more efficient at identifying and attacking both foreign allergens and domestic precancerous cells (Il'yasova et al. 2009). Unlike the toxin hypothesis, this suggests that it is not allergies that are reducing the risk of cancer, but the hypervigilant immune system instead. As a result, it is uncertain whether the inverse allergy-cancer correlation is appropriate to use as evidence for the toxin hypothesis.

Nevertheless, the literature on allergies and cancer can be argued as more consistent with the toxin hypothesis. For example, the toxin hypothesis predicts that the inverse allergy-cancer association should occur specifically for cancers of tissues and organ systems that are directly exposed to carcinogens from the external environment and from which the toxic substances can be expelled by allergy symptoms. Conversely, the immunosurveillance hypothesis predicts that the inverse association should be present for cancers

of all tissues and organ systems. A comprehensive review of the literature conducted by Sherman et al. (2008) indicated that research findings are more often consistent with the former prediction, suggesting that the allergy-cancer association may in fact provide suitable, albeit merely correlational, evidence for Profet's toxin hypothesis.

Allergies and Protection Against Venom

Within recent years, a line of experimental evidence has emerged that demonstrates a protective value of allergic capability. These experiments have particularly utilized venoms as they consist of highly toxic components that can cause severe and life-threatening tissue damage and, perhaps unsurprisingly, also have a high allergenic propensity. For example, Marichal et al. (2013) conducted a study in which they injected a group of mice with small doses of honeybee venom (simulating one or two stings), triggering production of venom-specific immunoglobulin E (IgE) antibodies. IgE antibodies are a critical component of the allergic response as they precipitate the release of chemicals, such as histamine, that cause the typical allergy symptoms. The research found that the mice had significantly better outcomes when challenged three weeks later with near-lethal doses of the venom compared to a naïve control group of mice. Specifically, they were three times more likely to survive, had less severe sublethal reactions, and experienced a lower risk of anaphylactic shock. Further, mice who were genetically lacking IgE or the IgE receptor, Fc ϵ RI, did not experience this acquired protective immunity against venom. The authors concluded that key elements of allergic reactivity (IgE-related responses) are critical for enhancing host resistance to harmful venoms, thus supporting the toxin hypothesis.

Conclusion

Profet's hypothesis that allergies are an adaptation to protect against toxins provided a rather provocative explanation for why they exist. The idea may

have initially generated criticism, but it has been increasingly advocated by the scientific community, as encouraged by the growing amount of supporting evidence. The hypothesis certainly requires more testing though and it may be worthwhile for researchers to investigate the potential benefit of allergies for a wider range of toxins, in line with the diversity of allergens. Regardless of the outcome, the hypothesis has provided a refreshing viewpoint on allergies and has stimulated novel questions for allergy research. Ultimately, it is hoped that improving the functional understanding of allergies will pave the way for some concrete developments in the prevention, diagnosis, and treatment of this growing phenomenon.

Cross-References

- Darwinian Medicine and Survival Problems

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Alliance

- Cooperation Among Fishes

Alliance Formation

- Coalitional Relationships

Alliance Formation Theory

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Synonyms

[Evolution of human male homosexuality](#), [Evolutionary theory of homosexuality](#)

Definition

A theory holding that homosexual behavior in human males derives from selection for behavior that reinforces male alliances.

Introduction

The incidence of exclusive same-sex sexual preference (exclusive homosexuality) in humans is greater in men than in women and varies across cultures and historical periods (LeVay 2011). The incidence in contemporary Western cultures is estimated to range between 2 % and 6 % (Barthes et al. 2013). Exclusive homosexuality is an evolutionary paradox, because it does not contribute to reproduction; consequently, it is unclear how genes that may contribute to it are inherited and maintained in the population. The trend in theory and research has been to identify a single explanation. However, recently, some authors have made compelling arguments for more

complex and multicomponent explanations that involve both ultimate (evolutionary) and proximate (environmental, developmental) factors (e.g., LeVay 2011; Poiani 2010).

The alliance theory of male-male sexual behavior in humans posits the development of one of the components that may contribute to the existence of exclusive homosexuality in humans: the evolutionary component. It takes into account theory of human evolution and unique species-specific aspects of human evolution. Nonexclusive homosexual behavior occurs in many animals (Bagemihl 1999), and its causes and functions may be similar in some species and quite different in others (Poiani 2010). Consequently, human homosexual behavior should be studied in the context of the evolution of humans and closely related species. The expression of homosexual behavior among primates varies across species and tends to be confined to Old World monkeys, apes, and humans. This suggests both shared phylogenetic origins and current adaptive value (Poiani 2010).

The Alliance Theory

The alliance theory holds that homosexual behavior reinforced alliances between hominin (human ancestor) males that contributed to their ability to survive and ultimately to find female mates and reproduce (Kirkpatrick 2000; Muscarella 2000, 2006). This may have been particularly adaptive in the case of juvenile males who are likely to have been peripheralized or pushed to the outer edge of the group for some period of time as is seen with juveniles in other species. The juveniles remain peripheralized until they are able to work their way up the male dominance hierarchy. At this time they are vulnerable to predation, intra-species aggression, and lack of resources. The use of homosexual behavior as sociosexual behavior that reinforces alliances is seen in other primates. Dyadic relationships increase the status of both individuals, and their alliance allows both to more effectively defend against aggressors and prevent the taking of resources such as food. The expression of homosexual behavior in human males across history and across cultures can often be

interpreted as supporting alliances between the individuals (Kirkpatrick 2000). There may have been even greater selection pressure for the expression of homosexual behavior as a mechanism of alliance formation in humans because of a factor unique to human evolution.

The Role of Dominance Hierarchies

As described in the alliance theory, one of the most important aspects of human evolution was the development of complex social organization and the characteristics that allowed for this including the abilities to cooperate, form alliances, and live in a dominance hierarchy. Dominance hierarchies would have been in flux for hominins, and one's positions of subordination and dominance would have changed across the lifespan due to developmental changes and changes in the membership of the hierarchy itself as a function of births, deaths, illness, and injury. Human males in particular appear to have evolved numerous behavioral characteristics that facilitate the development and maintenance of within-coalition dominance hierarchies (Geary et al. 2003). In many social animals homosexual behavior serves a sociosexual role for the expression and maintenance of positions of dominance or subordination in a hierarchy and for the establishment of pair-bonds that lead to alliance formations (Poiani 2010). This is particularly evident in humans' closest primate relatives, chimpanzees and bonobos (Muscarella 2000). Homosexual behavior in humans is speculated to be an exaptation, that is, it may have evolved originally as a sociosexual behavior related to the expression of dominance and subordination and selection acted upon it further, because it also contributed to the development and reinforcement of alliances that contributed directly to survival and indirectly to reproduction (Muscarella 2006).

Conclusion

The alliance theory actually describes selection for bisexual behavior, that is, nonexclusive

homosexual behavior under certain circumstances and heterosexual behavior, which is the sine qua non of reproduction and the passing on of genes that may be related to homosexual behavior. The theory does not account for exclusive homosexual behavior which is posited to be due to an interaction between the species-specific and genetically influenced expression of homosexual behavior characteristic of humans and developmental, ecological, cultural, and psychological factors (Kirkpatrick 2000; LeVay 2011; Muscarella 2006; Poiani 2010). The alliance theory does not address female homosexual behavior although it may also be related to alliance formation (Muscarella 2000; Poiani 2010). However, the evolutionary nature of human female dominance hierarchies and coalitional strategies is very different from that of human males (Geary et al. 2003), which may affect the expression of homosexual behavior in human females (Muscarella 2015). The alliance theory has heuristic value, but to date, there is no empirical evidence that supports it.

Cross-References

- [Cultural Differences in Sexual Socialization](#)
- [Evolution of Cooperation](#)
- [Evolution of the Brain, The](#)
- [Living in Groups](#)
- [Same-Sex Relationships](#)
- [Sex as Bonding Mechanisms](#)
- [Why Humans Are Unique](#)

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Alliances

- ▶ In-Group Versus Out-Group
- ▶ Prisoner's Dilemma Outcomes
- ▶ Science and Morality

Allocare

- ▶ Access to Alloparents

Allocation of Attention

- ▶ Selective Attunement to Adaptive Problems

Allogrooming

- ▶ Cooperative Grooming

Allomother

- ▶ Access to Alloparents

Allomothering

- ▶ Aunt Care
- ▶ Mothers and Maternal Grandmothers and Childhood Survival

Alloparenting

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Synonyms

Babysitting; Caregiving; Communal breeding; Cooperative breeding; Cooperative childrearing

Definition

Caregiving by nonparental caregivers, who provide direct and/or indirect investments to a child

Introduction

Who helped you develop into the person you are today? Most of us may think about a parent or parents, but many of us would also recognize the important role of other people. Perhaps it's a teacher, a grandparent, or a neighborhood friend. The fact that we are supported by many people in our childhood is, in fact, very unusual: In non-human mammals, support – or investments – for juveniles are typically and solely provided by the biological mother. Only 9–10% of mammals display parental care, where biological fathers are additionally involved in raising offspring, without the support of other helpers (Kleiman and Malcolm 1981). In humans, we see a notably different system of facultative fathering, where

biological fathers may or may not provide investments into their children, combined with a range of additional caregivers beyond the biological parents. These additional caregivers, or alloparents, can include siblings, grandparents, and extended kin, as well as nonrelatives such as step-parents, friends, and neighbors.

Support from alloparents, meaning “other parents,” is arguably an obligate human characteristic. This is because, compared to other primates, humans have an extended childhood and adolescence: while the conceptualization and timing of adulthood does somewhat vary between cultures, broadly speaking, humans do not become “mature” and self-sustaining until their mid-teens to early 20s. During childhood and adolescence, we experience a prolonged period of physical growth and skills development, making us dependent on sustained support from parents and alloparents to survive, develop, and successfully reach adulthood. Nonparental caregivers are therefore *necessary* for successful reproduction and childrearing in humans – although who supports parents and how varies cross-culturally.

But how did alloparenting evolve? Why do alloparents help in childrearing, and how do they influence parental fitness? This chapter provides an overview of alloparenting in humans, outlining different types of alloparenting, broadly addressing the evolution of alloparenting and providing a brief review of key alloparents in humans across cultures.

Defining Alloparenting

In its essence, alloparenting is a transfer of time, energy, and/or resources to non-offspring, with opportunity costs against any other behavior. This can be conceptualized as *alloparental investments* into a non-offspring which, all things being equal, is expected to increase non-offspring biological fitness (with fitness meaning the ability to survive and reproduce). Humans join the 3% of mammalian species where alloparenting is the norm, where successful reproduction and offspring survival is dependent on the help from

nonparental caregivers (Lukas and Clutton-Brock 2012).

To date, research on alloparenting in humans is often referred to as the “cooperative breeding literature.” However, there has been some debate among researchers on whether humans should be classified as cooperative breeders at all. Partly, this may be the outcome of some confusion and variation around what cooperative and communal breeding means between disciplines. These terms are often used ambiguously, and sometimes interchangeably, likely exacerbated by the fact that “communal breeding” and “cooperative breeding” are often unaccompanied by clear definitions.

Is Alloparenting the Same as Cooperative Breeding?

In the nonhuman animal literature, cooperative breeding is defined as a system where a dominant female monopolizes breeding, aided by subordinate and nonbreeding alloparents who forgo their own reproduction. In contrast, communal breeding refers to a system where multiple females reproduce, often pooling their resources and young (Lukas and Clutton-Brock 2012). Confusingly, humans have been argued to be both cooperative and communal breeders. The long pre- and post-reproductive life stages in humans have been interpreted as evolved characteristics of reproductive suppression, which is a defining characteristic of cooperative breeding (Lukas and Clutton-Brock 2012): Older, reproductively mature children may temporarily “forgo reproduction” and help care for their younger siblings, while grandmothers have been argued to have a long post-reproductive lifespan to help care for their grandchildren. At the same time, mothers rarely, if ever, monopolize reproduction in human groups. As a species, we typically live in groups of multiple parents with children, where parents and alloparents share resource and care. This pattern seems to be similar in feature to communal breeders.

Clearly, humans do not fit neatly into either category of communal or cooperative breeding as strictly defined. Instead, humans cooperate broadly and flexibly around reproduction and childrearing, with alloparenting being a norm.

With this context, in this chapter we purposely avoid labelling humans as cooperative breeders. Instead, we stick to the terms *alloparenting* and introduce the term *cooperative childrearing*. The word “cooperative” is maintained, as there is no denying that alloparenting is a cooperative act (reviewed in more detail below). However, by directing attention to “childrearing,” which is uniquely attributable to humans and children, it clarifies that the human system varies from cooperative breeders in the strictest sense. In humans, alloparenting does not necessarily mean individuals forgo reproduction, while recognizing that some alloparents do.

How is Alloparenting Conceptualized?

Alloparenting is an inherent part of cooperative childrearing. However, like cooperative and communal breeding, alloparenting as a term has been defined, conceptualized, and categorized in different ways within and between disciplines. This is perhaps reflective of the fact that alloparents can invest in different ways, with different pathways of investment transfer. To fully capture the diversity in alloparental investments, alloparenting in humans can be conceptualized in three distinct ways: (1) provisioning vs caregiving, addressing the types of alloparental investments, (2) direct vs indirect, addressing the pathways of alloparental investments, and (3) additive vs substitutive, addressing alloparenting systems.

Types of Alloparental Investments: Provisioning Versus Caregiving

Alloparental investment behaviors can be broadly categorized into *provisioning*, which is a transfer of resources to parents and/or children, and *caregiving*, which is a transfer of time and energy to care for the child. Alloparental investments via provisioning can involve any form of resource, including food, wealth, and other materials, and the generation of resources (i.e., production) is often an important aspect of provisioning. For example, hunting behavior by men in forager populations are often conceptualized as provisioning activities. Similarly, in developed populations, grandparents providing financial transfers to parents and grandchildren can be

conceptualized as provisioning. Alloparental investments via caregiving include physical care and feeding children, as well as teaching and play. For example, across societies, older children or adults often carry infants and young children, which is a type of caregiving activity.

It is important to note that production activities are often incompatible with caregiving. This means alloparents, like parents, are generally unable to do both things at the same time (Emmott 2015). In the Hadza hunter-gatherers of Tanzania, for example, mothers are reportedly not able to carry toddlers while they go out and forage for food, and so must leave these relatively young children in camp (Blurton Jones et al. 2005). Similarly, in developed populations, the conflict between employment and providing childcare is widely recognized (e.g., see Allen 2003), as unsurprisingly not many workplaces allow people to bring children on a regular basis. Because of these difficulties in combining provisioning and childcare, alloparents may specialize in providing a particular type of investment.

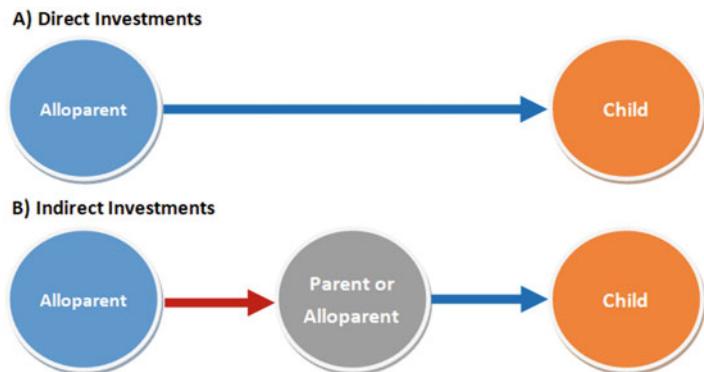
Pathways of Alloparental Investments: Direct Versus Indirect

Because alloparenting in humans exists within a social network, alloparenting behaviors can be described in terms of the pathway it takes for the time/energy/resources to be transferred to the child, or how alloparental investments into children “arrive.” Broadly, there are two types of alloparental investment pathways: direct investments and indirect investments.

Direct investments are defined as any form of alloparental time/energy/resource which is transferred directly to the child (Fig. 1). For example, in the Gussi of Western Kenya, mothers reportedly assign “sibling alloparents” to their toddlers who become partly responsible for carrying, feeding, and generally looking after the younger sibling (LeVine et al. 1996). In the UK, stepfathers have been found to provide care to their unrelated young children, including playing with children, reading to them, and feeding them (Emmott and Mace 2014). In Japan, a traditional custom called “otoshidama” exists where kin and non-kin adults gift money directly to children over the New Year

Alloparenting,

Fig. 1 Representation of (a) direct investments and (b) indirect investments by alloparents. Children always receive direct investments. Indirect investments can be transferred to another investor (parent or alloparent) who utilizes it to provide direct investments



period. Under this custom, children generally have the autonomy in how they spend their otoshidama money, and parents are not involved in the “financial transfer” apart from perhaps providing some advice to their children on the ways to spend the money (personal observation by author, EHE). In all these examples, alloparents invest in children *directly* without going through other caregivers and parents.

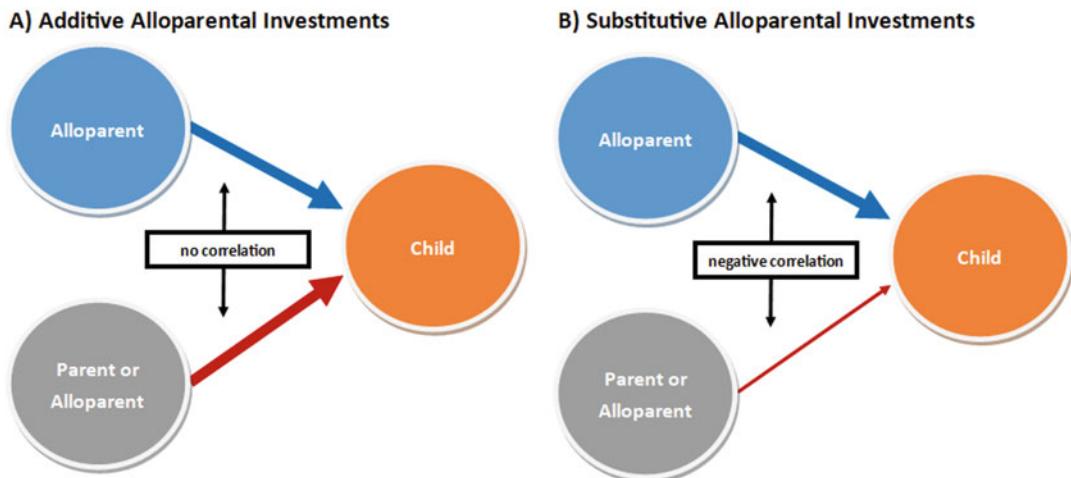
Note, direct investments do not necessarily require direct contact between the alloparent and child. In the Agta foragers from the Philippines, for example, the majority of observed childcare could be defined as passive, proximity-based care without direct engagement. Here, children stay in camp and play together while adults forage, but one or two older adolescents or older adults would stay behind to “keep an eye” on the children (personal observation by author, AEP). Some may question whether such a minimal investment activity is, in fact, meaningful direct alloparenting. However, regardless of the level of effort involved in passive childcare, alloparents are still likely to be experiencing opportunity costs as they could be doing other activities. While passive childcare is often viewed as an “inferior” type of direct investments in Western cultures, passive childcare can be crucial because, regardless what the caregiver is doing for the majority of the time, alloparents are able to react and help the child when required (Meehan et al. 2013).

Indirect investments are defined as any form of alloparental time/energy/resource transfer made to an individual, who then *converts* the gained

time/energy/resource into direct investments to the child (Fig. 1). To put it differently, the transfer from an alloparent to the child is fully mediated by an “intermediate” person. Indirect investments can, for example, be directed towards the parent who then uses this extra support to provide care to the child. In rural Ethiopia, maternal grandmothers were found to frequently contribute to heavy domestic tasks, while paternal grandmothers contributed to agricultural labor, which were both associated with greater child survival (Gibson and Mace 2005). Here, while grandmothers were not directly engaging with the children, their indirect contributions to household production and labor were likely “transferred” into child quality. Such activities by alloparents can be classified as indirect investments, as the alloparent raises resources or frees some time for the parent, who is then able to direct investments towards the focal child.

Alloparenting Systems: Substitutive Versus Additive

Within the cooperative childrearing system, direct and indirect alloparental investments do not happen in isolation but exists within a dynamic network of caregivers around the child and parents. All things being equal, alloparental investments are expected to have a beneficial effect on child quality. However, whether or not alloparenting has a “net benefit” for child quality depends on if and how other caregivers react to that alloparenting. Broadly, alloparenting can be *additive*, where it does not influence the level of maternal or paternal investments, or it can be *substitutive*,



Alloparenting, Fig. 2 Representation of (a) additive alloparental investments and (b) substitutive alloparental investments by alloparents. In additive alloparental invest, the amount of alloparental investments do not influence parental investments. In substitutive alloparental

investments, there is a negative correlation in the investments between the alloparent and parent (or another alloparent), where an increase in alloparental investments are associated with a decrease in parental investments

where mothers and/or fathers reduce their investments which is “topped-up” by alloparents. While alloparenting under both systems are expected to benefit parental fitness, substitutive alloparenting is not expected to lead to higher child quality. Depending on the quality of alloparental investments, substitutive alloparenting may even have a detrimental effect on child fitness.

Additive alloparental investments are transfers of time/energy/resources into the child, which does not influence the investment behavior of mothers and/or fathers (Fig. 2). This has sometimes been discussed as “constant breeder input,” where parental investments are insensitive to the behavior of alloparents (Kushnick 2012). Whether alloparenting is additive – as in, whether parental investments are insensitive to the help from others – may depend on whether the parental investment behaviors are replaceable. For example, breastfeeding is (usually) dependent on the mother, and alloparents may have less scope to influence breastfeeding compared to other types of parental investment behaviors (Kushnick 2012), particularly in contexts where formula milk is not readily available.

In an additive alloparenting system, children always experience a “net gain.” Additive

investments are therefore expected to lead to higher child quality, and it may be more likely to be found in contexts where parents optimize child quality over quantity (and therefore parents do not “reduce” investments when others provide help). For example, in a UK sample, contact with maternal and paternal grandparents were not associated with differential levels of maternal or paternal caregiving (Emmott 2015), suggesting grandparental direct investments in this population may be additive. In contemporary China, living near maternal grandparents and availability of them as alloparents was not associated with differential levels of maternal caregiving (Chen et al. 2000).

Substitutive alloparental investments are transfers of time/energy/resources into the child, which then “releases” parents from having to make those investments (Fig. 2). Parents then redirect their energy into other activities, helping them achieve higher fitness. This is sometimes referred to as “load lightening,” where the more help parents receive from alloparents, the less investments they provide to their children (Kushnick 2012). For example, in the Maya and Pume, for every 10% increase in direct alloparental care was associated with a 25% decrease in the probability of maternal caregiving, estimated to be a potential

saving of 165 kcals per day (Kramer and Veile 2018). This suggests that alloparents in these populations were allowing mothers to withdraw from childcare, giving them extra time and energy to carry out other activities. Similarly, in the Aka foragers of the Central African Republic, grandmother caregiving was associated with a reduction in maternal childcare and an increase in maternal foraging activities (Meehan et al. 2013), suggesting grandmothers were substituting maternal caregiving which allowed mothers to divert her time and energy into production.

With substitutive investments, alloparenting does not necessarily lead to a “net gain” for children due to the reduced investments from mothers and/or fathers. For example, in the Maya and Pume example previously mentioned, direct alloparental care was not associated with increased physical child quality, measured by child weight (Kramer and Veile 2018). In fact, if the alloparenting quality is inferior, receiving substitutive investments from alloparents could lead to *reduced* child fitness. For instance, in the UK, availability of grandmothers as alloparents has been associated with lower levels of breastfeeding (Emmott and Mace 2015), presumably as grandmothers are able to “substitute” infant feeding via formula, thereby increasing the incentives for mothers to stop breastfeeding. Given the benefits of breast milk for infant development, such substitutive alloparenting may not be beneficial for children. Similarly, in the Agta foragers, maternal and paternal grandmothers have been observed to become the main caregiver of an infant while the mother temporarily left camp to look for work. However, because this led to breastfeeding cessation, and grandmothers did not have access to formula and/or clean water, it was not uncommon for these infants to become very malnourished, parasitized, suffer from severe gastrointestinal disease, and sometimes die as a result (personal observation by author, AEP). In such cases, alloparenting, despite all the best intentions, does not lead to benefits for the child.

While substitutive investments do not necessarily lead to higher child quality, they may nonetheless increase parental fitness via increased

fertility. Such substitutive investment systems may be more prevalent in populations where it is adaptive for parents to optimize child quantity over quality. For instance, in contemporary Thailand, residence with paternal kin after marriage was associated with higher fertility for parents, but it did not influence child outcomes (Snopkowski and Sear 2013). The consequence of increased fertility may also be increased sibling competition, with potentially negative consequences for child outcomes (Lawson et al. 2012).

Whether alloparenting is substitutive or additive may vary between maternal and paternal kin: From an evolutionary perspective, there is an unequal cost to reproduction between the sexes, where males can reproduce “cheaply” by providing relatively unlimited sperm, while females pay a higher cost due to their larger, limited eggs. In mammals, this is followed by a long gestation and lactation period for females, which is energetically expensive. Because of this asymmetry in the costs in reproduction, we hypothesize a sexual conflict between the sexes where the optimal number of offspring is expected to be higher for males than females. Given this mismatch, there may be greater incentives for paternal kin (i.e., father’s family) to help parents achieve higher fertility by providing substitutive alloparental investments, while maternal kin (i.e., mother’s family) may be better inclined to help parents achieve higher child quality. For instance, in the China example mentioned above, living near or with paternal grandparents was associated with reduced maternal caregiving (Chen et al. 2000), which could be because paternal grandparents “released” mothers from providing childcare so she could reinvest this energy into activities which lead to higher fertility. Similarly, in the Karo Batak subsistence agriculturalists of Indonesia, receiving help from paternal kin was associated with mothers increasing farmwork, while receiving help from maternal kin was associated with mothers spending more time carrying children (Kushnick 2012). This could be because paternal kin facilitated higher levels of maternal production which can be transferred into higher fertility (because female reproduction is limited by resources). In contrast, maternal kin may have

facilitated higher levels of investments into existing children, thereby increasing child quality.

The Evolution of Alloparenting in Humans

When considering the evolution of alloparenting in humans, it is important to note that alloparenting behavior in itself has been observed across many species. In nonhuman primates, allo-mothering (which includes alloparenting and fathering) is common, having been described in 74% of the 154 species where data is available (Tecot and Baden 2015). However, in most species, this behavior is not a defining feature of their breeding system, and may even be “misfired” alloparenting whereby caregiving behaviors are misdirected to non-offspring.

In contrast, alloparenting in humans is arguably a defining feature of human childrearing and is observed across human populations: In the Aka foragers, infants have been found to have, on average, 21 different caregivers which include kin and non-kin (Meehan et al. 2013). In the Hausa of Nigeria (sub-Saharan agriculturalists), children had 4.8 different caregivers on average (LeVine et al. 1996). In contemporary developed populations, parents rely on relatives such as grandparents, aunts, and uncles for childcare, as well as more formal arrangements such as day-care centers and crèches (Allen 2003; Langer and Ribarich 2007).

How did alloparenting evolve to become a diverse yet obligate human characteristic? Researchers have argued that alloparenting is both a cause and consequence of our unusual life-history, which involves a “premature” birth of infants, essentially helpless for a substantial postnatal period, followed by an extended childhood and adolescence. The combination of prematurity and slow growth means that human offspring are particularly dependent on alloparental investments for survival and optimal development into adulthood. It has been hypothesized that the level of alloparenting required is so high in humans that mothers were unable to successfully raise children without alloparents in our

evolutionary history (Hrdy 2009). It has also been hypothesized that alloparenting coevolved with other species-typical characteristics such as short interbirth intervals leading to multiple dependent children, and a long, post-reproductive lifespan (Hrdy 2009).

Underpinning the species-level evolution of alloparenting and cooperative childrearing are individual-level selection pressures. For the recipient, the fitness benefits of alloparental support seems intuitive, where children and parents who receive time, energy, and/or resources have improved survival and reproduction (Sear and Coall 2011). But why do alloparents help, given that it is associated with some form of cost? As with any form of cooperation, the evolution of such helping behaviors is puzzling due to a “free rider” problem: Those who receive help but do not help in return gain the largest fitness benefit, meaning the “free rider” phenotype would rapidly spread through the population, resulting in the population no longer being cooperative. Therefore, assuming selection pressures act on individual traits, alloparenting would only evolve if there are some kind of fitness benefits from helping. Outlined below are the hypothesized individual fitness benefits for alloparenting which may explain the evolution of cooperative childrearing, focusing on indirect fitness benefits (what alloparents gain via improving the survival/reproduction of their relatives) and direct fitness benefits (what fitness benefits alloparents gain by improving their own survival/reproduction).

Indirect Fitness Benefits

An individual’s inclusive fitness is the sum of their own fitness (i.e., direct fitness) and the fitness of kin (i.e., direct fitness). Therefore, alloparents may gain indirect benefits by improving the fitness of their relatives. This means alloparenting can evolve via kin selection, where a costly behavior can be selected for if the fitness benefits gained by the receiver (B), weighted by the coefficient of relatedness between the helper and the receiver (r), is larger than the fitness costs incurred by the helper ($rB > C$). In case of additive alloparental investments, investing in related children

is expected to increase the alloparent's inclusive fitness if this resulted in increased survival and future reproductive success of that child. In case of substitutive alloparental investments, alloparenting may increase inclusive fitness by facilitating parents who are relatives to decrease parental investments into a specific child, allowing them to invest more in fertility (i.e., having more children) and/or increasing investments in other children.

If kin selection is an important aspect of alloparenting, we would expect alloparents to preferentially help relatives. Evidence strongly supports the role of relatedness as a driver of alloparenting in humans: For example, across traditional societies, maternal grandmother presence has been found to be more likely to be associated with higher child survival compared to paternal grandmother presence, supposedly due to higher relatedness certainty amongst maternal kin (Sear and Mace 2008). Similarly, in contemporary societies, maternal grandparents have been found to invest more in their grandchildren than paternal grandparents (Pollet et al. 2009).

However, regardless of relatedness, when benefits of cooperation are low, the motivation to allomother can diminish and alloparenting may consequently be withheld. In humans and other animals, evidence suggests that alloparenting is sensitive by broader "pay-offs," which can be influenced by factors such as reproductive value, resources/wealth and local competition (Sear and Mace 2008). While kin selection and indirect fitness benefits are a pervasive explanation for cooperative behavior, it is important to note that it is not the *sole* explanation for alloparenting. In humans, parents and children frequently live amongst and cooperate with friends and other nonrelatives. Even if parents, children and alloparents are related, alloparents may help for different reasons – gaining both direct *and* indirect fitness benefits. Just because two individuals are related does not mean their cooperation is *only* motivated by indirect fitness benefits. To fully understand why alloparents provide help, it is essential to consider what individuals gain beyond indirect fitness benefits.

Direct Fitness Benefits

Kin selection is unlikely to explain all cases of alloparenting, as cross-cultural evidence suggests humans frequently help raise unrelated children. Instead, alloparents may be motivated to help raise children because they gain a "direct benefit" leading to higher fitness. For instance, individuals may gain valuable parenting experience which improves their parenting skill, leading to higher reproductive success in the future. Alloparenting may also serve as a costly signal which helps alloparents access reproductive opportunities, or it can be part of a reciprocal relationship in the broader cooperative social system. All these pathways may increase the individual's fitness, promoting the maintenance of cooperative childrearing.

Learning-to-Mother/Parenting Experience

The learning-to-mother hypothesis, first proposed by Jane Lancaster, posits that young, non-reproductively active females may alloparent to learn and develop their mothering skills, since more experienced mothers tend to have better infant outcomes. This has been broadened to parenting more generally, where male and female helpers could gain direct benefits via caregiving skills development (Kramer and Veile 2018). Such "parenting practice" could be adaptive for alloparents if offspring are highly vulnerable and dependent on high quality care for survival.

To date, this hypothesis has been mainly discussed in the context of female alloparenting found amongst nonhuman primates. For example, in female vervet monkeys, alloparenting experience before their first birth was associated with higher survival of their firstborn infants (Fairbanks 1990). However, for this hypothesis to be convincing, there are some questions which need to be addressed: First, if infants are so vulnerable, why would mothers allow inexperienced, unskilled individuals to provide childcare? This is likely to *cost* mothers and infants rather than help, and in fact this has been proposed as one of the reasons why alloparenting is not more widely observed among primates (Hrdy 2009). Second, does alloparenting actually lead to parenting skills development and higher

reproductive success in adulthood? The evidence is currently sparse. For example, an analysis of Mayan data found that girls who spent more time in allocare did not have more surviving children as adults (Kramer and Veile 2018). Importantly, the parenting experience hypothesis only applies to direct alloparental investments, involving direct care, and does not explain any form of indirect investments commonly observed among humans. Nonetheless, future studies could investigate the parenting experience hypothesis in humans, for example by explicitly testing whether caregiving by pre-reproductive individuals lead to higher parenting skills in later life.

Costly Signaling and Mating Effort

The Bateman's principle states that male reproductive success is limited by access to females, while female reproductive success is limited by access to resources. This means females across species are generally the choosier sex in terms of reproduction, and males need to compete and advertise their quality. Men may therefore opt to incur the cost of alloparenting as a way to signal his quality, known as "costly signaling." Costly signaling via provisioning for mothers and children may be a particularly important factor for male alloparenting in humans: While nonhuman primate males rarely share food with others, hunting followed by extensive food-sharing is observed widely across forager populations. Some have argued that hunting and food-sharing by men function as a costly signal, where men "show off" their health and skill, becoming more attractive to potential reproductive partners. For example, in the Mermain islanders of Australia, men cooperatively hunt turtles which are shared with the group, meaning turtle-hunters provision parents (indirect alloparental investments) as well as children (direct alloparental investments). In this population, turtle hunting has been argued to be a form of costly signaling as hunting turtles successfully require high levels of skill, which is socially recognized (Smith et al. 2003). Compared to other men, turtle-hunters have more reproductive partners (Smith et al. 2003), suggesting this provisioning activity in this

particular population may be directly benefiting male reproductive success.

Given female reproduction is limited by resources, men could also provide allocare in exchange for mating opportunities, similar in concept to a reciprocal exchange (see "[Reciprocity](#)" section below). Alloparenting by stepfathers is one such example, where it has been hypothesized that stepfathers provide care to stepchildren in order to form and maintain a reproductive pair with mothers (Anderson 2000). In the USA, stepfathers were on average less educated and had lower levels of income than fathers (Anderson 2000). Partnering with mothers (rather than women with no children) and helping raise their children may be a way to overcome their "lower provisioning potential," allowing them to successfully partner with a woman and eventually have their own children (Anderson 2000).

Of course, alloparenting as costly signaling and mating effort is primarily applicable to men, or at least for individuals seeking reproductive opportunities – and does not explain alloparenting by other individuals such as women, children, and post-reproductive adults. It is also important to note that whether male provisioning and caregiving functions as a costly signal may depend on population context: In the Tsimane forager-horticulturalists from Bolivia, for example, patterns of caregiving by men suggested that men were unlikely to be providing alloparental childcare as a costly signal. This is because men tended to provide care when a child's mother was absent rather than when the child's mother was present (Winking et al. 2009). This suggests that men provided childcare based on the need of alloparenting, rather than the opportunity to "show-off" their potential parenting skills to women. Overall, the costly signaling hypothesis is limited by its ability to alloparenting more generally and is likely to be only applicable to a small proportion of male alloparents.

Reciprocity

Alloparenting may exist as part of a reciprocal cooperative interaction, understood as "I'll scratch your back if you scratch mine." Such cooperation can evolve if the cost of helping

someone in the present is outweighed by the benefits the helper receives in return at some point in the future, lessened by the probability that this benefit may or may not occur. In humans, the probability of not receiving the later benefit (i.e., not getting your back scratched) may often be small as we have repeated interactions with the same individuals across large sections of our life. Individuals can also be picky about who they interact with, and may preferentially assort with individuals who cooperated with them previously (an in turn, excluding those who do not cooperate).

Researchers have found significant support for reciprocity driving cooperation across different domains of human behavior, although few have explicitly explored the role of reciprocity in childrearing. An exception is work by Jaeggi et al. (2016) who demonstrate the importance of reciprocity in explaining alloparental caregiving in the Tsimane forager-horticulturalists from Bolivia. In developed populations, reciprocal interactions around alloparenting often involve financial payment, such as professional nannies and childminders (e.g., see Allen 2003), but studies have also described alloparenting between neighbors and friends as part of a reciprocal arrangement. Interestingly, work in other species suggests that the fitness payoffs of cooperating are higher when the environment is marginal and unpredictable (Jaeggi et al. 2016), and living in larger groups, cooperating and pooling resources can be an adaptive strategy to buffer against environmental fluctuations. In humans, cooperative childrearing may therefore have evolved to mitigate risks that come with less secure, more variable environments. In this system of reciprocal helping, individuals ultimately end up benefitting as they provide help when they can afford to do so, in exchange for help later on when they are in need.

To summarize, alloparenting can be conceptualized as a cooperative behavior involving immediate costs to the helper and benefits to the recipient. Ultimately, alloparenting is hypothesized to only evolve if there is some form of fitness benefit to the helper. In humans, alloparents likely gain benefits in different ways

depending on the context, where alloparenting for close kin brings indirect and direct fitness benefits, while alloparenting for nonrelatives, friends, and strangers is expected to be associated with direct fitness benefits. This multifaceted cooperation likely facilitated and coevolved with the unique human life history, ultimately leading to cooperative childrearing from such a broad range of alloparents becoming an obligate human characteristic.

Key Alloparents Across Cultures

Who helps with childrearing and how they help varies across societies. This is not surprising given the many different selection pressures which encourages (or discourages) alloparenting, meaning the costs and benefits for alloparenting is likely to be context dependent. Nonetheless, there are particular alloparents in humans who have been frequently identified as important for parents and children.

Grandparents

The “Grandmothering hypothesis” states that the unusual postmenopausal lifespan in humans evolved due to the importance of grandmother support for successful reproduction and childrearing (Hrdy 2009). It posits that reproductive cessation through menopause facilitates allo-mothering, in that grandmothers can care and provide for their grandchildren without experiencing reproductive conflict with the mother. Studies have shown that grandmothers are more willing to provide alloparental investments (Gibson and Mace 2005). Alloparental investments from grandmothers may be particularly important during the “costly” period of infancy and young childhood, when children are particularly dependent on others for support.

Grandparents, particularly maternal grandmothers, may be important alloparents in humans. Assuming paternity certainty, grandmothers are 25% related to their grand-offspring, and therefore gain significant indirect fitness benefits due to this cooperation. A review of kin presence and its associations with child survivorship found that

maternal grandmother presence was positively correlated with child survival in 69% of studies on traditional, natural fertility populations ($n = 46$, Sear and Mace 2008). Paternal grandmothers were positively associated with child survival in 53% of studies ($n = 17$, Sear and Mace 2008). Literature on grandmothering in developed populations also highlight they are important providers of childcare and financial support and may be particularly important for children's psychological and socio-emotional development (Sear and Coall 2011).

However, the importance of grandmothers as alloparents may be context dependent. In developed populations, grandparents may be particularly important caregivers when families are under stress and/or in need of support (Sear and Coall 2011), meaning if families are "doing well," grandmothers may not be particularly important for children and parents. In the Aka foragers, grandmother absence (thereby lack of grandmother alloparenting) was only associated with a negative effect on child developmental outcomes in patrilocal camps, where mothers lived with the father's relatives (Meehan et al. 2014). The authors suggest the association between grandmother absence and poorer child outcomes was not observed in matrilocal camps, because the availability of other maternal kin as alloparents in these camps buffered the "loss" of a grandmother. This highlights that, while grandmothers are important alloparents in a range of cross-cultural populations, wider alloparental networks can also be important for parents and children. Whether or not grandmothers are key alloparents may therefore depend on who else is around to help beyond grandmothers.

Siblings and Other Children

In higher-fertility populations, children often have multiple siblings who can be important caregivers, who frequently provide a lot of the direct alloparenting a child receives (Kramer and Veile 2018). Importantly, in the Pume and Maya, childcare from siblings was not associated with significant decreases in economic activities or education, suggesting children were not suffering from opportunity costs due to their helping

(Kramer and Veile 2018). This suggests that children, and siblings in particular, may be very willing alloparents as they do not suffer enduring fitness costs from being alloparents. Indeed, studies have shown the "benefits" siblings may bring to children: in the Gambia, older sisters were associated with increased survival of younger siblings (Sear and Mace 2008).

However, children can also be competitors for parental investments and household resources. As such, having a large number of siblings, and high levels of sibling competition, may lead to poorer fitness outcomes for children (Lawson et al. 2012). While studies to date investigating the number of siblings and child outcomes in different populations have returned mixed results (Lawson et al. 2012), a large-scale study using data from 27 countries across sub-Saharan Africa found that higher fertility (and therefore more siblings) was associated with higher child mortality, highlighting the possible detrimental effect sibling competition (Lawson et al. 2012). Again, this highlights the importance of local context. In situations where resources or investments are plentiful, siblings may serve as very helpful alloparents. However, in situations where siblings need to compete with each other for resources or investments, siblings may hinder rather than help.

Beyond siblings, other unrelated children can certainly be alloparents. This may be particularly important in societies where children spend time together as a group, such as in the Hadza foragers where children and young adolescents stay in camp and play while adults hunt and forage (Blurton Jones et al. 2005), as well as in developed and developing populations where children spend an extended period of time with each other at school. Among the Aka foragers, where a range of alloparents care for children, unrelated children are described as an important part of the wider caregiving network (Meehan et al. 2013). While children caring for children is not a well-recognized form of caregiving in Western contexts, and in fact sometimes conceptualized as harmful, it is a widely observed behavior which is likely to impact child quality – and studies show children make meaningful contributions as alloparents (Meehan et al. 2013).

Peers of Parents and Other Households

In communal breeding species, other mothers and parents – who may or may not be related – are important sources of support as they pool resources to raise offspring. In humans, parents may form a collaborative network with other households because they live nearby, where parents and alloparents to collaborate to raise children. Often, other households in the collaborative network are relatives: For instance, among the Pimbwe, the number of maternal aunts and uncles who were likely of reproductive age (i.e., mother's adult siblings) was associated with higher child weight, particularly for families with low socioeconomic status where parents and children “in need” benefitted by receiving help from aunts and uncles (Hadley 2004). The benefits of aunts and uncles have also been reported in developed populations, where they are often important caregivers and sources of support for children (Langer and Ribarich 2007). It is important to note, however, that aunts and uncles are not necessarily expected to be beneficial alloparents, and it is likely to be dependent on local context. In situations where parents experience local resource competition with their adult siblings, the presence of aunts and uncles may even be detrimental.

Given that humans live in complex groups and display high levels of cooperation with unrelated individuals, there is potential that non-kin peers and households are also important alloparents. However, at present, the literature on alloparenting by unrelated peers is generally limited, while there is work on the importance of diverse and unrelated social networks. In the Agta (Philippines) and BaYaka (Republic of Congo) foragers, nonrelatives were essential components of mothers' social networks. In these populations, mothers who were directly connected (in terms of proximity) to many individuals in their social network, be them kin or non-kin, had higher fertility. This suggests that having access to a large number of different types of helpers may be important for parents to successfully reproduce (Page et al. 2017). Having a diverse and

flexible social network may be more adapted to tackle variable and unpredictable environments experienced by many hunter-gatherers. In contrast, relying on a limited number of co-resident relatives, who have their own childcare and subsistence demands, may not be an optimal strategy to ensuring childcare demands are met. Overall, this suggests that both individuals beyond your household *and* your relatives are likely to be important alloparents – at least in forager populations – but this requires further exploration. We can also hypothesize that such unrelated peers and households may be of particular importance in low-fertility populations with neolocal norms, as family members may simply be unavailable for alloparental support.

Institutional Alloparents

In many developed settings, the demographic transition and smaller family sizes have meant parents have fewer relatives to rely on as alloparents. This has also coincided with strong nuclear family norms where parents are perceived as primary caregivers of children (Emmott 2015). Arguably, the cooperative childrearing system in developed populations now rely less on informal social networks, but more so on institutional alloparenting where the state and other institutions provide or organize support to help raise children. This includes professional workers whose role is to support families and children, such as social workers and teachers, as well as financial provisioning and subsidies via welfare payments and tax breaks. In Nordic countries, for example, childcare is perceived to be a joint responsibility between the parents and the state, and consequently the state guarantees subsidized or free formal childcare for parents (Emmott 2015). Studies show institutional alloparenting across developed populations may be beneficial for children, with formal childcare associated with better child development (Melhuish 2004). However, the quality of caregiving by institutional alloparents are known to vary, and poor-quality care may have detrimental effects on children's outcomes (Melhuish 2004).

Conclusion

Alloparenting is a diverse yet cross-culturally observed behavior which exists as part of the cooperative childrearing system in humans, hypothesized to have coevolved with our unusual life history. Important alloparents include grandparents, children and siblings, and other households – and in developed populations, institutional alloparenting is provided where the state provides financial transfers for families and/or organizes “professional alloparents.” However, who provides alloparenting and how they help varies within and between populations.

The motivation for alloparents to help raise children depends on the indirect and direct fitness benefits they gain from cooperating. Therefore, in trying to understand the ultimate reasons behind alloparenting (or why alloparenting exists), it is important to consider a multitude of factors such as what individuals gain from helping kin, if they learn new skills, if they achieve social standing, or whether helping now ensures that they receive help in the future. Nonetheless, in particularly harsh environments, co-operators may become competitors for resources. In this sense, an evolutionary approach to alloparenting predicts variations in the structure and nature of cooperative childrearing systems depending on the local population context. In some populations, particular types of kin may be important – such as grandparents and siblings. In other populations, it may be fellow parents and other households who mainly contribute and support childrearing. Whatever the form of cooperative childrearing systems, however, what is clear is that humans require additional support from alloparents for successful childrearing and reproduction.

Cross-References

- Adoption Preferences
- Childcare
- Child Care
- Consolidating Familial Power
- Cooperation

- Cooperation Among Nonchimpanzee, Non-human Primates
- Forms of Adoption
- Function of Adoption
- Grandfather Investment Versus Grandmother Investment
- Grandparenting
- Helping
- Kin Selection
- Maternal Grandmother Invests Most
- Mothers and Maternal Grandmothers and Childhood Survival
- Nonhuman Reciprocal Altruism

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Alloparenting and Female Same-Sex Behavior

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Synonyms

Bisexuality; Helpers at the nest; Same-sex behavior

Definition

The alloparenting hypothesis posits that female sexual fluidity – “situation-dependent flexibility in women’s sexual responsiveness...that makes it possible for some women to experience desires for either men or women under certain circumstances, regardless of their overall sexual orientation” (Diamond 2008, p. 3) – was selected because it facilitated the acquisition of and bonding to an alloparent (a non-biological caregiver for one’s offspring).

Introduction

As Darwin outlined in *The Descent of Man* (1871), reproduction is the engine of evolution. Sexual selection favors traits that increase an organism’s ability to reproduce; therefore, seemingly counterproductive behaviors such as same-sex sexual activity and romantic relationships

pose an evolutionary puzzle. Although there have been several hypotheses put forward to attempt to explain same-sex sexual behavior in men [cite relevant Encyclopedia entries here], relatively little has been posed to explain such behavior in women. One exception is Kuhle and Radtke's (2013; see also Kuhle 2013) alloparenting hypothesis positing that sexual fluidity in women evolved as an adaptation that increased ancestral women's abilities to form pair-bonds with females who could help them rear children to reproductive age.

Alloparenting

Alloparenting has been observed in an array of species and is particularly common in our primate cousins (Hrdy 1999). Among squirrel monkeys, relatives and non-kin engage in reciprocal alloparenting of infants (Roulin 2002; Williams et al. 1994). Among Japanese macaques, mothers allow other females to hold, watch, and protect infants (Bardi et al. 2001; Redmond 2008). Bonobo females form strong pair-bonds that last the duration of their lives (Furuichi 2011; Kano 1992). When a female reproduces, other females are significantly involved in the life of the young bonobo (De Lathouwers and Van Elsacker 2004; Furuichi 2011; Kano 1992). To cement pair-bonds within the troop, female bonobos engage in various forms of sex with troop members, especially with females who may serve as allomothers.

In humans, Kuhle and Radtke (2013) argue that alloparenting may have been a way for ancestral women to acquire a second form of parental investment for their children in the face of paternal desertion, death, or divestment of resources. Hrdy (1999, 2007, 2008) surmises that without cooperation from both kin and non-kin alloparents, humans may have been unable to flourish as a species because human infants are so altricial. Close kin are not always the dominant allo-caregiver; unrelated women often contribute substantial allomothering across cultures (Bentley and Mace 2009; Hrdy 1999; Meehan 2009).

Sexual Fluidity

Relative to men, women are more likely to report bisexual attractions than exclusive same-sex attractions (Baumeister 2000; Diamond 2006, 2007, 2008; Peplau 2001; Peplau and Garnets 2000). Additionally, US women aged 18–44 years are more than twice as likely as men to report being attracted to and having had sexual contact with members of the same sex (Chandra et al. 2011). Women's fluid sexuality is also evidenced physiologically (Chivers 2005, 2010). As opposed to men, women do not experience a significantly greater genital arousal from stimuli of their preferred versus non-preferred sex (Chivers and Bailey 2005; Chivers et al. 2004).

For the present purposes, a fluid sexuality is one that is potentially sexually responsive to both sexes (but not necessarily at the same point in time). It avoids a focus on changes in one's sexual identity or sexual orientation.

Sexual Fluidity as a Conditional Female Mating Strategy

According to the alloparenting hypothesis, sexual fluidity increased ancestral women's reproductive success by diminishing the costs of four adaptive problems that resulted in a deficiency of paternal investment and by promoting the acquisition of allomothering investment from unrelated women: (1) an absence of paternal investment due to rape, (2) reduced paternal investment due to paternal defection, (3) reduced paternal investment due to paternal death, (4) and reduced paternal investment due to a dilution of resources (Kuhle and Radtke 2013). Under this view, most heterosexual women are born with the capacity to form romantic bonds with both sexes. Female sexual fluidity is a conditional reproductive strategy where the pursuit of men is the default strategy, and same-sex sexual responsiveness is triggered when inadequate paternal investment occurs or when women with alloparenting capabilities are encountered. Sexual selection is hypothesized to have designed sexual responsiveness mechanisms in women that are sensitive to the situations and

experiences that were recurrently associated with the availability of paternal and allomothering investment over evolutionary history. The alloparenting hypothesis makes 14 testable predictions. Although there are several studies relevant to the first three predictions (see original article), no empirical evidence yet exists that bares upon predictions 4–14.

1. Relative to women who have never been abused by their male mates, women who have experienced abuse by male mates will be more likely to have subsequently engaged in same-sex sexual behavior.
2. Relative to women who have never been raped by men, women who have been raped by men are more likely to have subsequently engaged in same-sex sexual behavior.
3. Relative to women who were never abused as children, women who experienced physical or sexual abuse by men during childhood or adolescence will be more likely to have subsequently engaged in same-sex sexual behavior.
4. Women whose husbands divested in them for the sake of other women are more likely to have subsequently engaged in same-sex sexual behavior (especially if they have children) relative to women whose husbands' investment did not diminish from being diluted among other women.
5. Women whose husbands deserted them are more likely to have subsequently engaged in same-sex sexual behavior (especially if they have children) relative to women whose husbands remain mated to them.
6. Women whose husbands have died are more likely to have subsequently engaged in same-sex sexual behavior (especially if they have children) relative to women whose husbands are alive and investing in them.
7. In the absence of paternal defection, desertion, and death, wives of husbands whose investment has diminished are more likely to have subsequently engaged in same-sex sexual behavior (especially if they have children) relative to women whose husbands' investment is sufficient.
8. A woman's mate value (MV) will be an important moderating variable on her likelihood of engaging in same-sex sexual behavior. All things being equal, lower MV women will be more likely than higher MV women to engage in same-sex sexual behavior in the face of male abuse, rape, divestment, desertion, and death because they are less able to acquire sufficient paternal investment from other men.
9. Women who have formed deeper, emotional friendships with women who exhibit alloparenting potential are more likely to have engaged in same-sex sexual behavior than women with fewer such friendships.
10. Women who experience extreme stress associated with childrearing are more likely to report having engaged in same-sex sexual behavior than women without such stress.
11. Women with an unrestricted sociosexuality (Jackson and Kirkpatrick, 2007; Simpson and Gangestad, 1991) will be more likely to engage in same-sex sexual behavior than women with a restricted sociosexuality. The more willing and comfortable a woman is in engaging in casual sex without love, commitment, or closeness, the more likely she is to experience a dearth of paternal investment postpartum and hence need allomothering investment.
12. Women with few kin available to alloparent will be more likely to engage in same-sex sexual behavior than women with abundant alloparenting help from kin.
13. Women will be more likely to engage in same-sex sexual behavior during non-fertile versus fertile phases of their menstrual cycles. In the context of a plural marriage, same-sex sexual behavior during ovulation comes with opportunity costs that detract from reproduction. However, such behavior during non-fertile phases could promote the forming and grooming of alloparenting relationships among women.
14. If sexual fluidity serves to promote female-female bonds, heterosexual women who evidence high levels of fluidity (e.g., the most nonspecific patterns of genital arousal) should have a larger number of close female friends compared to heterosexual women with lower levels of fluidity.

But Why the Sex?

Sex is an effective means of forming, increasing, and sustaining pair-bonds between people (Brigman and Knox 1992; Hazan and Diamond 2000; Leigh 1989; Meston and Buss 2009). Sexual behavior with male mates promotes women's feelings of commitment to these partners (Meston and Buss 2009). A similar process of sexual behavior-induced commitment is likely to occur between female partners. As female same-sex behavior in bonobos appears to increase both the survival of the mother and her offspring (Furuichi 1989; Hohmann and Fruth 2000; Parish 1994, 1996), it is likely that future research will reveal that sexual relations between female bonobos increase pair-bonding and help ensure that a mother's offspring are cared for by alloparents (Radtke 2012). The alloparenting hypothesis suggests that psychological mechanisms underlying a similar process of same-sex sexual behavior in the service of alloparenting evolved in human females and is particularly likely to be triggered among women who encounter an absence of paternal investment, or the availability of allo-mothering investment.

Conclusions

The alloparenting hypothesis entwines several diverse phenomena including (a) female sexual fluidity in human and nonhuman primates; (b) heterosexual women's potent genital arousal to both sexes; (c) the rates of rape, physical abuse; and sexual abuse as a function of sexual orientation; and (d) the ubiquity of alloparenting among human and nonhuman primates. The alloparenting hypothesis also outlines 14 testable predictions, 12 of which specify variables that will shunt some women into forming same-sex romantic bonds that facilitate alloparenting. No other hypothesis for sexual fluidity is as wide ranging or as falsifiable.

Since the engine of evolution is reproduction, same-sex sexual behavior appears to be an enigma. However, it is resolved if, instead of hindering reproduction, the trait actually

facilitates it. In light of the alloparenting hypothesis, a trait that formerly appeared maladaptive – sexual behavior between women – is recast as an adaptive outcome. This hypothesized contingent adaptation may have increased ancestral women's ability to form pair-bonds with women who helped them rear children to reproductive age in the face of male rape, death, desertion, and divestment of resources, as well as during stressful childrearing times, or simply when a suitable allo-mother presented herself. Being born with the ability to go both ways may have been beneficial to ancestral women.

Cross-References

- [Alloparenting](#)
- [Alloparenting and Grandparenting](#)
- [Sexual Identity](#)

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Alloparenting and Grandparenting

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Definition

A system of parenting where people other than the parents act in a parental role and help raise children that are not necessarily their own.

Introduction

As the social animals we are, we have evolved in ways that promote cooperation because

individuals who help each other are more likely to survive in threatening environments than those who do not cooperate. Additionally, because the end goal of evolution is not necessarily to survive but to reproduce and pass one's genes on to future generations, we have evolved mechanisms that will increase the chances of survival of our offspring. One such mechanism involves having other members of the group aid in the rearing of a child, a term that is known as alloparenting. The following section describes how alloparenting works, and why people may willingly help raise a child that is not theirs.

Alloparenting

According to Bentley and Mace (2009), alloparenting is when children are cared after by individuals who are not their biological parents. This includes uncles, aunts, grandparents, siblings, or even other members of the community that are not necessarily immediately genetically related to the children. Because females in general tend to have higher parental investment, it should not come off as a surprise that other females of the group are more likely to help a mother with her child than are men. Additionally, because offspring are the future of one's genes, an individual female engaging in alloparenting would have to make sure her child will not incur any harm while in the care of other members. As a result, individuals whom the mothers believe will give the child back without injury are more likely to be trusted by the mother (Hrdy 2009). Non kin members may engage in alloparenting behaviors, but it is typically individuals who are blood-related to the child who are more likely to do so, which supports kin selection theory. An aunt helping raise her nieces and nephews shares more genetic makeup with them than a random member of the community, and thus getting them into the future allows some of her genes to survive as well. Meanwhile, non kin members may also provide help, but the reasons and mechanisms for it may differ from those of family members. While kin selection theory

explains why uncles, sibling, and grandparents engage in alloparenting, reciprocal altruism theory may shed light on why non kin will also help rear a child. A female may agree to care after a child that is not hers because she knows that the child's mother may be more likely to return the favor and care after her own offspring if the need ever arises.

Grandparenting

A very common form of alloparenting is grandparenting. Grandparents have an influence over the development of their grandchildren (Szinovácz 1998) and can affect a grandchild's behavior in both direct and indirect ways, such as directly interacting with them and offering advice. It is not uncommon for the older members of a society to help care after the young. Additionally, when it comes to grandparents, it is the mother's parents who typically invest more in grandchildren than the father's parents. This may be due to differences in paternal certainty; the mother's mother can be absolutely sure that her grandchildren are hers, and although the mother's father has a chance that his daughter is not his, which would mean the grandchildren share no genetic makeup with him, he can at least know the children are the mother's. Grandparents from the father's side, however, have no way of knowing if his son has been cuckolded and if any grandchildren are theirs. As a result, the maternal grandmother tends to invest more than the paternal grandmother, and the same goes for the grandfathers.

A prevailing question in evolutionary psychology is why women stop being fertile at a given age. After all, if the end goal is the further reproduction of one's gene, shouldn't natural selection favor longer reproductive periods? Hrdy's (2009) grandmother hypothesis offers a possible explanation of why women experience menopause. This hypothesis suggests that women become infertile at a certain point in their life to stop focusing on having children and to start focusing on taking care of the children and grandchildren

they already have. Infertile women in hunter-gatherer societies still collect as much food and work as much as they did during their reproductive years. This means they can provide for any kin they may have, and because grandchildren share a portion of their genes with their grandmothers, investing in the survival of the young would have benefits for the grandmothers' genes. By staying active in caring for her children and grandchildren, an elderly female can help her daughter eat and stay healthy so that the daughter can focus on bearing more children and provide extra resources to ensure the children's survival. To support this idea, women with a strong relationship with their mothers are more likely to have more children themselves and to start having them at a younger age than women who do not have close relationships with their mothers. Additionally, grandchildren of grandmothers who did not live long enough to help their daughter reproduce are less likely to survive past infancy.

Conclusion

Alloparenting is an effective strategy to increase the likelihood that one's offspring survive. Members who are not genetically related to a child may still help raise him or her, but perhaps because of an unspoken expectation that the favor be returned (reciprocal altruism), whereas other kin members such as uncles, aunts, siblings, and grandparents may aid in the rearing of a child because the child is still a vehicle of some of the kin member's genes. Additionally, grandparents, particularly grandmothers, seem particularly prone to invest time in their grandchildren.

Cross-References

- ▶ [Differential Parental Investment](#)
- ▶ [Maternal Investment](#)
- ▶ [Parental Investment and Sexual Selection](#)
- ▶ [Sexual Conflict and Sex Differences in Parental Investment](#)

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Alloparents

- ▶ [Grandparenting](#)
- ▶ [Higher Survival with Older Siblings](#)
- ▶ [Kinship and Emotional Closeness](#)
- ▶ [Presence of Siblings](#)

Allopreening

- ▶ [Cooperative Grooming](#)

Aims

- ▶ [Charity](#)

Alpha, Beta, and Gamma Males

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Synonyms

Male status; Rank order; Social hierarchy

Definition

The ranked order of males within a group.

Introduction

The terms alpha, beta, and gamma male are typically used to describe an individual's position within a social hierarchy. In linear hierarchies, alpha males are the highest-ranking males within a group, followed by beta, and then gamma males. While this section is focused on male social status, it should be noted that females can also form strong social hierarchies. Dominance hierarchies can commonly be found in taxa exhibiting group living, where frequent conflict among individuals can occur. Individual rank can be used to predict the outcome of agonistic interactions between males and thus be used to deter some of these aggressive encounters. This section will discuss some examples of how these terms are used across a variety of taxa.

Nonhuman Primates

Much of the research on dominance hierarchies comes from studies on nonhuman primates. In these groups, a male's rank is based on a combination of age, health, competitive ability, and even maternal status. As such, males achieving alpha status are usually in their prime. While these hierarchies can be relatively stable, a male's ranking is not permanent. One's status can change as other males enter or leave groups or through rank changes within a group (Hamilton and Bulger 1990). Since challenges to alpha males can result in severe injury, males will often remain in their natal group until they reach their physical peak. The tenure of any alpha male can vary greatly among species but can be very short-lived, in some cases shorter than 6 months (Hamilton and Bulger 1990).

The position of an alpha male can incur significant costs to the individual. Higher-ranking males participate more in activities related to policing group conflicts and are often under threat

of takeover by other males. However, one primary advantage of maintaining alpha status is obtaining higher reproductive fitness compared to other males in the group. Alpha males have priority access to ovulating females and fertilize a significantly higher proportion of offspring during their tenure compared to males in subordinate positions (Jack and Fedigan 2006). In multi-male groups, the reproductive skew between alphas and other males can be striking, but there is large variation among primates (Hagar 2003). Some of this variation in reproductive skew is likely driven by social interactions between alphas and other males. Males of varying status will form alliances, which can either reinforce current male rankings or overthrow an established alpha. In return for their help in these endeavors, alphas may "exchange" breeding opportunities with these subordinates (Snyder-Mackler et al. 2012), leading to higher reproductive success of beta or gamma males.

Canines

The term alpha male is often used in association with canines to designate the highest-ranking male within a pack. Much of the early work on social hierarchies in canines came from studies of captive wolf populations. In these populations, multi-male and female groups can consist of non-related individuals, which form structured social hierarchies in both sexes (Rabb et al. 1967). The alpha male and female are the main breeding pair and can behaviorally restrict the courtship of other adults in the pack (Rabb et al. 1967). While relatively stable, changes in social status can occur if an alpha is removed or becomes injured. Also, alphas can form alliances with other males to protect and shield one another during attacks (Rabb et al. 1967). However, it is possible that if the status of the alpha male declines, so does the status of his associated males.

The packs of wild populations are very different than those of captive populations. In the wild, packs tend to consist of familial groups that include parents and their offspring (Mech 1999). Although multifamily packs can exist, this is rare.

The alpha male and female are the primary breeders of the pack. Once offspring reach a certain age, they will leave the natal pack to form their own in a different territory (Mech 1999). Alpha males are also responsible for scent marking their specific territories (Peterson and Page 1988), which can be maintained over multiple years. When conflicts arise between packs, it is the alpha individuals that primarily participate in these aggressive interactions (Peterson and Page 1988).

Like wild wolves, African wild dogs (*Lycaon pictus*) form familial packs consisting of an alpha breeding pair, their offspring, and sometimes the siblings of one of the alphas. The siblings are subdominant to the alpha pair but will cooperatively participate in hunting and protecting the offspring (Malcolm and Marten 1982). While there are some instances of subdominants mating with one of the alpha pair, the proportion of offspring subdominant males successfully fertilize is currently unclear.

Birds

Dominance hierarchies are often associated with group living; however, alpha/beta relationships can occur in non-group-living species. In the lance-tailed manakin (*Chiroxiphia lanceolata*), males form long-term cooperative breeding groups, with one male being dominant to one or more unrelated males. This species has a lekking mating system where males and females congregate and compete for mates during the breeding period. Alpha and beta males cooperate in performing elaborate mating displays to attract females. The energetic investment that beta males make in the partnership can be costly. They can engage in excess of three million duet calls and spend more than 1000 h performing displays during their time with an alpha male (McDonald and Potts 1994). However, alpha males obtain the majority of the reproductive success from these pairings, and beta males rarely mate. Beta males do eventually benefit by the fact that they are more likely to become an alpha male if they have participated in these cooperative

groups (McDonald and Potts 1994). Succession in this group is hierarchical with beta males moving into the alpha position once it is vacant.

Marine Isopods

While the terms alpha, beta, and gamma are usually related to male rank within social hierarchies, it should be noted that this is not always the case. In the marine isopod (*Paracerceis sculpta*), these terms are used to describe three different male reproductive morphs (Shuster and Wade 1991). The morphs are genetically determined by a single autosomal locus and represent alternative mating strategies. Alpha males are the largest morph and defend females within the central cavity of intertidal sponges (spongocoels). Beta males are intermediate in size and resemble females. These males mimic female behavior to enter spongocoels occupied by alpha males and females. Gamma males are much smaller than the other two morphs and effectively sneak into occupied spongocoels. The reproductive success of each morph is dependent upon the relative density of males and females within the spongocoel. When only one female is present, the alpha male fertilizes the majority of the offspring (Shuster and Wade 1991). As the number of females increases, the reproductive success of beta and gamma males increases and can surpass the alpha male. Across natural populations, the average reproductive fitness of each morph is relatively equal (Shuster and Wade 1991).

Conclusion

Social hierarchies can dictate how individuals interact with one another within a group. In group-living species, male ranking is typically correlated with male reproductive success, with alpha males receiving most of the mating opportunities. Beta and gamma males will contribute to the group and may form alliances with an alpha, sometimes in exchange for mating opportunities. Beta males may also cooperate to increase their likelihood of obtaining the alpha position once it

becomes vacant. While these ranked terms often indicate male social status, it should be noted that they can also be used to describe different male alternative reproductive tactics in many taxa.

Cross-References

- ▶ [Making the Best of a Bad Job](#)
- ▶ [Mating Strategy Equilibria](#)
- ▶ [Sneak Copulation as an Alternative Mating Strategy](#)

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Alteration

- ▶ [Genetic Predispositions](#)

Alternating Attention

- ▶ [Selective Attending](#)

Alternative Adaptive Peaks

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Synonyms

[Alternative Strategies](#); [Adaptive Polymorphisms](#); [Adaptive Variation](#)

Definition

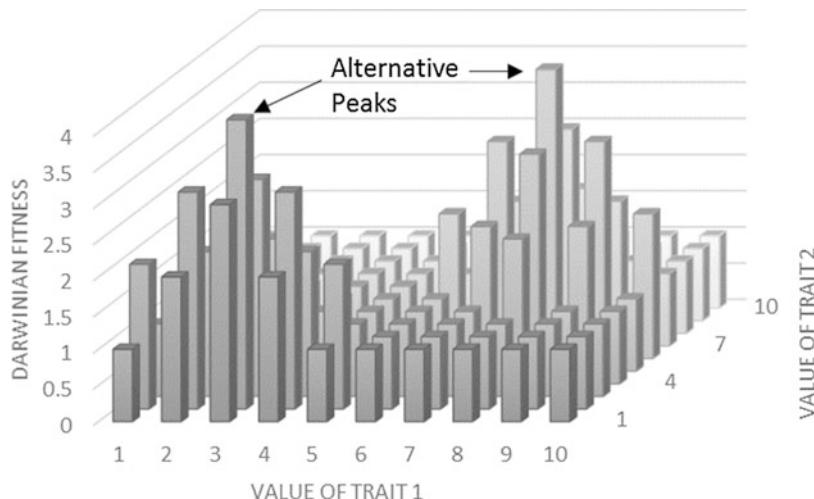
A set of two or more phenotypic states that result in higher fitness than other states. This is in contrast to situations in which there is a single optimal phenotype, with all variation surrounding that optimum being maladaptive.

Introduction

Sewall Wright introduced the concept of the fitness landscape to visualize the relationship between an organism's genotype or phenotype and its Darwinian fitness (Wright 1932). In most such visualizations, fitness is represented on a vertical Z-axis, such that the highest points on the landscape produce “adaptive peaks” centered over phenotypic combinations (on the X and Y axes) that have the highest fitness (Fig. 1). Adaptive processes, specifically natural selection or learning, are expected to move the phenotypes of populations or individuals from lower points on the landscape towards the

Alternative Adaptive Peaks, Fig. 1 A 3-axis fitness landscape with alternative adaptive peaks.

The horizontal axes represent the phenotypic state of two traits (1 and 2), while the vertical axis represents the Darwinian fitness of individuals with particular combinations of traits. In this landscape, there are two alternative adaptive peaks: Trait 1 = 3, Trait 2 = 2, and Trait 1 = 8, and Trait 2 = 6



adaptive peaks. In some cases, there will be more than one peak on an adaptive landscape, alternative adaptive peaks (Fig. 1).

The fitness landscape is likely to be dynamic, such that the height and position of peaks are shifting when any aspect of the environment (including the social environment) changes (Lewontin 1978). When populations find themselves in valleys, adaptive processes should drive their phenotypes to the nearest peak. In some cases, populations can climb toward local peaks (local optima) that are shorter than the highest peak (global optimum), thus expressing phenotypes that are less optimal than other possible phenotypes. Traditional gradualist models of evolution predict that it will be difficult for populations on a local optimum to shift to a higher optimum as the population must first pass through an adaptive valley, in which phenotypes are less fit than they were at the local optimum. Sewall Wright argued that some combination of large mutations and genetic drift would allow small subpopulations to form phenotypes distant enough from local maxima that they reach the valleys (or saddles) of landscapes where selection will allow them to climb higher alternative peaks.

Alternative Adaptive Peaks

The fitness landscape metaphor has been used to help explain the persistence of adaptive genetic

and phenotypic variation in populations, for example, the existence of personalities in humans (Nettle 2011). Populations with two or more behavioral strategies with equal fitness payoffs can be visualized as a landscape with two or more “alternative adaptive peaks” of equal height. There are two general situations in which such alternative peaks are expected to arise; where there is negative frequency or density dependent selection and where individuals within populations live in environments that vary across space and time.

Negative frequency-dependent selection occurs when the fitness advantage of a behavioral or phenotypic strategy decreases as it is more commonly used. Biological sex ratios represent an example of this type of selection, as whichever sex is more common tends to have lower fitness, thus maintaining a 50:50 sex ratio in most animal species (Maynard Smith 1978). Frequency-dependent selection can be visualized on a dynamic adaptive landscape as the lowering of peaks as they become occupied, and the concurrent rising of less occupied peaks (Arnold et al. 2001). The frequency of each strategy is expected to reach a stable equilibrium when the fitness of individuals using each strategy is equal, when peaks are of equal height.

A classic model of behavioral strategies maintained by negative frequency selection is the producer-scrounger polymorphism of foraging animals (Barnard and Sibly 1981). Producers

invest energy to find or prepare food before consuming it, while scroungers rely on food found and prepared by scroungers. The first individual to scrounge will typically achieve higher fitness than producers, because it has potential access to the food produced by the rest of the population. However, as the frequency of scroungers increases (and the frequency of producers decrease), the fitness payoff for scroungers gets progressively lower, until it matches that of the producers. At this point, the height of adaptive peaks is equal and the frequency of each strategy is at a stable equilibrium.

It has been hypothesized that psychopathy (a cluster of traits including egocentrism and a lack of empathy) is maintained in human populations via negative frequency-dependent selection (Mealey 1995). As with the scrounger strategy, this hypothesis argues that the selfish/cheating behavior only thrives when a larger portion of the population is cooperative and susceptible to exploitation by psychopaths.

A related concept, “competitive disruptive selection,” describes situations in which what would be a single adaptive peak under low competition conditions becomes a stable local minimum when that peak becomes occupied at higher population densities. This would favor the diversification of phenotypes around that minimum. For example, in high population density conditions, where competition for prey is intense, stickleback fish with morphology that differs from the mean are at an advantage in specialized foraging (Svanback and Bolnick 2007).

Alternative peaks may also arise and maintain consistent variation when individuals within populations live in different environments. In this case, one horizontal axis might represent the habitat in which an individual found, while the other represents a trait that its utility depends on habitat. For example, the fitness payoffs for life history strategies, such as early investment in reproduction, depend on features of the habitat in which organisms are living. In a now-classic example of life history variation, Austad (1993) demonstrated that opossums living on islands where there was little risk of predation invested less in early reproduction and more in later

reproduction compared to mainland opossums, where predation greatly reduces the probability of surviving long enough to reproduce later in life.

Adaptive Peaks and Personality

Applying adaptive hypotheses to explain human behavioral variation (e.g., personalities) is a relatively new endeavor, and thus, few studies have been published to date. Gangstad (2011) points out that low amount interculture variation in personality, compared to the consistently large intra-population variation, indicates that heterogeneous environments probably do not account for persistence of personality. This pattern instead favors the hypothesis that within environment, processes, like negative frequency dependence, maintain this variation. For example, Sulloway (2011) suggests that birth order effects may be driven by processes akin to competitive disruptive selection, as competition over roles and/or resources within human families favors to development of differences among siblings.

Conclusion

Adaptive peaks and the fitness landscapes on which they reside are useful metaphors for understanding adaptive evolution and development. However, as with most metaphors, the fitness landscape is limited in several ways. In particular, the fitness of individuals surely relies on more than two interacting traits, but our ability to visualize multi-dimensional landscapes that result when three or more traits influence fitness is limited. Moreover, the instability of the landscape – the degree to which its shape may change from moment to moment makes it difficult to use the landscape to predict where population phenotypes will be moving at evolutionarily relevant timescales (Kaplan 2008).

Cross-References

- ▶ [Adaptation and Natural Selection](#)
- ▶ [Adaptationist Program, The](#)

- ▶ Cultural Variation
- ▶ Daniel Nettle
- ▶ David Buss
- ▶ Evolutionary Personality Psychology
- ▶ Frank Sulloway (1996) on Birth Order
- ▶ Frequency-Dependent Selection
- ▶ Game Theory
- ▶ Individual Differences
- ▶ Life History Strategies
- ▶ Personality
- ▶ Sex Ratio

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Alternative Mating Tactic

- ▶ Sneak Copulation as an Alternative Mating Strategy

Alternative Reproductive Tactics

- ▶ Making the Best of a Bad Job

Alternative Strategies

- ▶ Alternative Adaptive Peaks

Altriciality Life Span Hypothesis

- ▶ Grandmother Hypothesis, The

Altriciality Lifespan Hypothesis

- ▶ Grandmother Hypothesis of Menopause

Altruism

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Synonyms

Cooperation; Game theory; Prisoner's dilemma

Definition

when an organism behaves in ways that produce benefits for others with a cost for himself.

Introduction

Evolution is based in adaptive value traits that prevail (reproduce) in a limited-resource environment. Thus, fierce competition should be inevitable. Paradoxically, altruistic acts are widespread in nature and an organizing principle in human societies (Nowak 2006). Hamilton (1963) described the evolution of altruistic behavior as a stable strategy in kinship relations, pointing that such acts are costly to the individual but beneficial to his genes, therefore being a fitness-enhancing strategy. However, cooperative acts are also observed among non-kin, in one-shot interactions (Boyd et al. 2003; Fehr and Gächter 2002; Gächter et al. 2008), and in highly diverse societies (Henrich et al. 2006). When fitness is measured in terms of genetic combined to cultural reproduction, new beneficial forms of altruistic acts can emerge (Nowak 2006). From the enormous amount of data on the subject of altruism, it is possible to describe five scenarios that may favor the occurrence of cooperation as a stable fitness-enhancing strategy: kin selection, direct reciprocity, indirect reciprocity, group selection, and spatial cooperation (Nowak 2006).

Kinship Altruism or Inclusive Fitness

Kinship altruism was first proposed by Hamilton (1963) as a mathematical model to quantify probabilities for altruistic behavior. It states that an altruistic behavior could be a stable strategy when it helps the agent to increase the frequency of his genes in the gene pool. Therefore, it should be directed toward relatives, in the proportion of the relatedness, and only when gains are greater than the losses imposed to the agent (Hamilton 1963, 1964). This description is known as Hamilton's law for kinship altruism.

This model gained solid support from research on brotherly care in female eusocial hymenoptera. These haplodiploid insects show varying degrees

of relatedness with sisters fathered by the same male presenting 0.75 of genetic similarity, mother and brood presenting 0.5, and brothers and sisters presenting only 0.25. Research shows, as predicted by Hamilton's law, that brotherly care in these species varies in a direct relation with the relatedness coefficient (Hare and Trivers 1973; Mueller 1991; Sündstrom et al. 1996).

Direct Reciprocity

Proposed by Trivers (1971) as a model to describe conditions in which natural selection favors altruistic behaviors toward non-kin and even between individuals of different species. As predicted by Hamilton (1963, 1964), in direct reciprocity interactions, the altruistic act may be maintained when the costs for the agent are low and the benefits to the recipient are great (Trivers 1971). Alongside the costs of the act, another critical variable for the occurrence of direct reciprocity altruism is the number of interactions.

The scenario of the prisoner's dilemma (Gale et al. 1951) has been the main model for predictions about direct reciprocity. In the dilemma, two criminals have been apprehended suspected of commit a serious offense. There is no evidence linking the men to this crime. To produce some evidence, the prosecutor proposes a plea bargain to both men in separate: if one of them confesses and implicates the other, the confessor will be set free for compliance, and the other will be imprisoned for 10 years. If both confess, both will remain in jail for 5 years. If none of them confess, both can be convicted of a minor crime and stay in jail for 1 year.

In one-shot interactions between two encounters, the most stable strategy is to defect, that is, to implicate the other (Axelrod 1984; Nowak 2006; Nowak and Highfield 2011; Trivers 1971). By defecting, the encounter is paying no costs and earning benefits. In fixed-number repeated interactions, the most profitable strategy may be the tit for tat (Axelrod 1984), to cooperate in the first interaction (do not confess), and repeat the previous action of the encounter in subsequent interactions, but always to defect in the last interaction. This is so because when the probability of future interactions is high, to cooperate may be an

individually selected strategy once it can be reciprocated. The recipient will also be compelled to reciprocate the cooperation, because, if he defects, the first cooperator may curtail any new cooperative actions toward him. Considering that cooperate is to pay low costs to produce great benefits, he may be losing more fitness by not to reciprocate. But, as it is a fixed-number interaction, the last interaction is identical to a one-shot interaction; thus, defection is again the more beneficial choice (Axelrod 1984). Cooperation, as the best strategy, may only emerge when the two encounters meet repeatedly in an unknown number of interactions and both are able to produce similar amounts of benefits at similar amounts of effort (Trivers 1971).

Additional evidence suggest that a *win-stay, lose-shift* strategy may be more profitable in direct reciprocity interactions than was *tit-for-tat* (Nowak 2006; Nowak and Highfield 2011). The rule in its strategy is to cooperate at the first interaction and then to repeat your own previous choice after winnings and change it otherwise.

Indirect Reciprocity

Altruism is also observed in ephemeral interactions, with no possibility for direct reciprocation. In such scenarios, there is also a benefit for cooperate, in the form of reputation building (Nowak 2006; Nowak and Highfield 2011; Wedekind and Milinski 2000). A person may help a stranger in need because this stranger is a known cooperator. Reputation is here understood as an image score, the person's status within the group, which is assessed by the members of the group and taken into account in social interactions (Wedekind and Milinski 2000).

In a model designed to show the evolution of cooperation through reputation, Nowak (Nowak and Highfield 2011) created a simulation in which each agent meets another only once and is given a choice to provide help or not. For every aid, one unit is added to a personal public score. Nonetheless, for every defection, one unit is removed. It is not possible to know how many times a specific agent cooperated or not, and the "helping score" or image score is only known by a fraction of the population; thus, different agents

have differing levels of information about the same individual. Results showed that when cost-to-benefit ratio is sufficiently low and the amount of information about the encounter's reputations is sufficiently high, cooperation favors a good reputation. Similar results have been found in experiments with humans (Wedekind and Milinski 2000) and nonhuman animals (Bshary and Grutter 2006).

Transmission of reputation depends on third parties' participation and mechanisms for reputation spread like simple observation, gossip, and eavesdropping (Bshary and Grutter 2006; Nowak and Sigmund 2005; Tomasello 2016). Because of the need for information transmission, indirect reciprocity is more probable in small groups or in subgroups of bigger populations (Leimar and Hammerstein 2001; Nowak and Sigmund 1998).

Group Selection

One of the most controversial issues in the puzzly field of altruism is if selection can act on groups as units. The concept of group selection was proposed by Darwin to account for scenarios where intense between-group competition favors costly behavior that improve performance at group level. These costs would be reverted in individual benefits because in frequently cooperative groups, individuals may fare better (Nowak and Highfield 2011).

Defenders of this position present evidence from theoretical (Wilson 1975; Wilson and Sober 1994), simulation models (Boyd et al. 2003; Nowak and Highfield 2011), and laboratory experiments (Fehr and Gächter 2002; Gächter et al. 2008; Gürerk et al. 2006) showing that groups where cooperators abound are richer and less prone to extinction.

In simulation models (Nowak 2006; Nowak and Highfield 2011), similar groups with varying levels of cooperation and defection (pure cooperator, pure defector or mixed group) were created. Members only cooperate or defect within its group, and individuals may reproduce in proportion to individual payoffs. But groups also reproduce. At a certain group size, the group splits in two and the poorest group is extincted. Results showed that group selection favors

pure cooperator groups. However, within mixed groups, defectors reproduced faster than cooperators. That is, in within selection, defectors do better, but in between groups, more cooperators correlate with faster reproduction. Boyd, Gintis, Bowles, and Richerson (2003) also observed the positive effect of a higher number of cooperators on maintenance of stable cooperation, but with better results in groups where altruistic punishment (a costly act to punish defection) was present.

Other important aspect in group selection is migration. In Nowak's model (Nowak and Highfield 2011), migration had a detrimental effect, undermining cooperation. He concluded that for the evolution of group selection, migration must be maintained at low rates. Adversely, in Boyd, Gintis, Bowles, and Richerson (2003) model, immigrants were able to imitate patterns of cooperation and altruistic punishment, maintaining cooperation at high stable levels.

Critics of the idea of group as units of selection are based on the argument that the outcomes of a highly cooperative group act on within-group selection, having between-group selection as a second-order product (Dawkins 1994; Wilson 1973). The basic argument is that for group selection to be a pressure in evolution, group extinction rates must be high enough to compete with individual selection, which is highly improbable in nature (Wilson 1973). That is, group selection may be possible, but does not account for the evolution of cooperation in real-life situations.

Spatial Cooperation

In well-mixed populations where every member has equal chances to interact to one another, defectors tend to be more successful than cooperators (Nowak and Highfield 2011). But it is a common feature in real-life social organizations that some organisms interact more often than others (Nowak 2006; Nowak and Highfield 2011). Some theoretical works have taken into account how the geographic disposition of the agents may influence the occurrence of

cooperation (Killingback and Doebeli 1996; Maynard Smith 1982; Nowak and May 1992).

In simulation models (Nowak 2006; Nowak and Highfield 2011; Nowak and May 1992), members of a group are distributed in a chessboard-like field. Each member interacts only with its eight neighbors in a prisoner's dilemma. After each interaction, the winner earns the loser's spot. Those members were programmed to act as pure (unconditional) cooperators or pure defectors (for variations in strategy, see Killingback and Doebeli 1996). Variation across simulations occurred in the amount of each type of member and its position on the chessboard. Results from interactions were displayed by color pattern; at each trial, blue cells represented cooperators and red for defectors, green showed cells previously occupied by a defector and taken by a cooperator, and yellow showed ex-cooperative cells. General results showed the coexistence of cooperation and defection across different starting frequencies of cooperators versus defectors, with either static or shifting configurations. Average frequency of cooperative interactions ranged around 31.78%, independently of the scenario. Authors concluded that cooperation is a stable strategy, even in the absence of variables as kinship, reciprocity, and altruistic punishment.

Real-life studies in spatial ecology have shown the presence of stable strategies of cooperation in neighbor's interactions (MacLean and Gudelj 2006; Momeni et al. 2013; Nadell et al. 2016). For opposing results, see Hauert and Doebeli (2004). However, the generality of such conclusions is still to be known, once literature, especially from *public goods games* (PGG), suggests that organisms are primarily conditional cooperators (Chaudhuri 2010; Gächter and Thöni 2007; Rabin 1993).

Conclusion

Although costly, altruism is a widespread pattern of behavior present in various species. It may be so because altruistic acts are more probable when

costs to the altruist are low compared to benefits to the recipient and the altruist may be directly benefited by inclusive fitness, in kinship altruism, or in future interactions by reciprocity and other proximal mechanisms.

Proximal mechanisms as reputation, reciprocity, and altruistic punishment may require complex cognitive functions as remembering, language, mind theory, and so on (Nowak 2006; Nowak and Highfield 2011; Tomasello 2016). Thus, altruism may reach its full complexity only in human interactions.

Cross-References

- ▶ [Altruism in Kin Selection](#)
- ▶ [Cooperation Among Fishes](#)
- ▶ [Cooperation Among Nonchimpanzee, Non-human Primates](#)
- ▶ [Cooperation in Social Carnivores](#)
- ▶ [Cooperation Varies with Genetic Relatedness](#)
- ▶ [Emotional Closeness Predicted by Relatedness](#)
- ▶ [Evolutionary Paradox: Adoption](#)
- ▶ [Group Selection](#)
- ▶ [Hamilton's Rule and Genetic Relatedness](#)
- ▶ [Hamilton's Rule and Kin Investment](#)
- ▶ [Hamilton's Rule and Theoretical Implications](#)
- ▶ [Helping and Genetic Relatedness](#)
- ▶ [Helping and Inclusive Fitness Benefits to Helper](#)
- ▶ [Helping and Reproductive Value of the Recipient](#)
- ▶ [Helping More Likely with Close Kin than More Distant Kin](#)
- ▶ [Moral Language Regulation](#)
- ▶ [Moral Tribes](#)
- ▶ [Observation of Altruism](#)
- ▶ [Primate Cooperation](#)
- ▶ [Prisoner's Dilemma and Cooperation](#)
- ▶ [Prosocial Behavior](#)
- ▶ [Reciprocal Altruism](#)
- ▶ [Reputation and Altruism](#)
- ▶ [Rescuing Strangers](#)
- ▶ [Selection for Cooperative Relationships](#)
- ▶ [Significance of Helping](#)

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Altruism Advertises Cooperativeness

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Synonyms

Prosocial behavior

Definition

Altruism refers to benefit provisioning behavior, and cooperation is defined as exchange between two or more individuals which is mutually beneficial.

Introduction

Altruism is defined as a behavior that is beneficial to a receiver but costly to the altruist (Trivers 1971). Altruism is a phenomenon which causes evolutionary theorists trouble when tying it into the overall play of evolution. Why be altruistic to someone you do not know?

The reason why altruism is a puzzling phenomenon is because it is costly in nature. Being altruistic has also been argued to be costly to an individual's fitness, beneficial to the receiver's fitness but at a cost to the altruist. Because of the fitness deficit between altruist

and recipient, Sanchez and Cuesta (2005) argue that altruism should therefore cease to exist over time if it provides us with no direct evolutionary advantage(s). However, we observe altruism in everyday life; giving up one's seat for an elderly person on public transport, helping someone by carrying their shopping, or stopping to help someone in an accident.

Evolutionary theorists have spent decades exploring the psychological mechanisms that drive altruism towards those we are not related to (see Kurzban et al. 2015 for a recent review). According to the principles of natural selection, altruism must have evolved in order to convey benefits to others and to increase one's fitness, otherwise, due to its costly nature, it should not have evolved.

There are several explanations to explain the signaling purpose of altruistic behavior. Explanations derive from individual selection where the altruist expects reward from his or her action (this suggests that altruism is selfish as opposed to selfless – see Ruse 2012). Further explanations derive from indirect and direct reciprocity (Roberts 1998), where altruistic behavior evolves through engaging cooperatively with others. Reputation building has also been proposed (Nowak and Sigmund 1998), where altruism increases one's reputation through continued cooperation with others, thus suggesting a good reputation can be sought from displays of altruism, which signal cooperative intent towards others. Multilevel selection has been used to explain the evolution of altruistic behavior, arguing that natural selection, when operated on a group level, increases the survival of a group. For example, if a group contains more altruists compared to other groups, it increases the likelihood that the group which contains altruistic people will outperform and have increased longevity compared to the group of non-altruists. In relation to cooperativeness, although altruism (at face value) is a costly endeavor, multilevel selection diminishes the personal cost of altruistic behavior, as altruism may advertise cooperativeness through multilevel selection by increasing the survival of a group (Wilson 2015).

Altruism is crucial, on a societal and individual basis, as we need to be both on the receiving end of altruism and be engaging in altruistic displays to survive, particularly through being chosen as partners in cooperative ventures (Ruse 2012). Throughout our evolutionary history, cooperation has been crucial in increasing survival. Even today, cooperation is just as important to governments maintaining relationships with one another, personal and social ventures, with kin or non-kin alike. The decisions we make in everyday life, whether they involve family, friends, acquaintances, enemies, or strangers with whom you are walking along the street, are influenced by conflict and cooperation. Day to day decisions such as deciding whether to confront a colleague about taking advantage of your good nature or deciding whether to deal with the free rider in a group task are both influenced by cooperation or conflict.

For altruism to evolve, the benefits associated with these traits should provide benefits through reciprocating altruistic behavior, leading to cooperation (Kurzban et al. 2015). If the benefits of cooperation are greater than the cost of cooperation, benefits can be accrued by continuously cooperating with those who cooperate with us.

Cooperative tendencies refer to a variety of behaviors and traits. For example, cooperation can encompass altruism, furthering the notion that altruistic behavior signals or advertises cooperative intent (Baumard et al. 2013). Reciprocal altruism (Trivers 1971) suggests that people are altruistic towards others when there is a mutual benefit in being so. This theory suggests that altruism is rewarded through reciprocation, suggesting the benefits of altruism somewhat match, or exceed, the costs of engaging in the altruistic act (Trivers 1971), implying the interaction is repeated, and the recipient will reciprocate in the future, thus leading to cooperative behavior. One of the conditions set by reciprocal altruism is that the altruistic cost should provide a larger benefit to the receiver than the altruist. Manktelow (2012, p. 80) states "If you take a benefit, then you pay a cost." Evidence suggests that humans

are not simply altruistic in order to gain immediate benefits, but altruistic behavior may lead to immediate and/or future gains through cooperative ventures (Stevens and Hauser 2004).

Being cooperative may not always benefit an individual in the short-term and may in fact be costly in the short-term, but actors may “recoup their losses in the future” (Stevens and Hauser 2004; p. 60). Reciprocal altruism has been extensively studied in a range of economic contexts, and due to the societal importance of cooperation, humans have developed cognitive functions to ensure cooperation is embedded into our society, which may also be a reason why cheater detection and free riders are (generally) punished in society. After all, in order to monitor social exchange fairly and prevent others from reaping benefits without paying a cost, we must detect and punish cheaters (Manktelow 2012).

Conclusion

In summary, altruistic behavior can often signal cooperative intent when communicating with others. This can be through direct observation, through reputation building, indirect, and direct reciprocity.

Cross-References

- ▶ [Altruism](#)
- ▶ [Cooperation](#)
- ▶ [Prosocial Behavior](#)

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Altruism Advertises Generosity

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Synonyms

[Cooperation](#); [Public goods](#); [Reciprocity](#)

Definition

Public altruistic actions advertise about personal qualities such as generosity, which can be a signal of abilities, resources, and good social opportunities.

Introduction

Altruism is the intention to benefit others at a cost to oneself (Van Vugt and Van Lange 2013). Altruistic behavior and generosity are in the micro-foundations of social order (Simpson and Willer

2015). Some theories were developed to explain animal and human prosocial outcomes as generosity and cooperation in the evolutionary context: the kinship altruism and the reciprocal altruism theories (Hamilton 1964; Komter 2010), which indicate that altruistic behavior could contribute to increase survival chances among genetically related and non-related individuals. More recently, the competitive altruism theory (Van Vugt et al. 2007) proposed that altruism is the process through which individuals attempt to outcompete each other in terms of generosity, because altruism enhances the status and reputation of the giver (Hardy and Van Vugt 2006).

Altruistic behavior advertises some desirable underlying quality that is costly to obtain and therefore hard to fake, such as resource control, genetic endowment, health, or vigor (Barclay 2010). Generous behavior is one of the many forms of advertising some qualities as potential exchange partners (Van Vugt et al. 2007). Human generosity includes volunteering, donating to charities, and informal helping that contributes to the society's common good. Although generosity is not restricted to human beings, it is a critical part in our evolution as cooperative beings and plays an important role for the maintenance and further evolution of the species (Komter 2010, Glanville et al. 2016).

Along this entry, we discuss how altruism advertises generosity and what is the role that this public generosity plays in the evolutionary fitness of human societies by showing some contributions of altruistic behavior to the survival chances.

Public Generosity as a Status Signal

The reason that organisms cooperate with genetically related individuals can be easily understood by Hamilton's inclusive fitness theory, the kin selection theory. Helping members of your kinship increases your chance to survive because natural selection would favor behaviors that benefit either the organisms themselves or those who share their genes (closely related kin) (Hamilton 1964; Van Vugt et al. 2007). On the other hand,

reciprocal altruism theory (Trivers 1971) offers an explanation about being altruistic toward unrelated organisms. This behavior could be selected if the receiving party is reciprocal to the giver at some point in the future. Thus, providing benefits to other individual leads to reciprocation, which serves the survival chances of all parties involved (Komter 2010).

The reciprocal altruism can be a problem once altruists may be exploited by individuals who fail to reciprocate (Hardy and Van Vugt 2006). So how the cooperation is maintained if the reward of generous acts toward genetic strangers is not certain? Reputation and visibility may be important forces accounting for human generosity and cooperation (Komter 2010). Hardy and Van Vugt (2006) indicate that altruistic actions are in fact a signal about the altruist personal qualities. When altruism is socially displayed, a reputation can be built: the altruistic acts can signal abilities, resources, and good social opportunities, representing more attractive partner because of the signal to provide future benefits (Barclay 2010). Also, altruistic benefits increase social status and thus the likelihood to be chosen as a mate or ally (Hardy and Van Vugt 2006).

Indirect reciprocity theory (Alexander 1987) proposes that altruistics sometimes receive community rewards and support as a compensation because of the public good that these individuals bring to the community (Hardy and Van Vugt 2006). As reward, the group may foster reputation, status, and prestige of the altruistic individual before the group for being generous (Komter 2010). On the other hand, by contributing and building a good reputation of generosity, this individual becomes more attractive to future exchange partners, and its public generosity acts as a signal of evolutionary fitness (Hardy and Van Vugt 2006; Komter 2010).

Although the reciprocity system promotes altruism and cooperation, when reputations are at stake, this is likely to induce a process of competitive altruism because the individuals attempt to outcompete in terms of generosity to have status and reputation as altruistic act consequence (Hardy and Van Vugt 2006). Thus, who behave in generous or cooperative ways receive reputational

rewards as a powerful force that shape prosocial action (Simpson and Willer 2015). According to Hardy and Van Vugt (2006), competitive altruism emerges if the behavior is costly for the actor to display; the behavior is easily observable to others; the signal is a reliable indicator of some underlying trait or characteristic of the signaler; the behavior benefits the actor who displays it in the long run.

Under these circumstances, altruistic and cooperative individuals become more central in the network because of their reputational benefits of prosociality (Komter 2010). The visibility of altruistic actions advertises qualities of generosity and leads to more prosocial behaviors in the community, which create social ties grounded on the selective advantages of altruism (Komter 2010; Simpson and Willer 2015).

Conclusion

Concluding, the public nature of altruistic actions provides a good opportunity to advertise one's generosity. When acts of altruism toward genetic-related or non-related ones are public, they advertise about desirable traits and qualities that cannot be easily observed, such as generosity, which advertises good exchange partners. A practical implication is that altruism in society can be fostered by encouraging people to publicly display their generosity (Hardy and Van Vugt 2006) and that groups can flourish if their constituent members move beyond narrow self-interest (Simpson and Willer 2015).

Cross-References

- ▶ [Altruism](#)
- ▶ [Evolution of Reciprocal Altruism](#)
- ▶ [Indirect Benefits of Altruism](#)

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Altruism Among Nonkin

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Synonyms

[Nonhuman reciprocal altruism](#)

Definition

Nonkin altruism is helping nonrelatives at a cost to one's lifetime reproductive success. By this definition, a strategy of nonkin altruism cannot evolve and persist. If an “altruistic” trait is adaptive, then “altruists” that pay a cost in the short-term to help a nonrelative must gain a net reproductive benefit in the long-term, in which case

the behavior is not altruistic but rather mutually beneficial.

Introduction

The concept of altruism is of great interest to both psychologists and evolutionary biologists, but it has different meanings in each context, which creates a semantic problem for the field of evolutionary psychology and other social sciences concerned with the evolution of human cooperation (West et al. 2011). In psychology, altruism often refers to *intentions and motivations* to help others without regard to one's own self-interest. In evolutionary biology, however, altruism refers to a behavior that increases the recipient's direct fitness (lifetime reproductive success), while decreasing the actor's fitness (Hamilton 1964; West et al. 2007).

Evolutionary Altruism

According to the standard inclusive fitness definition of altruism (Hamilton 1964; West et al. 2007, 2011), altruism between nonkin cannot be evolutionarily stable. Altruism can only be explained by *kin selection*. To understand why, remember that altruists, under this definition, will have on average fewer surviving offspring over a lifetime relative to nonaltruists, resulting in the eventual loss of the altruistic trait in the population. The only way genes underlying the altruistic trait could remain in the population is if genetic relatives, carrying those genes, gain increases in reproduction that counter the loss in reproduction of the altruist (indirect fitness). For this reason, altruism towards nonkin is not common and it is nonadaptive when it does occur.

So why is the term “altruism” heard so frequently? Some authors define altruism as a helping behavior that is costly to the actor in the **short term**. Under this definition, altruism among nonkin is *cooperation* that is initially costly, where *cooperation* is defined as a behavior that benefits another individual (see ► “[Reciprocal Altruism and Cooperation for Mutual Benefit](#)”). However,

for any cooperative behavior to evolve, ultimately the benefits must outweigh the initial costs. For example, *reciprocal altruism* is one mechanism of recuperating costs. By giving you my food when you are hungry, I decrease my current fitness by putting my life slightly at risk (a short-term cost). But later if you feed me when I am hungry, then I gain a net benefit from my earlier investment (higher fitness). In this and many cases where the term “altruism” is used, the behavior is not truly altruistic because there is no net cost to lifetime reproductive success. Because of this problem, the term *reciprocal altruism* is often replaced by the term *reciprocity* or *reciprocal cooperation* with the understanding that reciprocal altruism is not truly altruistic (Carter 2014). For information on other forms of cooperation please see ► “[Reciprocal Altruism and Cooperation for Mutual Benefit](#)”.

Group Selection

Rather than measuring fitness changes relative to the entire population, some authors measure these changes relative to the social group. This definition is used by the *group selection* or *multilevel selection* framework for modeling social evolution, which uses an alternative set of definitions than the traditional definition given above, which are used by *inclusive fitness theory*. Although they can sound quite distinct in words, these two modeling approaches are mathematically equivalent (Lehmann et al. 2007; Marshall 2011; West et al. 2007).

Let us examine how these differences play out using a very simple scenario. Imagine that two warring tribes, the Reds and the Blues, are fighting over resources. The Reds are highly cooperative and vicious fighters. The Blues are not so cooperative, but there are many more of them. Let us assume that all the individuals in both tribes are on average genetically unrelated. Within the Reds is a class of individuals known as Fighters. These warriors have a genetic predisposition to fight and if necessary give up their lives for the good of their tribe. The Blues do not have any individuals willing to do this. Due to the Fighters in the Red Tribe,

the smaller tribe of Reds is beginning to outbreed and outcompete the larger tribe of Blues over a few generations. Let us say that the average fitness of Blue individual is therefore only 0.1. The average fitness of Red individual is let us say 2. But because the Red Fighters were more likely to die during combat and gained no reproductive advantage over other Reds, let us say their average fitness is 1. The question is now, "Is the Fighter trait altruistic?"

Without doing any math at all, it can be seen how inclusive fitness theorists and multilevel selection theorists might answer this question differently. If the Fighters are compared to the whole population, then they are not altruists because the Fighter trait gives them a direct reproductive advantage over the Blues (and hence a benefit relative to the average individual in the population). So, from an inclusive fitness perspective, the Fighter trait would be considered cooperative because it benefits other Reds, but not altruistic, because by helping their tribe succeed, they also help increase their own reproductive success relative to the whole population. In contrast, a multilevel selection approach might view a Fighter as an altruist, because they gained less of an advantage over the Blues, compared to the other Red individuals who were not Fighters. From this perspective, they are altruists *within* the Red tribe. It is important to keep in mind that, if the Fighter trait is adaptive, it must increase the actor's net *inclusive fitness*, regardless of whether it is considered altruistic or not.

Psychological Altruism

Returning to the concept of altruism from a psychological perspective (motivation), how does it relate to the evolutionary definition? First, it is important to note that evolutionary altruism is not necessary to explain psychological altruism. If people who truly cared about the wellbeing of others (i.e., showed psychological altruism) were also on average more likely to survive or reproduce, then this motivational tendency is not evolutionarily altruistic but rather cooperative. Psychological altruism can be explained by many nonaltruistic forms of cooperation enforced by punishment, reciprocity, or indirect reciprocity that lead to

psychological tendencies to care about others under certain contexts or with certain cues. Alternatively, cases of psychological altruism might not be due to any evolutionary process. Evolution explains heritable variation in traits, not specific actions or behaviors and certainly not specific thoughts and motivations. Psychological altruism is a mixture of inherited traits and acquired social norms.

Conclusion

Psychological altruism between nonkin is common and widespread and does not pose an evolutionary puzzle. Evolutionary altruism poses a puzzle whose solution depends on how you define altruism. If altruism is defined as a behavior that on average decreases the actor's lifetime fitness, then altruism is not expected to ever evolve among nonkin. However, under other definitions that measure costs on smaller time intervals or relative to group members, nonkin altruism can be evolutionarily stable.

Cross-References

- [Altruistic Punishment Enhances Reputation](#)
- [Nonhuman Reciprocal Altruism](#)
- [Reciprocal Altruism and Cooperation for Mutual Benefit](#)

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Altruism and Costs to Altruist

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Synonyms

Benefit and cost asymmetries; Benefit to another at cost to self; Cost-benefit analysis; Costs of cooperate; Reproductive benefits must outweigh costs

Definition

The act of producing a benefit to a recipient generates a cost to the behaver.

Introduction

Natural selection may only favor behaviors that benefit the organism performing them. However, altruistic acts, where an individual pay a cost to produce a benefit to another, are widespread in nature. Seen in isolation, altruistic acts may seem counterproductive, and selection should pressure against them. But when analyzed in a wider perspective, including variables such as kinship, reciprocity, reputation, altruistic punishment, and so on, altruistic behavior turns to be a case of reciprocal interaction with benefits to both sides. One of the key features in this wider analysis is the cost-to-benefit analysis.

Cost and Benefit Toward Kin and Nonkin

A

It is possible to define costs and benefits as states or resources that an organism may pursue or avoid, respectively (Woodford 2019). They are effects of particular behaviors that affect locally the individuals involved in the interaction but also affect the gene pool of the population (Hamilton 1963; Woodford 2019). In evolution, the ultimate goal of any organism is to maximize fitness by reducing costs and increasing gains (Buss 1988). That is the same idea in the rule of cost-benefit analysis: the individual may choose the alternative with higher benefits at lower costs. In the evolution of altruism, the same rationale must be applied: the amount of help perceived (benefit) must be greater than the amount of effort (cost) expended, both measured in terms of reproductive success (Hamilton 1963, 1964; Trivers 1971).

Hamilton (1963, 1964) was the first to propose a description of the controlling variables for altruistic acts to emerge. In his prediction, based on kinship altruism, one important aspect was “if the advantage conferred is large enough compared to the personal disadvantage” (Hamilton 1963, p. 355). The coefficient of relatedness is a critical parameter to predict how an altruistic act is more or less advantageous in terms of natural selection. But even in order to increase inclusive fitness by helping kinship, cost has limits. Costs may be compensated in a direct proportion of genetic relatedness. In Hamilton’s example, in altruistic acts toward siblings, advantage must be at least twice the cost; for half-brothers, profit must be four times the cost; and so on.

Trivers (1971) proposed the description for a stable altruistic interchange between nonkin also based on cost-to-benefit ratio analysis. For reciprocal altruism to thrive, two unrelated individuals must alternate the roles of behaver and recipient with the behaver paying a low cost for a great benefit (he suggested a proportion of 1/20 cost for 1/2 gain), and each individual must be able to pay similar amounts of the cost for similar amounts of gain in future (an undetermined number of) interactions. Individuals may be compelled to altruism in direct reciprocity scenarios because of the certainty of future gains. They are paying

low costs to earn greater benefits in future interactions. Defection in this case means the curtailing of possibilities of substantial help at low costs.

Empirical supporting evidence presents the probability of an altruistic act as aligned to cost-to-benefit analysis in kin and nonkin reciprocal interactions. In Stewart-Williams (2007) study, 295 participants completed a questionnaire about probabilities of offering differing levels of help (low-cost, medium-cost, or high-cost help) to siblings, cousins, acquaintances, or friends. Results showed that for low-cost help, participants were akin to help friends more often, followed closely by siblings, cousins, and then acquaintances. For medium-cost help, siblings and friends were preferred and chosen equally. In high-cost help, siblings would receive more help than any other with cousins and friends in second place with similar results. When reciprocity was at stake, help was more probable to acquaintances, showing a pattern of conditional cooperation expected in nonkin interactions. Such results confirms the predictions about cost-to-benefit ratio analysis: (1) unconditional (nonreciprocal) altruism is preferentially directed to kinship in proportion to the relatedness; (2) the bigger the costs, the fewer and more related the recipients; and (3) reciprocity as a conditional altruistic act is directed to nonkin (for similar results, see Webster (2003)). These predictions are also observed in anthropological data (Essock-Vitale and McGuire 1980) and simulation models (Boyd and Richerson 1992).

In social discounting analysis, it is possible to measure the value of producing a gain to another person with a cost to oneself, at a given social distance (Jin et al. 2017; Jones and Rachlin 2009). Therefore, social discounting may be a measure for the probability of an altruistic act given a certain degree of nearness. Jones and Rachlin (2009) had 103 participants completing questionnaires about three dimensions of discount. On the social discount questionnaire, participants were asked to make an imaginary list of the 100 closest persons to him. The dearest person should be the number one in the list. The last person should be a mere acquaintance. Based on this order, the participants were exposed to a series of hypothetical

choices between keeping some money to themselves and forgoing it in order to give some money to a person from the list. The amounts of money were manipulated at each trial in a way that the amount for the participant suffered a constant decrease while the amount for the other person was fixed. Values started from \$85 for the participant or \$75 for one person of the list until \$0 for the participant or \$75 for someone from the list.

Results showed a direct relation between social proximity and giving up the money for himself in the benefit of a relative or close friend. Many participants changed from money to himself to money to a close person when the decrease in his amount reached \$70, that is, as soon as the benefit for himself was below the benefit to another.

Second-Order Costs: Altruistic Punishment

Cost-to-benefit analysis predicts the occurrence of altruism even concerning second-order costly acts as altruistic punishment. This pattern of behavior may occur in public good scenarios, where each member of a group can benefit from a limited common resource. The maintenance of the good is a shared responsibility. Each member may pay a cost $c > 0$ to produce a benefit b to the common good being $b > c$ (Gintis 2000). Increases in the marginal value of the public good have a double effect: enhancement of the benefits from contribution and reduction of the net costs for contributions (Goeree et al. 2002). Decreases in its value tend to lead to a collapse of the good, the tragedy of the commons (Hardin 1968). Three patterns of behavior can be observed in public goods scenarios: to free ride, benefit from the good without paying any costs; to cooperate only, by paying costs only for the maintenance of the good; and to punish free riding, by paying costs either to the maintenance of the good and to punish free riders.

Altruistic punishment may be worth the cost, only when the cost-to-benefit ratio to the punisher is low, that is, small costs impose great losses, and the frequency of punishing acts declines over time (Boyd et al. 2003). But although the extra costs, altruistic punishment pays back. Evidence shows

that altruistic punishers are preferred partners in interactions (Gürerk et al. 2006; Henrich 2006; Nelissen 2008) and they receive more help in future interactions (dos Santos et al. 2010). Besides, groups composed by altruistic punishers are richer, with members cooperating more often and in higher amounts, compared to groups without punishers (Fehr and Gächter 2002; Gächter et al. 2008; Gürerk et al. 2006). Compared to the total amount earned by cooperators only, the losses in the average amount earned by punishers are under 2% (Gürerk et al. 2006). Additionally, cooperation typically collapsed in the absence of punishment with increasing in free riding frequencies over time (Fehr and Gächter 2002; Boyd et al. 2003; Gürerk et al. 2006).

Reputation and Costly Signaling

Altruism is worth the cost even in one-shot interaction with no possibility for reciprocation or punishment for free riding. Such scenario should lead to complete noncooperation, but this collapse can be prevented as long as it contributes to a good image score or reputation (Nowak 2006; Nowak and Highfield 2011; Wedekind and Milinski 2000). Reputation may function as a costly signaling. Costly signaling theory states that altruistic acts return to the behaver as social influence (Gintis et al. 2001). When individuals honestly incur in costs to provide others, they build a reputation as more capable physically and economically. Those traits increase the attractiveness of helpers enhancing their chances to be chosen as sexual partner, ally, or friend, therefore enhancing reproductive success (Barclay 2011; Griskevicius et al. 2007). In costly signaling, the cost-to-benefit ratio is subverted: the more costly the act, the bigger the benefits to the behaver (Jordan et al. 2016).

When reputation is at stake in an economic game (contributions to the group were public), participants contributed with higher amounts (Fox and Guyer 1978; Hardy and Van Vugt 2006; Milinski et al. 2002). Reputation as high contributor paid back as good cooperators were preferred partners in future interactions (Hardy

and Van Vugt 2006); it boosts cooperation in a population, even when such behavior is initially rare (Gintis et al. 2001); and it may prevent the collapse of a public good (Milinski et al. 2002).

It is possible that to cooperate in one scenario may signalize the probabilities of to cooperate in another. Jones and Rachlin (2009) found a parallel between social discounting and cooperation in public good scenarios. Participants who chose to forgo more money to benefit a dear person contributed more with the public good.

The common link among such different scenarios favoring altruism is that part of the benefit returns to the behaver (Brown and Vincent 2008; Nowak 2006). Brown and Vincent (2008) demonstrated that when there is no direct benefit for cooperation, the only stable evolutionary strategy is complete noncooperation.

Conclusion

Theoretical models and the supporting empirical evidence place the cost-to-benefit analysis at the center of the altruism issue. Cost-to-benefit ratio analysis provides accurate revisions about the probability of occurrence of an altruistic act in a myriad of interactions. Thus, an altruistic act can be understood as an individual, selfish strategy that has the helping of others as a mean to an end (Brown and Vincent 2008; Dawkins 1989; Woodford 2019). Brown and Vincent (2008) consider an altruistic act as *enlightened self-interest* behavior and opposed to *tragedy of commons* behavior, to free ride. That is, even in self-interest, to help others is qualitatively different from free ride, and evidence presented here suggest that altruism may be a more profitable selfish strategy.

Cross-References

- [Benefit and Cost Asymmetries](#)
- [Benefit to Another at Cost to Self](#)
- [Cost-Benefit Analysis](#)
- [Costly Signaling and Altruism](#)
- [Costs of Punishing](#)
- [Reproductive Benefits Must Outweigh Costs](#)

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Altruism and Watching Eyes

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Synonyms

Cues of being watched; Eyespots; Observation cues; Prosocial; Social cues; Surveillance cues

Definition

Altruism is a highly prosocial behavior whereby an individual will promote the welfare of others at a cost or risk to themselves. People tend to participate in more altruistic behaviors when they feel like they are being watched by others. The “watching eyes” effect is the phenomenon whereby an image of a pair of eyes can positively influence a person’s altruistic behavior.

Introduction

Altruism is an act that promotes the welfare of others at the cost to the self. It has been the subject of much interest within behavioral sciences (see chapters ► “Kin Selection Hypothesis” and ► “Reciprocal Altruism” for further details). Humans however are unusually ubiquitous in displays of altruism toward unrelated strangers and will often engage in competitive altruism (Roberts 1998). *Being seen* to be altruistic by group members could have a number of fitness

benefits. These may include access to mates, resources, and future reciprocal help. For a full background, see topics on costly signalling, competitive altruism, and indirect altruism. It may also promote in-group favor and reduce social ostracism. Such is the strength of the reputation of *being seen* to be altruistic, that even subtle cues of being watched, such as by a pair of eyes, can be enough to promote prosocial behavior. In a seminal paper, Haley and Fessler (2005) demonstrated that prosocial behavior could be manipulated by the presence of visual eyespots. Since 2005, there have been a plethora of laboratory, online, and real-world studies which have supported the “watching eyes” effect. However, in their recent meta-analysis, Northover et al. (2017) suggested the strength of the watching eyes effect is mixed and highlight at least 18 studies in the last 9 years which have obtained nonsignificant results. Significant effects of the watching eyes effect may be therefore conditional on features of the environment, quality of the surveillance cue, participant traits, or methods of data analysis (Northover et al. 2017).

Reputational Fitness Benefits of Being Seen to Be Altruistic

Much of human behavior has evolved as a consequence of living in large social groups. For example, when observed, we change our behavior to fit in line with what is socially desirable. As the saying goes, “No man is an island.” Displays of altruism, in particular, has been shown to increase when observed by other group members. For example, in a public goods game study, Hardy and van Vugt (2006) found that donations to group funds significantly increased when donations were made public rather than private. This suggests there are reputational fitness benefits for showing off altruism. These may be twofold: One, it reduces the chance of violating social norms and being ostracized from the group. Two, it heightens chances of future reciprocal help (indirect altruism) and access to resources and mates (costly signalling). From an evolutionary perspective, it pays for someone to behave altruistically when being observed. Those ancestors that increased altruism when watched by others would be at a

fitness advantage over those who did not. But how strong is this evolutionary drive to be *seen to be* an altruist – do we actually need to be watched or do we just need to feel as though we are being watched by others?

Altruism and the Watching Eyes Effect

Research has shown that even subtle cues of being watched can have a significant influence on individuals' altruistic behavior, with some studies showing that this effect can be invoked by simply displaying a pair of eyes on a computer screen or on a poster. In their seminal study, Haley and Fessler (2005) conducted a series of dictator games (psychological scenarios which are used to explore unselfish behavior) and found that a stylized image of a pair of eyes on a computer screen substantially increased generosity among participants (Fig. 1).

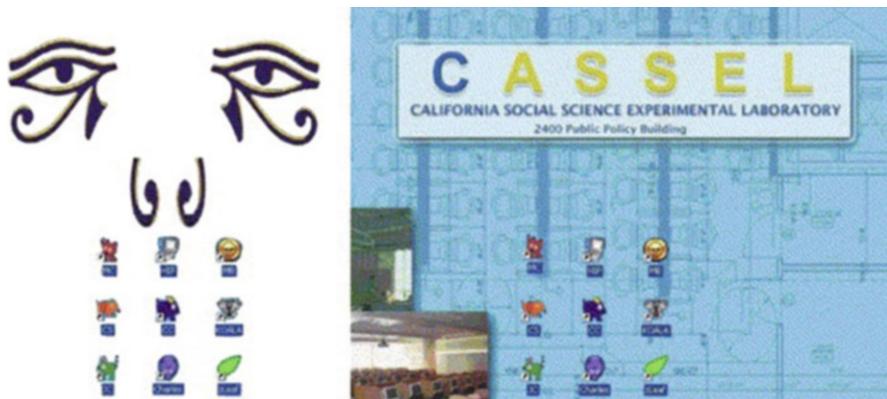
Burnham and Hare (2007) further supported this and showed that feeling of being watched are so intrinsic that even being observed by a robot could increase cooperation. They compared donations to six rounds of a public goods game and found that individuals "watched" by images of a robot; "Kismet," presented on their computer screen, contributed 29% more than the subjects without Kismet. However, since Haley and Fessler's (2005) paper was published, there have been both successful replications and null findings reported in the literature. In a 2013 replication,

Nettle et al. (2013) found that while the watching eyes effect did not significantly increase the mean amount of money donated, it did significantly increase the probability of donating something rather than nothing (combined odds ratio 1.39). This suggests that while the watching eyes effect may not increase the donations of the already generous, it could elicit donations from those who may not have originally done so.

Bateson et al. (2006) went further to examined the effect of an image of eyes on contributions to an honesty box and found that when people were exposed to an image of eyes on a nearby noticeboard, they gave three times more money than when they were exposed to an image of flowers. This suggests the watching eyes effect may help at reducing free riders (those who take more from the group than giving back) and encourage group norms (Fig. 2).

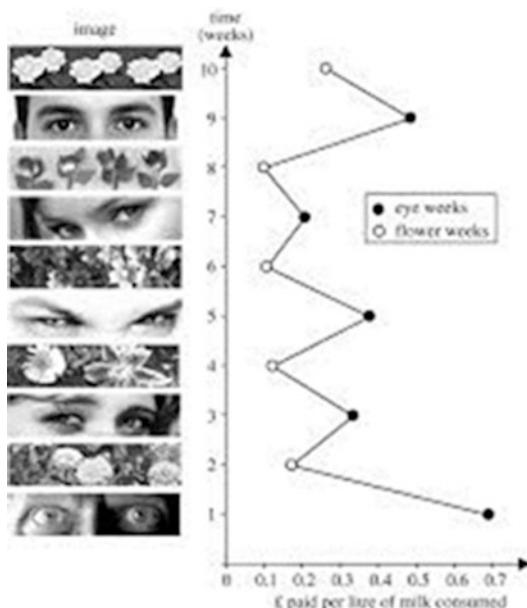
Studies which followed found that prosocial behaviors such as generosity (e.g., charity donations), morality (e.g., a drop in bicycle theft and increased voter turnout), and green behaviors (e.g., a reduction in littering) were substantially enhanced under conditions of "being watched" by images of eyes (for an overview, see Northover et al. 2017).

However, the strength of the watching eyes effect depends on how the eyes themselves are presented. For example, across three studies, with a total of 612 participants, Manesi et al. (2016) found that the gaze of the eyes made a difference; compared to averted eyes or closed eyes, only



Altruism and Watching Eyes, Fig. 1 Eyespots (left) and control (right) desktop displays. (Image of eyes taken from Haley and Fessler's 2005 paper)

direct eye gaze elicited the desire to help others. Furthermore, the emotion of the eyes can be important. When unkind eyes were compared to kind eyes or a control (images of trees), Pauwels et al. (2017) found that only unkind eyes increased the first mover's motivations to cooperate in a prisoner's dilemma game. In other words, unkind eyes boosted initial cooperation. The authors suggest unkind eyes urge the first mover to live up to the expectation of the interaction partner and conform to social norms (Fig. 3).



Altruism and Watching Eyes, Fig. 2 Image of eyes taken from the Bateson et al. 2006 paper

If a simple image of a pair of eyes on a computer screen or poster is enough to positively influence prosocial behavior, then these results point to a potentially low-cost and simple way of encouraging prosocial behavior in a much wider range of contexts such as reducing food waste, reducing energy consumption, and reducing littering. In fact, the “watching eyes” effect has been used in advertising campaigns by the HMRC aimed at tax evaders and by Keep Britain Tidy in reducing dog fouling.

Other potential avenue of the “watching eyes” effect is in online charity giving. Online charitable donations have been decreasing despite that charities can reach many more potential donors via the Internet than they can via more traditional fundraising methodologies (e.g., door to door canvassing). However, previous studies of the “watching eyes” effect in online environments have failed to find significant results (e.g., Saunders et al. 2016). It has been suggested that this could be because as the online environment is a truly anonymous setting, the eye cues are not effective in making people *feel* like they are being observed, and it is the belief of being watched by another person which is critical in generating the “watching eyes” effect. There is a growing literature which has started to cast doubt on the effect of watching eyes with recent, comprehensive meta-analyses finding no support for the “watching eyes” effect (e.g., Northover et al. 2017). At best, the results have found the “watching eyes” effect to be inconsistent or have found the effect to be heavily conditional on a range of factors. These include the



Altruism and Watching Eyes, Fig. 3 The two types of eye cues, kind eyes (a) and unkind eyes (b), and the control cue (c). (Image of eyes taken from the Pauwels et al. 2017 paper)

environment (e.g., whether the behavior was public vs. anonymous), the type of eye cue (e.g., photo vs. stylized eyes, perceived valence of the eyes image, gender of the eyes image, etc.), participant traits (e.g., gender), or the method of data analysis to name a few factors (see Northover et al. 2017 for a comprehensive list). In short, the finding of more recent research suggests the “watching eyes” effect may not be effective in *all* environmental context.

Since Haley and Fessler’s (2005) influential study, there has been an exponential growth in the use of the Internet with the introduction of companies such as Google and Facebook (to name just a couple). In a time where we are constantly exposed to images of people via the Internet or television and are used to feelings of being watched (e.g., CCCTV), perhaps we have become habitualized to these cues and images of eyes are no longer effective in evoking feelings of being observed. The mixed results suggest that any effect of monitoring cues is to some extent dependent on the characteristics of the environment and the specific watching stimuli used. If researchers can pinpoint the characteristics of the environment and the stimuli which can evoke the watching eyes effect, this would provide an inexpensive method of encouraging prosocial behavior which can be utilized in a range of applications from online charitable donations to reducing energy waste.

Conclusion

The “watching eyes” effect posits that altruistic behaviors could be encouraged by making people feel that they are being observed. Despite promising early studies, recent results have become mixed, and there is now doubt to whether the “watching eyes” effect exists in all environmental contexts. However, the “watching eyes” effect is still a potentially fruitful research avenue. By exploring more rigorously the conditions under which subtle cues of being watched could enhance prosocial behaviors, the findings could lend itself as an inexpensive way to encourage a broad range of prosocial actions.

Cross-References

- [Charity](#)
- [Costly Signaling and Altruism](#)
- [Eyespots](#)
- [Game Theory](#)
- [Indirect Benefits of Altruism](#)
- [Kin Selection Hypothesis](#)
- [Prisoner’s Dilemma and Cooperation](#)
- [Prosocial](#)
- [Reciprocal Altruism](#)
- [Reciprocal Altruism and Cooperation for Mutual Benefit](#)
- [Reputation and Altruism](#)

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Altruism Between Relatives

► $C < R_b$

Altruism Defined by Benefits Conferred

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Synonyms

Cooperation; Kin selection; Prosocial; Reciprocal altruism

Definition

An act of altruism involves not just a cost to the altruist but also means that another individual will benefit in different ways from the act.

Introduction

The traditional view of evolution by natural selection emphasizes how individual organisms have adaptive traits that aid their *own* survival and reproductive success, so that they pass their own genes onto future generations. When people therefore think of natural selection, they think of traits that benefit an individual directly and often at the expense of others, such as aggression, competition, and dominance, come to mind. However,

equally important in the natural world are behaviors such as grooming, food-sharing, and charity, where an individual organism actually incurs a cost to help benefit another. This contribution will therefore explore why such altruistic behaviors, whereby an individual incurs a cost in order for another to benefit, can be adaptive if they are costly, by looking at the benefits conferred by these acts to others.

The Puzzle of Altruism

Charles Darwin himself recognized that altruism was a challenge to his theory of evolution by natural selection. He knew that it was a common and ubiquitous behavior observed in different species, and that for his theory not to be shown to be false, altruism needed to be shown to be adaptive. Darwin articulated this challenge clearly in *The Descent of Man* (Darwin 1871) when he wrote:

It is extremely doubtful whether the offspring of the more sympathetic and benevolent parents, or of those who were the most faithful to their comrades, would be reared in greater numbers than the children of selfish and treacherous parents belonging to the same tribe. He who was ready to sacrifice his life, as many a savage has been, rather than betray his comrades, would often leave no offspring to inherit his noble nature. The bravest men, who were always willing to come to the front in war, and who freely risked their lives for others, would on an average perish in larger numbers than other men.

Benefits to the Group

An early attempt to answer how altruism could be adaptive suggested that it is the group, rather than the individual, that is being selected for. Group selection (Wynne-Edwards 1962) suggested that individuals incur costs to be altruistic to others so that their group is more likely to survive. A typical example of this would be a group with a limited amount of food, where each individual group member incurs the cost of low food intake. By doing so, they ensure that all other group members can get enough to eat and therefore the group is maintained and can be successful. Although originally a popular view, theoretically group selection could not work, as a selfish

individual who invaded that group would take all the benefit of available food left by other altruistic group members, leaving the group depleted. In other words, an individual can always exploit any benefit of altruism conferred to a group.

However, in the previous two decades, the notion of selection of groups has made somewhat of a comeback, albeit under a different name. Multi-level selection states that, under certain circumstances, groups of organisms behaving in a certain way (e.g., altruistically) can be selected for in the same way that individual organisms can (Wilson and Sober 1994). As a result, the different levels or “nested hierarchy” of units (e.g., groups, individuals) can all be acted on by natural selection, meaning that all need to be considered when understanding how altruism has evolved.

Benefits to Genetic Relatives

According to William Hamilton (1964), we can look to our kin as the beneficiaries of our altruistic behaviors. This is because these individuals share a number of our genes, and by helping their own survival and reproduction, we in turn are increasing the likelihood that these genes of ours will be present in future generations (albeit in another’s body). This is the principle behind Hamilton’s theory of inclusive fitness and relates to kin selection. Furthermore, the amount of help given to relatives is positively correlated to the amount of relatedness we share with them (in other words, how many genes on average we share with them). Therefore, closer relatives such as siblings of offspring are more likely to benefit from our altruistic acts as we share a large number of genes with them (50%) than would our cousins with whom we share only 12.5% of our genes.

To fully understand how and when relatives can benefit from our altruism, we can use Hamilton’s rule, see Fig. 1.

Therefore the larger the value of relatedness, the greater the difference between the cost to the altruist and the benefit conferred on the recipient can be. An example could be that you are more likely to rescue your sister from a burning building (where there is both high benefit due to high

$$rB > C$$

r is the relatedness between the individuals

B is the benefit to the recipient of the act

C is the cost the actor incurs for performing the act

Altruism Defined by Benefits Conferred, Fig. 1 A summary of Hamilton’s rule

relatedness with your sister and also high costs of the act) than you are to your second cousin (where benefit is greatly reduced due to lower relatedness, whereas the costs of entering the burning building are still high).

There is plenty of evidence of the benefits conferred by kin selection in humans. For example, In the USA, individuals are more likely to inherit the wealth of close genetic relatives (Smith et al. 1987). Elsewhere, members of South American tribes are more likely to receive free labor from relatives (Hames 1988) and on the Pacific atoll of Ifaluk, individuals received more shared food from relatives (Betzig and Turke 1986).

Benefits to those Who Helped Previously

Hamilton’s theory of kin selection soon became an established means of explaining how altruism can confer benefits, but it still did not fully explain the many examples we see of altruistic acts, particularly those where the beneficiary is unrelated. In response to this, Robert Trivers developed the theory of Reciprocal Altruism (Trivers 1971). According to this theory, individuals will help another unrelated individual in the expectation that that individual will return the favor in the future. In order for this to occur, Trivers proposed a number of conditions that must exist; first the cost of performing the altruistic act must be less than the benefit that is conferred on the recipient; secondly, reciprocal altruism will only occur in species that are highly social, which ensures that there are regular interactions between individuals for such acts to occur (and be reciprocated); finally, reciprocal altruism will also only occur in species with the necessary cognitive capacities, such as long-term memory, reasoning and perception.

Because of these three conditions, reciprocal altruism has mostly been observed in primate species, such as male baboons who work together at times to usurp higher-ranking males for access to fertile females (Packer 1977) or chimpanzees who use reciprocal altruism for cooperative grooming (Brosnan and de Waal 2002). It can also readily be observed in our everyday lives and exists cross-culturally such as with food-sharing among Hiwi and Ache families (Gurven 2004). It has also been observed in less suspected species such as vampire bats, who share blood meals with others in a group in a reciprocal altruistic way (Wilkinson 1984).

Conclusion

Despite the initial view that altruism was contradictory to Darwin's theory of evolution by natural selection, neo-Darwinian thinkers identified that such selfless behavior can be adaptive for the altruist when the benefits that the receiver gains are examined more. The two traditional explanations for altruism, that of kin selection and reciprocal altruism, changed how psychologists and biologists thought about this behavior and showed that, via increased inclusive fitness or greater returns in the future, it is the altruist themselves who benefits. As such, it raises the question of whether these acts are true altruism or not, as the actual initial costs to an individual of such an act are eventually outweighed by the direct benefits they receive in the long term.

Cross-References

- ▶ [Altruism](#)
- ▶ [Indirect Benefits of Altruism](#)
- ▶ [Kin Selection](#)
- ▶ [Reciprocal Altruism](#)

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Altruism Displays Cooperative Potential

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Synonyms

[Conspicuous prosociality](#); [Costly signaling](#); [Impression management](#)

Definition

A conspicuous demonstration of outward prosociality in order to signal one's capacities and inclinations for helping and working with others.

Instances of cooperative activity among individuals that are not kin-related are generally rare

throughout much of the animal kingdom but are a prevalent and enduring feature of human societies; steeped as they are in massive social and cultural complexity. The ability and capacity to forge alliances and engage in cooperative endeavors with conspecifics has created the foundational conditions for humans to build social and normative institutions, develop commerce and legal codes, engage in warfare, and create public infrastructural works for common benefit (Fehr and Fischbacher 2003). Social norms, which establish benchmarks for situational social behavior, and the looming threat of punishment and sanction for those who transgress such norms, serve as the macro-level regulatory mechanism governing large-scale cooperation among humans. At the micro level, cooperation is undergirded by a suite of faculties within the human emotional repertoire, including prosociality, compassion, shame, guilt, and a sense of fairness and othermindedness (Gintis et al. 2003; Lehmann and Keller 2006).

Convergences in common evolutionary history have produced commonalities between humans and non-human primates in terms of the behaviors and preference structures which facilitate cooperation. Activities such as coalition building and support, mobilization of territorial defense systems, engagement in guardianship of children by extended family, and social grooming are all seen across the different primate species. Humans, however, differ markedly in terms of the scale, scope and manifest variety of their cooperative behavior. Cooperative interaction among humans regularly extends beyond the boundaries of the immediate group, and the resulting social ties often endure long after the individuals comprising them have moved beyond occupying the same physical space. Furthermore, humans, unlike our closest primate relatives, exhibit strong generalized preferences for performance outcomes which benefit *others* (Burkart et al. 2009).

A major source of insight from the hominid branching of the evolutionary history of primates has been the advent of cooperative breeding during the Pleistocene era. In this context, early humans, having been presented with novel environmental challenges due to changes in

geographic dispersal, needed to develop new foraging and subsistence strategies in order to acquire sufficient caloric resources in their new habitats (Johnson and Earle 2000). A key part of this overall stratagem was reliance by mothers on other guardians to assume some share of the burden of child-rearing – a phenomenon known as *alloparenting*. Under these conditions, it is thought that humans evolved an increasingly complex array of cognitive faculties purposed toward a kind of proactive prosociality, whereby individuals became more inclined to provide benefits to others in spite of their relatively distal genetic relatedness to them. While other primates engage in some degree of allopaternal care, the degree of kin relatedness in these primate societies is very high when compared to humans. This suggests that the selection pressures that have created the conditions for cooperative behavior among humans differ from those found among other primates (Kramer 2010; Van Schaik and Burkart 2010).

Perhaps the greatest differences in this respect are the dual evolution of cultural and physiological adaptations among humans, and the emergence of massive interdependence within our species. The centrality of information transmitted through culture to the human condition has no analogue in other primates, or indeed any other animal. Relative to other primates, ancestral humans occupied a greater diversity of physical environments and relied on a substantially greater breadth of resources, and therefore had to develop the requisite psychophysiological capacities to navigate these added complexities. Consistent with the cooperative breeding hypothesis, the complications inherent in these vast environmental parameters would have made single guardian child-rearing all the more difficult, and in turn created the conditions through which guardianship from other adults became an adaptive evolutionary imperative. Moreover, as universal participation in all affairs of group life – child-rearing included – became a necessity as humans learned to operate within environmental novelty, an effective and efficient means of transferring knowledge from one individual to another would have demanded additional adaptive solutions. Culture and language represent evolution's

answers to these adaptive puzzles (Smaldino 2014; Tomasello et al. 2012).

Taken together, the increasing interdependence found among ancestral humans, and the vehicle of culture for the efficient interpersonal transmission of survival-contingent information, meant that an effective signaling mechanism for cooperation was required within the human ecological niche. Ancestral humans had to be sure that a potential cooperator was both sufficiently interdependent within the group and a reliable source of accurate, culturally transmitted information. The uniquely human strain of altruism evolved precisely to fulfill such a need for an effective signaling mechanism. Consistent with costly signaling theory – whereby the performance of a costly altruistic act serves as a reliable signal of the altruist's trustworthiness and dependability – altruism functions as an outwardly observable display trait which attests to the cooperative potential of the altruist in question (Fehr and Fischbacher 2003; McAndrew 2002).

Furthermore, the unique complexity of human social structures provides an explanatory basis for the long-term, enduring, and dispersed nature of altruism in our species. Whereas other primates lack the sophisticated capacities for culture that we do, and as such their reputations for altruism are heavily constrained by the immediacy of the group in which they are embedded and the fleetingness of the acts performed and subsequent benefits accrued, the reputational benefits of a single act of altruism could potentially be realized by an individual human throughout the course of a lifetime. The singular performance of some suitably personally costly act might temporarily disadvantage an individual in a highly temporally constricted sense (a consideration which itself might preclude other primates from performing similar acts), but the same individual might amass a greater preponderance of social recognition benefits in the long run. In this sense, an emphasis on the “potential” component of cooperative potential is warranted. Other primates might recognize individual instances of costly altruistic behavior and make assessments of conspecifics accordingly, but there is little to suggest that non-human primates recognize such acts as being meaningfully reflective of the inclination of

altruists to perform other acts of altruism at some unspecified time in the future. Among humans, altruism serves just this end – showcasing itself as a hallmark for cooperative potential generally.

A

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Altruism in Kin Selection

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Synonyms

Altruism; Parental care; Inclusive fitness

Definition

When an organism behaves to produce benefits for his kinship with a cost for himself.

Introduction

The classical natural selection theory cannot account for scenarios where an animal behaves to promote benefits to others by paying its costs (Hamilton 1963, 1964). One possibility to explain such scenarios may be that the recipient of the altruistic act shares some genes with the behaver. The altruistic act, in this way, may reduce the behaver's fitness although enhancing his genes fitness, what is known as inclusive fitness. Therefore, altruistic acts toward relatives may be a fitness-enhancing strategy.

Hamilton's Law of Kinship Altruism

W. D. Hamilton construed his model for the selection of Altruistic acts on a criticism against the idea that an individual behaves in cooperative ways in the benefit of the species. Findings in population genetics at that time already pointed that general adaptive advantages on a group does not affect within group selection (Wright 1948). Besides, he was interested in a mathematical model that could account for predictions about the probability of occurrence of an altruistic act. The first step of Hamilton's law is the broadening of the concept of fitness. While fitness is a measure of an individual's ability to reproduce (Nowak and Highfield 2011), Hamilton (1964) proposed the concept of inclusive fitness as a measure for gene replication not dependent on individuals alone but encompassing also the relatives. That is, an organism may pass on his genes by reproducing and by helping kin to reproduce.

A costly act may favor the inclusive fitness, therefore being selected (1) when behaver and recipient share some genes, (2) in a direct proportion of the amount of genes shared, and (3) when cost-to-benefit ratio is high with small costs producing great benefits. This description was elaborated in the equation:

$$k > \frac{1}{r}$$

where k stands for the relative gain produced and r represents the coefficient of relatedness or the probability of sharing a gene. That is, altruistic acts will be more probable when the coefficient of relatedness exceeds the cost-to-benefit ratio.

The coefficient of relatedness is the key aspect of kin selection. It is classically expressed in Haldane's words that he would risk his life to save two brothers or eight cousins, but not less (Hamilton 1963; Nowak and Highfield 2011). Such calculation emphasizes the altruistic act as a selfish strategy (Dawkins 1976), based solely in the increasing of gene's fitness.

Evidence for nepotistic behavior abounds (Burnstein 2005). The classical model to draw predictions about kinship altruism come from the studies about brotherly care in female eusocial hymenoptera.

Studies on Brotherly Care in Female Eusocial Hymenoptera

Because of its haplodiploid reproduction, with males being haploid and females being diploids, the kinship coefficient in eusocial hymenoptera relatives takes a special course. Between sisters fathered by the same male, it reaches 0.75, bigger than the common kinship coefficient of 0.5 between mother and offspring and far superior than the kinship among hymenoptera sisters and brothers (0.25 on average). Such genetic configuration indicates that female hymenoptera produce more fitness by caring their sisters than by breeding or caring their brothers. Thus, studies about sexual behavior and brotherly care in female non-queen hymenoptera can shed light on predictions about inclusive fitness altruism.

Hare and Trivers (1973) showed that although the amount of males and females in haplodiploid colonies is similar, females weighed three times more than their brothers, meaning that their sisters, the workers, fed them more than theirs brothers.

Mueller (1991) observed possible bias in investment toward brothers or sisters in colonies

of *Augochlorella striata* bees where the foundress queen was either maintained or removed, being replaced by a worker. When a worker becomes the new queen, the other workers will no longer take care of siblings but of nephews and nieces. Results showed that in colonies with replaced queens, males weighed more than females and significantly more than the males from foundresses queen's colonies, suggesting that when kinship among workers and brothers and sisters is the same, there is a bias in investment toward brothers. Sündstrom et al. (1996) observed similar biases in colonies of *Formica exsecta* with monogamic or polyandric queens. In polyandric queen's colonies, the kinship between worker and offspring is equal for males and females, on average. Results showed that in colonies with singly mated queens, the elimination of male eggs is observed, a pattern absent in multiply mated queen colonies. Such evidence points to an inclusive fitness pattern of behavior from hymenoptera workers.

Proximal Mechanisms in Kinship Altruism

One of the major critiques about altruism in kin selection is based on the assumption that altruistic acts toward kin may not require gene sharing, but instead, behavioral characteristics that are preferred in social partners and maintained by proximal mechanisms, as reciprocity (Allen-Arare et al. 2008). That is, altruistic acts are better predicted by a history of reciprocal exchange interactions, regardless of the coefficient of relatedness (Allen-Arare et al. 2008; Chapais 2001; Moore 1992). Support for kin selection as a special type of interaction, apart from reciprocity, should demonstrate that higher frequencies of unreciprocated help happens among kin; the larger the cost, the more related must be agent and recipient; and reciprocal interactions are a necessary feature in nonkin help exchanges (Esock-Vitale and McGuire 1980).

Some anthropological data do support kinship altruism as a special kind of interaction that do not work as the same way as reciprocity. Esock-Vitale and McGuire (1980) resumed qualitative

anthropological descriptions in highly diverse human societies showing that the occurrence of unreciprocated help is more common (above chance level) among closer kin, with distant kin and nonkin reciprocating gifts. While unreciprocated gifts or aid among kin is usually ignored, when it happens among nonkin, consequences are gossiping, the rupture of social ties and the interruption of future gifts.

Morgan (1979) accompanied whale-hunting groups of Yupik Eskimo in Gambell Village, Alaska. Whale hunting is the major economic activity within this group and is a very risky activity with high rates of accidents and life threatens. For each crew, Morgan verified the coefficient of relatedness and its frequency in hunting. He observed that the most active groups had crews mostly composed by close relatives (all males) being either father and sons or brothers and their sons (coefficient of relatedness ranging from 0.33 to 0.55). Large families usually had more than one crew, so they could easily find backup members, and when one crew faced an accident, related crews usually came into aid. Crews composed by nonrelatives had unstable compositions and more difficult to find backup members, and when they faced accidents during hunt, they received less help. If kinship altruism could be reduced to a reciprocity exchanges, there should be no difference among family or nonfamily crews.

On the other hand, there are also evidences showing that reciprocity alone may account for some helping behavior among kin. Gurven et al. (2001) showed that in the indigenous reservation-living Ache people (forager-horticulturists), there is a widespread practice of food distribution between households with clear preference for a household recipient that contains at least one close relative, but the amount of food donated is contingent to previous food exchanges.

Jaeggi and Gurven (2013) showed in a meta-analysis on 32 independent studies on food-sharing behavior in human foragers and non-human primates that when controlling for reciprocity and kinship (only 10 studies), there was no difference in the frequencies of helping behavior, suggesting similar patterns toward kin and nonkin regulated by proximal variables.

Conclusion

Altruistic acts toward kin may be a fitness-enhancing strategy once it provides inclusive fitness and increases the frequency of a gene in the gene pool deemed to be the reproduction's success of an organism and its relatives. As predicted by the Hamilton's law, such acts are more probable the more related are the two individuals, with costs being lower than the benefits promoted. Such predictions find strong support in evidence among eusocial hymenoptera. Additional evidence, especially from primatology, suggest, however, that inclusive fitness may be less important for the maintenance of altruism among kin with proximal mechanisms like direct reciprocity and mutualism playing a major role (Allen-Arare et al. 2008; Chapais 2001; Moore 1992).

Cross-References

- ▶ [Altruism](#)
- ▶ [Cooperation Varies with Genetic Relatedness](#)
- ▶ [Genetic Relatedness](#)
- ▶ [Hamilton's Rule and Genetic Relatedness](#)
- ▶ [R = Coefficient of Relatedness](#)

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Altruism Norms

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Synonyms

Patterns of helping behavior; Prosocial norms

Definition

Altruism refers to any helping behavior whose intended goal is to improve another's welfare,

typically at some cost to the helper. Altruism norms are defined as the typical patterns of behavior seen surrounding these selfless acts. This chapter will summarize prototypical norms of altruism that are commonly seen in families and societies.

Introduction

Altruism norms have evolved and changed throughout the course of human history and can include things such as self-sacrifice, philanthropy, or just doing a good deed. It has been suggested that altruism is influenced in part by genetic factors but more so by the types of societies to which individuals are exposed (Bell et al. 2009). Altruism can be seen as an evolved mechanism that is molded to fit within the norms of different cultures, yet it operates automatically when loved ones, family members, or even strangers require help.

Kin Selection and Pro-family Norms

Engaging in altruistic behavior can be costly for an individual, but in certain scenarios it could be beneficial (evolutionarily) to better others rather than the self. For instance, if an individual were in a scenario where food needed to be rationed and food supplies were low, it might be more beneficial for this individual to allocate resources to those who would make better use of them (i.e., an elderly individual giving up food supplies to younger individuals). From an evolutionary perspective, this effect would be expected in familial environments as it is more important that the genes survive rather than the individual as copies of one's genes lead to greater genetic fitness than if one were to survive without reproducing. Research has shown that when placed into situations in which various individuals needed help, participants were more likely to help those who were more closely related to them as opposed to those more distantly related (Burnstein et al. 1994). In fact, when asked how likely they would be to donate an organ to someone who desperately needed an organ transplant, most

people preferred to donate their organs to those who were related to them rather than strangers (Borgida et al. 1992). While this could be the result of an individual learning that family takes care of family throughout their upbringing, children are also more willing to help their siblings rather than their friends (Tisak and Tisak 1996). While humans are excellent at recognizing when family members are in need, there are times where family members are forsaken in favor of non-family members.

Altruism Norms and Expectations of Altruism in Society

Although in most cases family would take priority, individuals often act altruistically toward other members of their society. Trivers (1971) believed that this behavior represents reciprocal altruism, or the idea that helping someone now may increase the likelihood of them helping us in the future. Reciprocal altruism affords both the helper and the recipient the possibility for reward, but this requires the helper to have a certain level of trust that the beneficiary will reciprocate at some point. Even though trusting another to reciprocate may be risky at times, engaging in altruism could increase one's genetic fitness. In fact, research has shown that people publicly punish selfish individuals to signal their lack of selfishness, and when individuals engage in costly helping (i.e., altruism), they are seen as more trustworthy by others (Jordan et al. 2016). While being seen as more trustworthy could certainly increase genetic fitness, research has found that people prefer to help attractive target figures. This could suggest that the goal is to increase their own genetic fitness through potentially reproducing with the attractive target figure (Farrelly et al. 2007). While the previous points are on ways in which altruistic behavior can be promoted, studies have shown ways to diminish the likelihood of altruistic behavior. Participants were asked to prepare a talk on the biblical Good Samaritan or a job talk, with the idea being that when they were asked to think about an altruistic figure (e.g., the Good Samaritan), they would, in turn, behave more

altruistically; the results did not support this, with neither being a significant predictor for altruistic behavior. These participants were randomly assigned to be told that they would be late, on time, or early to the following appointment prior to leaving. The researchers found that those participants who were told they were late for their next appointment were significantly less likely to help a stranger in need compared to the other conditions (Darley and Batson 1973). This implies that when helping others is detrimental (e.g., making us late to an important appointment), we are less willing to help them in their times of need.

While being on time can allow individuals to engage in altruistic behavior, recent research on gender roles in altruism has revealed another predictor of altruistic behavior. Rand et al. (2016) found that women are more likely to be expected to engage in altruism rather than men. Not only are women expected to be more altruistic, they experience greater punishment when failing to behave altruistically as compared to men. When participants were asked to use their intuition (rather than deliberation) when deciding to reciprocate an act of altruism, only women showed increased levels of altruism. Furthermore, when women described themselves with more masculine attributes (e.g., dominance), they were less likely to engage in altruism following a deliberation period. While women may be expected to be more altruistic, research has also found that when participants were asked to play games with others, they behaved in a more cooperative manner when they were told their decisions would be made public, rather than private (Hardy and Van Vugt 2006). Those participants who made public, cooperative choices were seen as having a higher social status than those who answered privately. While those are specific examples of individual groups, most societies tend to promote reciprocity norms through the golden rule. This idea seems to work well in societies as people prefer to help those who have helped them at some point in the past (Whatley et al. 1999), suggesting that helping another will result in the recipient of the help being more willing to provide their help at a later date to the helper.

Conclusion

The goal of this chapter was to cover altruism norms, specifically those in families and societies. Individuals tend to prefer to help family members rather than nonfamily members, but this is not always the case. Individuals may choose non-family members if the goal is not to necessarily pass on genetic fitness through bettering a family member but rather to secure a mate who displays some desired attribute (e.g., attractiveness). While most societies promote reciprocal altruism through use of the golden rule, individuals may choose to ignore a stranger in need if the cost is perceived to be too great. Additionally, certain traits or physical aspects of a person, such as trustworthiness or gender, may result in them being perceived to behave more altruistically in social situations, but, in general, people prefer to engage in altruistic behavior with those who have helped them in the past.

Cross-References

- [Altruism](#)
- [Kin Altruism](#)
- [Reciprocal Altruism](#)

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Altruistic Behavior

- ▶ Adaptive Problem of Detecting Kinship
- ▶ Alarm Calling and Kinship
- ▶ Kin Recognition

Altruistic Nepotism

- ▶ Alarm Calling Predicted by Inclusive Fitness

Altruistic Punishment

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Synonyms

Costly punishment; Moralistic punishment;
Strong negative reciprocity

Definition

A willingness to impose sanctions on norm violators at the punisher's own cost, in the absence of (immediate) material return

A

Introduction

Altruistic punishment is one of the central mechanisms and manifestations of *strong reciprocity*, the theory of which is regarded today as one of the most influential attempts at explaining the evolution of human cooperation (Bowles and Gintis 2011; Fehr and Fischbacher 2003, 2004; Fehr et al. 2002; Fehr and Gächter 2002; Fehr and Gintis 2007; Fehr and Henrich 2002; Fehr and Rockenbach 2004; Fowler 2005; Gintis et al. 2003, 2008; McElreath et al. 2003). It denotes a predisposition to cooperate with others and a willingness to punish at personal cost those who violate cooperative norms. This altruistic form of punishment has been well documented both in real life and in laboratory experiments. It is altruistic in the sense that it occurs even in situations where no future benefits for the punishing individual or the individual's genes are possible: in one-shot scenarios among strangers under conditions of strict anonymity (Bowles and Gintis 2011; Fehr and Fischbacher 2005; Gintis et al. 2003).

Experimental Evidence

In the laboratory, altruistic punishment has been observed most commonly in experimental games developed within the framework of game theory. In the *ultimatum game*, two players decide over the division of a fixed sum of money. Player A can make one proposal to player B, who can accept or reject it. If B accepts the proposal, the money is shared accordingly; if B rejects, both players receive nothing. Since the game is one-shot and anonymous, the self-interested outcome would be for player A to offer the lowest possible amount and for B to never reject. However, this outcome is almost never achieved: player Bs typically

reject offers lower than 30%, regarding them as unfair, and, anticipating this, player As typically offer around 50% (Fehr and Fischbacher 2005; Gintis et al. 2003).

In the ultimatum game, player Bs are directly affected by player As' proposal. There is evidence, however, that a number of people are willing to employ altruistic punishment against those who behave uncooperatively toward a third person (Fehr and Fischbacher 2004). In the *third-party punishment game*, players A and B take part in a *dictator game*. It has the same structure as the ultimatum game, except that here player B has no option of rejecting A's proposal; she/he has to accept whatever is offered. The game is anonymously observed by player C, who is not affected by player A's decisions. However, C is endowed by a fixed sum of money and has the opportunity to impose a fee upon A after witnessing A's offer. The fee is costly, for one-third of the decided amount is deducted from C's initial endowment. Nevertheless, in the experiment (Fehr and Fischbacher 2004), 55% of Cs punished A for offers below 50%, and the amount of punishment increased with the perceived unfairness of the offer. This tendency of disinterested third parties to use altruistic punishment is in line with the supposed role of strong negative reciprocity as a norm enforcement device in real-life situations, e.g., in the upholding of food sharing norms in hunter-gatherer societies (Bowles and Gintis 2011; Fehr and Fischbacher 2005).

Altruistic punishment has been well documented in multilateral experimental situations, as well. These typically resemble *social dilemmas*: n-person situations in which everyone would gain by cooperation but each individual has an incentive to gain at the expense of the others. The behavior that would be beneficial for all is less profitable for the individual than the selfish alternative, yet it would severely harm the interests of the community if everyone followed self-regarding strategies (Gintis 2009; Van Lange et al. 2007; Van Lange and Joireman 2008; Van Vugt and Van Lange 2006). The *public goods game* is one of the most widely applicable models for such dilemmas (Bowles and Gintis 2011; Camerer and Fehr 2004; Fehr and Gächter 2002; Gintis et al.

2003). This game typically consists of more than one rounds, in groups of $2 + n$ players. In each round, the players are provided with a certain amount of money, and they have to decide how much of it (if any) to contribute to a common account (i.e., the public good) and how much to keep in their own private account. The individual contributions are summed up and multiplied by a factor of usually 3. The resulting sum is then equally divided and added to the players' private accounts, independently of their individual contributions. In public goods games without costly punishment opportunity, the amount contributed to the public good gradually declines over time, which can be explained by the fact that those players who are inclined toward strong reciprocity do not cooperate at any cost – their cooperation is conditioned by the other group members' behavior. In the absence of other options, they signal their dislike of the free riders' strategy by lowering their own contributions. If, however, the players are given the option to use targeted, costly punishment against each other, the game unfolds differently. Sanctioning behavior follows the principles of strong negative reciprocity; the players who impose punishment even at their own expense are those who have an initially cooperative approach to the situation; sanctions are used against those participants who contribute nothing or only substandard amounts to the public good; and, the existence of punishment opportunities results in a stable and high level of contributions, thus re-establishing cooperation. Thus, by acting to raise the level of contributions to the public good, altruistic punishment itself serves as the so-called second-order public good (Bowles and Gintis 2011; Fehr and Fischbacher 2005; Fehr and Gächter 2002).

There is some controversy surrounding the external validity of the experimental findings. In particular, Guala (2012) has argued on the basis of anthropological evidence that the results do not translate from the laboratory to the field. While his critique has sparked intense debate, it seems true that in real-life circumstances people may strive to find other solutions beside costly punishment; alternatively, under the right circumstances, the mere threat of sanctions or purely symbolic

forms (gossip) can serve as incentives for cooperation (Van Lange et al. 2014).

Proximate Mechanisms

It has been suggested that in the experimental scenarios described above, the sole motivation for sanctioning behavior is strategic: the punishers' desire to maximize their payoffs relative to the punished individuals (Price et al. 2002). However, there is evidence indicating that this is not the case. In a prisoner's dilemma experiment by Falk et al. (2005), the cost of punishment was the same for the punisher and the punished player, so it was not possible to influence and affect the difference in payoffs via sanctioning. However, almost 60% of players who cooperated in the game imposed substantial amounts of punishment on defectors. It seems that costly punishment is to a large extent motivated by the negative emotions strong reciprocators feel when observing unfair decisions and the positive emotions induced by their own sanctioning behavior (Bowles and Gintis 2011; Declerck et al. 2013; Fehr et al. 2002; Fehr and Camerer 2007; Rilling et al. 2002). Studies combining neuroimaging methods with economic games have shown that both first-person and third-person punishment behavior activate reward-related brain regions (De Quervain et al. 2004; Strobel et al. 2011). Thus, it seems that humans are endowed with proximate mechanisms that render altruistic punishment pleasurable even when it yields no financial gains.

The punishment mechanism seems to be especially sensitive to structural modifications to the experimental situation. It is highly relevant whether the punishment is costly or cost-free, whether it comes from other members of the group or from an external observer, whether the group composition is stable or changes from round to round, and whether the participants are able to keep track of the earnings of each other during the game; group size and even the nationalities of the players are important modifying features as well (Balliet et al. 2011; Falk et al. 2005; Fehr et al. 2008; Hermann et al. 2008; Nikiforakis

2010). The effectiveness of costly punishment seems to be more pronounced in cultures with higher levels of interpersonal trust (Balliet and Van Lange 2013). At the same time, punishment can serve roles other than the sanctioning of unfair behavior. In some public goods game-type experiments, it has been found that a small but hardly insignificant proportion of the punishment was imposed on those cooperators who earned above average during the earlier rounds of the game (Bochet et al. 2006; Falk et al. 2005). Placing sanctions on cooperators may also serve as revenge; in the case of the so-called antisocial punishment, the defectors retaliate for the punishment they received before from the cooperators themselves (Hermann et al. 2008).

Evolutionary Origins

Costly punishment might yield pleasurable feelings, yet the finding that it is not the most economically beneficial strategy in public goods games (high contributors, who neither receive nor give out punishments, are the most successful) raises the question of the possible evolutionary origins of such an altruistic strategy. The answer may be found in the theories of multilevel selection and gene-culture coevolution. According to the literature (Bowles and Gintis 2011; Gintis et al. 2003), in the relevant evolutionary period of the Pleistocene, intergroup competition constituted a formidable force in the dynamics of human evolution. Human groups often had to face dispersal or extinction threats due to wars, famines, environmental disasters, etc. Groups with a relatively high proportion of strong reciprocators enforcing cooperation norms were much more likely to survive such events. Moreover, humans have unique cognitive and emotional capabilities enabling us to create and communicate social norms, among which are norms of altruism, cooperation, and the suppression of within-group competition. In such circumstances, within-group selection forces acting against strong reciprocators weaken to the extent that eventually they invade a population of self-regarding types (Bowles and Gintis 2011; Fehr and Fischbacher

2005; Gintis et al. 2003; Richerson and Boyd 2004). The use of moralistic punishment as a norm enforcement device may spread among the members of an entire population through the mechanism of conformist transmission, the behavioral norm of imitating the most successful members in a community (Bowles and Gintis 2011; Richerson and Boyd 2004).

Conclusions

We have seen the experimental evidence for altruistic punishment, the central behavioral expression of strong reciprocity, and there is every reason to suppose it is prevalent in real-life situations, as well. The main motivation behind this tendency lies in proximate mechanisms shaped by evolutionary forces and conditions that rendered this behavior, in spite of its costs, invaluable in the upholding of social norms.

Cross-References

- ▶ [Altruistic Punishment and Strong Reciprocity](#)
- ▶ [Cross-Cultural Punishment](#)
- ▶ [Costs of Punishing](#)
- ▶ [Evolution of Cooperation](#)
- ▶ [Free Riding](#)
- ▶ [Game Theory](#)
- ▶ [Gene-Culture Coevolution](#)
- ▶ [Multilevel Selection Theory](#)
- ▶ [Strong Reciprocity](#)

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Altruistic Punishment and Strong Reciprocity

A

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Synonyms

[Costly punishment](#); [Moralistic punishment](#); [Strong negative reciprocity](#)

Definition

A willingness to impose sanctions on norm violators at the punisher's own cost.

Introduction

The theory of *strong reciprocity* is regarded today as one of the most influential attempts at explaining the evolution of human cooperation (Bowles and Gintis 2011; Fehr and Fischbacher 2004, 2005; Fehr et al. 2002; Gintis et al. 2003). It denotes a predisposition to cooperate with others and a willingness to punish at personal cost those who violate cooperative norms. This altruistic form of punishment has been well documented both in real life and in laboratory experiments. It is altruistic in the sense that it occurs even in situations where no future benefits for the punishing individual or the individual's genes are possible: in one-shot scenarios among strangers under conditions of strict anonymity (Bowles and Gintis 2011; Fehr and Fischbacher 2005; Gintis et al. 2003).

Experimental Evidence

In the laboratory, altruistic punishment has been observed most commonly in experimental games developed within the framework of game theory. In the *ultimatum game*, two players decide over the division of a fixed sum of money. Player A can make one proposal to player B, who can accept or

reject it. If B accepts the proposal, the money is shared accordingly; if B rejects, both players receive nothing. Since the game is one shot and anonymous, the self-interested outcome would be for player A to offer the lowest possible amount and for B never to reject. However, this outcome is almost never achieved: player Bs typically reject offers lower than 30%, regarding them as unfair, and, anticipating this, player As typically offer around 50% (Fehr and Fischbacher 2005; Gintis et al. 2003).

In the ultimatum game, player Bs are directly affected by player As' proposal. There is evidence, however, that a number of people are willing to employ altruistic punishment against those who behave uncooperatively toward a third person (Fehr and Fischbacher 2004). In the *third-party punishment game*, players A and B take part in a *dictator game*. It has the same structure as the ultimatum game, except that here player B has no option of rejecting A's proposal; he/she has to accept whatever is offered. The game is anonymously observed by player C, who is not affected by player A's decisions. However, C is endowed by a fixed sum of money and has the opportunity to impose a fee upon A after witnessing A's offer. The fee is costly, for one-third of the decided amount is deducted from C's initial endowment. Nevertheless, in the experiment of Fehr and Fischbacher (2004), 55% of Cs punished A for offers below 50%, and the amount of punishment increased with the perceived unfairness of the offer. This tendency of disinterested third parties to use altruistic punishment is in line with the supposed role of strong negative reciprocity as a norm enforcement device in real-life situations, e.g., in the upholding of food-sharing norms in hunter-gatherer societies (Bowles and Gintis 2011; Fehr and Fischbacher 2005).

Altruistic punishment has been well documented in multilateral experimental situations, as well. These typically resemble *social dilemmas*: n-person situations in which everyone would gain by cooperation, but each individual has an incentive to gain at the expense of the others. The *public goods game* is one of the most widely applicable models for such dilemmas (Bowles and Gintis 2011; Fehr and Gächter 2002; Gintis et al. 2003). This game typically consists of more

than one rounds, in groups of $2 + n$ players. In each round, the players are provided with a certain amount of money, and they have to decide how much of it (if any) to contribute to a common account (i.e., the public good) and how much to keep in their own private account. The individual contributions are summed up and multiplied by a factor of usually three. The resulting sum is then equally divided and added to the players' private accounts, independently of their individual contributions. In public goods games without costly punishment opportunity, the amount contributed to the public good gradually declines over time, which can be explained by the fact that those players who are inclined toward strong reciprocity do not cooperate at any cost – their cooperation is conditioned by the other group members' behavior. In the absence of other options, they signal their dislike of the free-riders' strategy by lowering their own contributions. If, however, the players are given the option to use targeted, costly punishment against each other, the game unfolds differently. Sanctioning behavior follows the principles of strong negative reciprocity; the players who impose punishment even at their own expense are those who have an initially cooperative approach to the situation; sanctions are used against those participants who contribute nothing or only substandard amounts to the public good; and the existence of punishment opportunities results in a stable and high level of contributions, thus reestablishing cooperation. Thus, by acting to raise the level of contributions to the public good, altruistic punishment itself serves as a so-called second-order public good (Bowles and Gintis 2011; Fehr and Fischbacher 2005; Fehr and Gächter 2002).

Proximate Mechanisms and Evolutionary Origins

It has been suggested that in the experimental scenarios described above, the sole motivation for sanctioning behavior is the punishers' desire to maximize their payoffs relative to the punished individuals. However, there is evidence indicating that this is not the case. In a prisoner's dilemma experiment by Falk et al. (2005), the cost of

punishment was the same for the punisher and the punished player, so it was not possible to influence/affect the difference in payoffs via sanctioning. However, almost 60% of players who co-operated in the game imposed substantial amounts of punishment on defectors. It seems that costly punishment is to a large extent motivated by the negative emotions strong reciprocators feel when observing unfair decisions and the positive emotions induced by their own sanctioning behavior (Bowles and Gintis 2011; Fehr et al. 2002). Studies combining neuroimaging methods with economic games have shown that both first-person and third-person punishment behavior activate reward-related brain regions (De Quervain et al. 2004; Strobel et al. 2011). Thus it seems that humans are endowed with proximate mechanisms that render altruistic punishment pleasurable even when it yields no financial gains.

The finding that costly punishment is not the most economically beneficial strategy in public goods games (high contributors, who neither receive nor give out punishments, are the most successful) raises the question of the possible evolutionary origins of such an altruistic strategy. According to Gintis et al. (2003) in the relevant evolutionary period of the Pleistocene, human groups often had to face dispersal or extinction threats due to wars, famines, environmental disasters, etc. Groups with a relatively high proportion of strong reciprocators enforcing cooperation norms were much more likely to survive such events. Moreover, humans have unique cognitive and emotional capabilities enabling us to create and communicate social norms, among them norms of altruism and cooperation. In such circumstances, within-group selection forces acting against strong reciprocators weaken to the extent that eventually they invade a population of self-regarding types (Bowles and Gintis 2011; Fehr and Fischbacher 2005; Gintis et al. 2003; Richerson and Boyd 2004). The use of moralistic punishment as a norm enforcement device may spread among the members of an entire population through the mechanism of conformist transmission, the behavioral norm of imitating the most successful members in a community (Bowles and Gintis 2011; Richerson and Boyd 2004).

Conclusion

We have seen the experimental evidence for altruistic punishment, the central behavioral expression of strong reciprocity, and there is every reason to suppose it is prevalent in real-life situations, as well. The main motivation behind this tendency lies in proximate mechanisms shaped by evolutionary forces and conditions that rendered this behavior, in spite of its costs, invaluable in the upholding of social norms.

Cross-References

- ▶ [Altruistic Punishment](#)
- ▶ [Costs of Punishing](#)
- ▶ [Evolution of Cooperation](#)
- ▶ [Game Theory](#)
- ▶ [Strong Reciprocity](#)

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Altruistic Punishment Enhances Reputation

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Synonyms

Altruism among nonkin; Group selection; Public goods game

Definition

The costly act of produce a loss to a noncooperative behavior enhances the reputation of a group as cooperative one.

Introduction

During the evolutionary history of the human species, some survival increasing activities were group ones, consisting in a public good (Fehr and Gächter 2002). Hunting, warfare, and protection of common resources are some good examples. In public good situations, each member of the group benefits from the good, and its maintenance is a shared responsibility. Some members of the group will pay costs for the maintenance of the public good, the cooperators, while others will benefit from the good without paying any costs, the free riders. Increases in the number of the free riders will lead to a collapse and consequent extinction of the public good, harming the whole group (Hardin 1968). One measure to prevent such increases is to punish free riders, in order to curb such behavior. Thus, altruistic punishment may be an evolutionary selected strategy to maintain high levels of cooperation in large groups of unrelated individuals.

However, the punishment of free riders means additional individually costly acts, creating a second-order public goods problem (Fehr and Gächter 2002; Gürerk et al. 2006). Paradoxically, altruistic punishment is widespread, present in

highly diverse human societies (Henrich et al. 2006).

In models concerning group selection, the punishment strategy may be sustainable because the reduction of free riding produced by the altruistic punishment may overcome the costs of punishment by producing a more cooperative group composition (Fowler 2005; Gächter et al. 2008; Henrich and Boyd 2001). Once cooperation is established, the costs of punishment would tend to decrease and be compensated by the increased frequency of cooperative interactions, and so, weakening individual selection operating against altruistic punishers (Boyd et al. 2003; Gächter et al. 2008). Those groups may also create a reputation as rich ones, attracting more immigrants (Boyd et al. 2003). Experimental procedures and simulation models have been proposed to demonstrate the evolution of altruistic punishment and its impact within and between group selection.

The Public Goods Game

The main experimental scenario for the study of altruistic punishment and group benefits is the *public goods game (PGG)*. In such game, each player starts with a personal fund, and, in one or multiple trials, each member of the group can contribute or not to a common fund. The amount donated to the common fund is then enhanced and equally divided by all group members. This game encompasses all the main features of a public good in real-life situations: the shared responsibility to the public good maintenance and the individual benefits from the public good regardless the amount of expenditures of each group member. In the study of altruistic punishment, one more feature is added. After the division of the common fund, any member of the group can give a part of his individual fund to produce a loss in the individual fund of another member. This act will be named altruistic punishment when the loss is imposed to an individual who free rides. Generally, the loss produced is bigger than the amount gave by the punisher and leaves the free rider with less resources he could've accumulated if he had cooperated.

Experimental data have produced mixed results regarding the theoretical model for selection of altruistic punishment. Such variation is deemed to several parameters that may influence the experimental observation of the phenomenon. Once altruistic punishment is more probable under a reciprocity situation, a scenario that favors its occurrence may have a long number of interactions (Gächter, Renner & Sefton (2008) suggest a number of 50 trials), a stable configuration where members won't be replaced (Gächter et al. 2008), the costs are relatively low to produce high losses on the punished (Boyd et al. 2003; Egas and Riedl 2008), or some information about the participant's cooperative behavior in previous trials (Barclay 2006). Contrarily, scenarios that may discourage altruistic punishment are characterized by single or few interactions, instability in the composition of groups, and no information about member's reputations (Fehr and Gächter 2002; Fehr and Rockenbach 2003). The effect of altruistic punishment on reputation may be correlated to some outcomes like average group earnings, the impact of punishment on punisher earnings, the presence of aversion inequity motivations, and immigration rate.

Benefits in Group Average Earnings

One of the arguments against the selection of altruistic punishment as a stable strategy is that the costs of punishment are both decreasing punisher's fitness and producing very small increments to group mean payoffs, that is, not compensating the losses (Boyd et al. 2003). Hermann et al. (2008) showed that in some circumstances, even altruistic punishers (also high contributors) may be punished by average contributors, suggesting that altruistic punishment strategy may also need strong social norms of cooperation in order to be reinforced.

However, some experimental data suggests that highly punitive groups are richer than no punitive ones. Gächter et al. (2008) exposed 207 participants in groups of 3 to 1 of 4 conditions: punishment available and 50 trials (P50), punishment available and 10 trials (P10), no punishment available and 50 trials (N50), and no punishment in 10 trials (N10). The authors found that the greater average profit in cooperation occurred in

P50 groups. Fehr and Gächter (2002) exposed 240 students in groups of 4, to 6 periods of a PGG in 1 of 2 conditions, punishment and no punishment. Results showed that average investments were higher in punishment conditions with cooperation increasing over time while having a sharply decrease reaching no cooperation at all in more than half of the groups in non-punishment conditions. Such results demonstrate that punishment available groups produce more cooperation and bigger net earnings, compensating the costs of punishment by increasing the amount donated by cooperators.

Number of Interactions and Reputation

On the role of the number of interactions, as suggested by theoretical models, repeated interactions raise cooperation probabilities. In Gächter, Renner, and Sefton (2008) study, the presence of a punishment option increased the average earnings in longer interactions (50 trials) and had the opposite effect on brief interactions (10 trials). In a complementary way, the presence of punishment in a scenario of single interactions produced less cooperation than in conditions where no punishment option was available (Barclay 2006 – study 2; Fehr and Rockenbach 2003). Such data highlights the major role of the number of interactions, instead of personal reputation, as critical for the emergence of beneficial outcomes of altruistic punishment.

However, altruistic punishment is also consistently observed in one-shot anonymous interactions where participants will play each trial with a different, unknown person (Fehr and Gächter 2002; Gürerk et al. 2006). Even in such scenarios, reputation can play a critical role. Two kinds of reputation may be considered: the individual reputation as a punisher, which may be a controlling variable when dealing with known persons, and the group's reputation as a cooperative one, operating in anonymous interactions.

Some data demonstrated that participants prefer to interact with altruistic punishers, when given the choice (Gürerk et al. 2006; Henrich 2006; Nelissen 2008), and help altruistic punishers in future interactions (Santos et al. 2010). In Gürerk, Irlenbusch, and Rockenbach (2006) study, the whole evolution of between-group

cooperation could be observed. They had 84 participants playing multiple (30) anonymous one-shot interactions. At each trial, the participant had to (1) choose to be in a punishing or punishing-free interaction; (2) choose to endow some or no contribution to a common fund; and, in punishing groups, (3) choose to recompensate (by giving one token of his own) or punish (by giving one token to produce a loss of three tokens) other participants.

Results showed that, at initial trials, most participants choose to be in a punishing-free interaction and donate smaller amounts in this condition, with almost half of participants acting as free riders. Still at initial trials, punishment was frequent in the punishing interaction with free riders obtaining heavier losses than in the punishing-free interaction. At the sixth interaction, there is a shift with most of the participants choosing to be at the punishing interaction. This proportion increases along trials with more than 90% of participants choosing this condition at final trials. In punishing interactions it is also observed increases in the amount endowed over time. It produced progressive increments in payoffs, compensating the losses from punishment acts. At the end of the trials, reduction in payoffs of punishers compared to non-punishers was less than 2%.

This data illustrates a probable scenario in real-life group configurations concerning cooperation: frequently cooperative populations may do better as a group in between-group selection, creating a reputation that attracts immigrants, who intend to benefit from it. If those immigrants imitate native's behavior by cooperating and punishing free riders, cooperation is sustained in a stable level.

In PGG procedures, some behavior patterns can be drawn. Most of the participants are conditional cooperators (Chaudhuri 2010), persons who measure their contributions on average contributions of others. Punishers are usually *strong reciprocators* (Fehr and Gächter 2002; Gürerk et al. 2006), persons with a predisposition to make above-average contributions and punish low contributors. These punishers may be willing to sanction free riders, even when they are third parties, not being affected in a specific episode (Fehr and Fischbacher 2004). They are preferred partners and are seen as more trustworthy, group

focused, and reputable than non-punishers (Barclay 2006). Punisheds tend to shift strategy by raising their future contributions, even when interactions are anonymous and/or one-shot, that is, the future interaction may not be with the punisher (Fehr and Gächter 2002; Gürerk et al. 2006; Raihani and Mc Cauliffe 2012). Thus, the punishment provides increases in cooperation rates in future interactions, benefiting population as a whole.

Equity Motivations

Some evidence have pointed that inequity aversion may be a trait linked to the maintenance of cooperation (Brosnan and de Waal 2014; Brosnan and Bshary 2016; Hughes et al. 2018; Raihani and Mc Cauliffe 2012). Rabin (1993) describes that conditional cooperation, that is, to cooperate (help) in cooperative groups and hurt the noncooperative ones by free riding, produces, respectively, mutual-max outcomes, with increase in other's payoffs, and mutual-min outcomes, when participants minimize each other's payoffs.

Fowler, Johnson, and Smirnov (2004) consider that two types of inequity are at stake in PGG: the individual amount of contribution compared to the average contribution and the net profit after the division of the public good resources. In the first situation, a free rider might be a person whose contribution fell below the average amount. In the second situation, a free rider might be the person who earned above-average net payoffs. Fehr and Gächter (2002) proposed that, in their procedure, altruistic punishment was driven by deviations from the average group endowments toward the public good. The more distant the participant's contribution from the average, the more this person was punished. Punishers were usually the strong reciprocators. Fowler, Johnson, and Smirnov (2004) offered a different interpretation for the same data. They assert that, in the referred procedure, payoff deviance is equal to contribution deviance. However, when a model drew from regression analysis considering the absolute values instead of deviance from the mean, results suggested that payoff was the critical controlling variable. This model showed that contribution had less effect on punishment probability when payoff is high and has no effect on punishment when

payoff is at its lowest. This analysis suggests that punishment is correlated to high net earnings instead of low contributions and the altruistic punishment may work for the reduction of inequality.

Raihani and Mcauliffe (2012) and Dawes et al. (2007) found similar results, showing that probability of punishment acts is correlated to free riding that produced inequality, but not by free riding alone. Besides, participants who reject inequality are most prone to punish free riding (Johnson et al. 2009).

The literature about inequity aversion suggests that the refuse of inequality may be a strategy to avoid free riders. In this way, the display of inequity aversion behavior patterns may increase the probabilities of having a cooperative interaction, thus, putting such trait as a reputation enhancer.

Simulation Models

Until here, discussions about the evolution of altruistic punishment are based in theoretical models and experimental data. With simulation models, Boyd et al. (2003) propose that between-group selection, measured on the basis of immigration rate, would be the selection pressure for altruistic punishment strategies. The model starts with the assumption that cooperative groups, those with high numbers of altruistic punishers, are less prone to extinction. In such groups, the frequency of punishers and cooperative behavior may be positively correlated, and individual selection against punishers must be weak, because it is a common behavior, so costs are shared. In simulations, authors manipulated population size in four levels 4 (usual limit for experiments), 16, 64, or 256 members and the presence or absence of altruistic punishment. The altruistic punishment was also manipulated in light punishment (cost of being punished as twice the cost of cooperate) and high punishment (cost of being punished as four times the cost of cooperate). Several other parameters were manipulated to address common group transformation characteristics.

Main results showed that frequency of cooperation tends to decrease as a function of population size, but this fall is sharply slower in groups with punishers. Besides, in light punishment situations, it does not sufficiently reduce the average payoff

of free riders, creating the ideal scenario for raisings in free riding frequencies. Other important result is that increases in cooperation are sustainable only when the costs of being a punisher decline over time. If such costs are fixed over time, cooperation declines.

One important measure of the success of the group was the immigration rate. Groups that did better in terms of average payoffs created a reputation of being rich ones, attracting more immigrants. These simulation findings add information that are too laborious to be included in experimental models like the impact of group size on cooperation, immigration rate, and the reduction of punishment costs as crucial to the increase in cooperation.

Conclusion

Theoretical models have trouble to explain how cooperation can emerge and be selected among unrelated individuals dealing with public goods. The altruistic punishment strategy offers an answer to this puzzle but also suffers from the problem of being, at first, an individual costly strategy. Experimental data and simulation models have shown that cooperation typically collapses in the absence of punishment (Fehr and Gächter 2002; Boyd et al. 2003). The possibility of punishment not only stabilizes human cooperation but also maintains it at high levels, with low costs for punishers and bigger profits compared to non-punishing collectivities (Fehr and Gächter 2002; Gürerk et al. 2006). That is, altruistic punishment may be critical for the maintenance of cooperation. Groups that present high levels of altruistic punishment are richer and less prone to extinction and have better reputation, attracting more immigrants.

Cross-References

- [Altruism](#)
- [Altruism Among Nonkin](#)
- [Altruism and Costs to Altruist](#)
- [Cooperation](#)

- Ingredients of Reciprocal Altruism
- Reciprocal Altruism and Group Living
- Reputation and Altruism

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Altruistic Rewarding and Punishment

- Strong Reciprocity

Altruistic Suicide

- Kin Selective Suicide

Amalgamated Families

► Stepfamilies

American Left

► Political Left, The

Amotz Zahavi

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Prior to work conducted by Amotz Zahavi, costly behaviors (those which appear to be fitness reducing and costly to perform) appeared to be counterintuitive to Darwinian selection. Zahavi, by proposing the handicap principle, sought to further explain the adaptive benefits of costly behaviors and why they are central to both natural and sexual selection. Zahavi revolutionized the way we view behavior, arguing “handicaps” are usually present to signal our fitness (Zahavi 1975). These handicaps can take physical form such as possessing the famous peacock’s large and “expensive” tail, or behavioral acts such as expensive purchases, often carried out to communicate or signal one’s superior fitness to others. Zahavi’s work has been applied to a wide range of disciplines including psychology, biology, and physiology, with strong applications to a wide range of species and behavior. His work has contributed to our understanding of animal, human behavior, communication, coloring, social hierarchy, and the development of physical qualities which serve a strong survival purpose.

Synonyms

The handicap principle

Definition

Exploring costly traits as signals.

Introduction

Amotz Zahavi was a pioneer in evolutionary theory, who proposed the famous *handicap principle*. In 2016, Zahavi was awarded a lifetime achievement award by Tel Aviv University for his work and contribution to the department of Zoology. Prior to this, he was awarded the Society for the Protection of Nature in Israel prize by the Israeli Ministry of Education for his contribution to the environment. He was also awarded the Fryssen Foundation’s International Prize for his work on social communication (Amotz Zahavi n.d.).

The Handicap Principle

Amotz Zahavi observed and provided a theoretical framework for understanding human and non-human signalling behavior. From mating displays, language, elaborative displays among a variety of species, Zahavi was fascinated as to why we use elaborate displays, which are often observed as “costly” in nature. The term costly here refers to the idea that the trait/behavior is expensive to perform (or a physical feature is expensive to possess), often leading to “waste.” To perform such an act, one must be able to afford such wastage, as it does not come “cheaply.” These traits/features can be elaborate, yet costly in nature, often performed to advertise one’s fitness.

Zahavi applied the handicap principle to a range of behaviors, including altruism. As an example, Zahavi argued that although traits such as altruism can often be viewed as behavior which is costly, it relays a signal of honesty, as those who can afford to bear the cost of being altruistic must be in some way superior compared to those who

are unable to bear the costs from engaging in an altruistic cost (Zahavi 1995, 2003). Furthermore, costly signalling theory has been used to explain costly displays of “expensive” traits such as prosociality, as it signals one’s ability to confer the benefits associated with altruistic behavior (Zahavi and Zahavi 1997).

One key facet of Zahavi’s work is that although sexual selection suggests that traits evolve to increase reproductive success, these traits can often be “copied” by rival mates. As a result, “true” handicaps are those that rivals are unable to imitate, thus relaying the fact that possessing a “true” handicap means the bearer is able to bear the costs of possessing the trait. For example, although Gazelles often perform “stotting” when escaping from predators, which can be seen as behavior which is costly (or Springbok’s leaping into the air when seeing a predator), it signals to the predator (and those around them) that the Gazelle can afford to expend their energy on this expensive act, thus signalling strength, deterring the predator. However, it is important to note that Zahavi argued that these traits had to be reliable and honest. It is not worth it for a Springbok to jump in the air if he or she is unable to run fast. Similarly, without an abundant supply of wealth, one is unable to waste it.

Costly Signalling Under Mate Choice

Stemming from costly signalling theory and the handicap principle, Zahavi was aware that certain expensive traits can be beneficial in mate choice. For example, from Zahavi’s work, theorists argue that several traits have evolved through sexual selection as handicaps in order to act as mating signals (Miller 2007), such as prosociality (see Bhogal et al. 2016, *in press*; Farrelly et al. 2007) and conspicuous spending (Miller 2009).

Conclusion

Amotz Zahavi’s contribution to evolutionary science has proved invaluable to our understanding of why we often handicap ourselves in social

interactions. The handicap principle has provided scholars from a wide range of disciplines with understanding of why we perform costly behaviors, and what these displays signal to others, often benefiting us in a variety of contexts, thus acting as adaptive behavior. The simplicity and complexity of the handicap principle extends to human and nonhuman species, explaining a plethora of traits and behaviors which were initially a puzzle to evolutionary theory.

Cross-References

► Mating

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Amphimixis

► Sexual Reproduction

Amputated Limbs

- ▶ [Phantom Limbs](#)

AN

- ▶ [Anorexia Nervosa](#)

An Abstract of an Essay on the Origin of Species and Varieties Through Natural Selection

- ▶ [On the Origin of Species](#)

An Essay on the Principle of Population

- ▶ [Malthus on Population](#)

Analogical Reasoning

- ▶ [Concept Formation](#)

Anatomical Adaptations for Fighting

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Synonyms

- [Combat; Physical Characteristics](#)

Definition

Anatomical adaptations for fighting include muscularity, body size, the structure of the fist, the protective skeletal buttressing of the face and skull, and the distribution of pain receptors. These features evolved as adaptations for success during males' long history of fighting with other males over status, access to resources, and reproductive opportunities. Because males fight more often than females the causes of selection on these traits would have been stronger on males. Accordingly, males exhibit greater expression of these physical traits than do females.

Introduction

We are a very violent species and although recorded human history shows high rates of violence, evidence from contemporary foragers indicates that we were even more violent as hunter gatherers. Violence, particularly between males, is part of our primate heritage.

As in other primates, humans exhibit important sex differences in the propensity for violence (Wrangham and Peterson 1996). Males are much more likely than females to fight each other to achieve status, access to resources, and reproductive opportunities. Males are more aggressive, on average, in many situations than are females (Archer 2004). Conflicts between men are more violent than those between women. In every culture for which there is information, male–male homicide rates are higher than male–female or female–female rates (Daly and Wilson 1988). Moreover, males are more likely than females to be involved in nonlethal fights (Collins 2008).

Before the invention of weapons, hominin fighting consisted of hand-to-hand combat involving the punching, slapping, kicking, and grappling commonly observed in modern chimpanzees, gorillas, and untrained humans (Wrangham and Peterson 1996). If the reproductive success of ancestral males was correlated with their success in fights, then the causes of selection on the physical traits that increased their chances of winning a fight would have been stronger on

males than on females leading to the prediction that males will exhibit greater expression of the traits that increase their chances of winning fights. Selection on the traits associated with fighting ability was likely intense because the potential loss of fitness consequences that can result from losing a fight (e.g., the loss of status, injury, or death) are severe.

Muscles

Victory in a fight comes from being able to punch, kick, grapple, or use hand-held weapons to dominate an opponent to the point of surrender, severe injury, or death. Prior to the use of firearms, human muscle power was used to propel primitive projectile weapons (e.g., boomerangs, darts, knives, spears, sticks, stones). Anatomical adaptations needed for the high speed, overhand throwing of projectile weapons first appear together in early *Homo* (Roach et al. 2013). Hand-to-hand combat and the use of primitive weapons favor bigger over smaller and stronger over weaker combatants. This is clearly demonstrated by the observation that in societies with combat sports, weight classes are used in competitions because discrepancies between competitors in body size influence the outcomes of fights. Therefore, if fighting was a more important cause of selection on males than females, then males should be bigger and stronger, on average, than females. Moreover, males should have greater upper-body strength than females because mainly chest, shoulder, and arm muscles are used during fighting and to propel primitive projectile weapons.

Sex differences in muscular size strength are well established. Males have more muscle mass in both absolute terms and relative to body mass than do females. Female muscle strength, even when controlling for differences in fat free body mass, limb or body size, ranges from 40 % to 75 % of male strength. The sex difference is even greater for upper-body than lower-body muscle strength indicating stronger selection on males than females for upper-body strength. Moreover, male muscle fibers are shorter and have greater angles

of pennation (i.e., the angle of the muscle fibers to the force-generating axis of the muscle) which contributes to sex differences in muscular strength (Chow et al. 2000).

The faster a fighter subdues his opponent the better and, indeed, most fights between males are very short, usually involving a few punches or kicks before they are over (Collins 2008). Even organized combat sports which frequently have rules that prolong fighting (e.g., gloves that reduce the risk of injuries to puncher's hands and the prohibition of tactics like biting and eye gouging) place a premium on competitors quickly defeating their opponents. In fighting competitions, episodes of fighting are typically short (e.g., Olympic Greco-Roman wrestling, 3 rounds of 3 min each, Ultimate Fighting Championship, championship professional mixed martial arts, 3 rounds of 5 min each). Except for professional boxing, in which championship bouts have the potential to last up to 36 min (12 rounds x 3 min/round), total fighting time, excluding the rest periods of 1 min between rounds, typically lasts no more than 15 min. The premium on quickly defeating an opponent during a fight favors the intense, rapid actions (e.g., punches, jabs, kicks) associated with the rapid, strong contractions characteristic of type II (fast-twitch) muscle fibers. Males have a greater proportion of type II fibers, on average, than do females, suggesting that the need to produce rapid, strong contractions required during fighting was a stronger cause of selection on males than females. In addition, male muscles are better able than female muscles to produce the anaerobic power necessary for the rapid, intense actions needed during fighting. For example, patterns of male muscle activation monitored during physical actions like those used during foraging, hunting, and fighting showed that jumping and punching accounted for 73 % of the incidences of maximum muscle activation and the size of the muscles of the back and leg were related more to the demands of the explosive power needed during fighting rather than either sprinting or long distance running (Carrier et al. 2015). The high heritability of the traits of muscles such as their size, static and

explosive strength, and trainability suggests a long history of positive selection on them, especially in males.

Human Fists

The hand is an important anatomical weapon. It is used to threaten, injure, and sometimes kill rivals. When clenched into a fist, it permits punching and striking with great force while simultaneously reducing the risks of hand injuries. The fist provides buttressing that increases the stiffness of the second metacarpo-phalangeal joint thereby transferring force through the thenar eminence, the fleshy pad proximal to the thumb, and compared to an open hand doubles the ability of the proximal phalanges of digits 2 and 3 to transmit punching force (Morgan and Carrier 2013). The structure of the human hand is consistent with the hypothesis that fighting was an important cause of selection on hand anatomy. Moreover, males, because they are larger, have bigger fists than females. The causes of selection associated with the use of fists during fighting likely contributed to this sexual size dimorphism because a larger fist delivers more force.

The Head and Face

Frequent fighting during human history would have been an important cause of selection shaping the anatomy of the human face. This is shown by the fact that the head and face are the most frequent targets during fights and getting punched in the face is responsible for most facial fractures in modern societies. Not surprisingly, males suffer more facial injuries than do females (Carrier and Morgan 2014). These patterns suggest that if fighting was an important cause of selection in hominins, then human faces should possess adaptations that reduce the risk of injury from being struck by fists. Traits that help protect the face from damage from fists include its flatness, robust bone structure, and enlarged jaw muscles (Carrier and Morgan 2014). In addition, blows to the head have less damaging effects on males than females

as shown by the fact that female athletes suffer a greater frequency of concussions than do males playing the same sports. This sex difference may result from males having stronger neck and jaw muscles, on average, because there are no sex differences in cranial thickness (Lynnerup 2001). The more robust faces and larger and stronger jaw and neck muscles of males suggest that their heads evolved to avoid damage during fighting. Consistent with this hypothesis is the observation that a male's strength and fighting ability can be accurately assessed from observing his face alone.

Pain Tolerance

Fighting involves both powerfully striking opponents and absorbing blows from them. Therefore, the ability to "take a punch" and continue fighting is advantageous to combatants. Individuals with low pain tolerance would be more likely to give up and surrender quickly during a fight. Therefore, if fighting was a more important cause of selection in males than females, then males should be more tolerant of pain than are females. Contrary to folk wisdom that females have a higher pain threshold than males, experiments show that males perceive a stimulus of given intensity as being less painful, are less likely to perceive a stimulus of given intensity as painful, and are more tolerant of pain than are females. Moreover, males have fewer pain receptors in their faces than do females (Mowlavi et al. 2005).

Conclusion

Several traits indicate that fighting was an important cause of selection on human anatomy, especially for males. The larger bodies of males and their greater upper body muscle mass, strength, and muscle characteristics are all adaptive for the intense, rapid, and forceful actions required for success during fighting. The structure of fists is adaptive for causing maximum damage to rivals without incurring injury. Faces, especially those of males, evolved in ways that minimize damage from being struck by the fists of rival combatants.

Finally, males have fewer pain receptors in their faces and are more tolerant of pain than are females, allowing them to better deliver and receive blows and continue fighting.

Cross-References

- ▶ [Aggression](#)
- ▶ [Combat Sport](#)
- ▶ [Team Sport](#)
- ▶ [Male Adaptations That Facilitate Success in War](#)
- ▶ [Male Adaptations to Assess Fighting Ability](#)
- ▶ [Male Warrior Hypothesis](#)
- ▶ [Male-Male Competition](#)
- ▶ [Men But Not Women Will Have Adaptations for War](#)
- ▶ [Physical Aggression](#)
- ▶ [Play Fighting in Boys](#)
- ▶ [Self-Assessment of Fighting Ability](#)
- ▶ [Sex Differences](#)
- ▶ [Sex Differences in Ability to Assess Fighting Ability](#)
- ▶ [Sex Differences in Aggression](#)
- ▶ [Sex Differences in Same-Sex Aggression](#)
- ▶ [Sexual Dimorphism](#)
- ▶ [Sexual Size Dimorphism](#)
- ▶ [Team Sport](#)
- ▶ [War](#)

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Ancestor Worship

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Synonyms

Animism; Indigenous religion; Shamanism; Totemism; Tribal religion

Definition

The communicated acceptance of the supernatural claim that dead ancestors influence, and/or are influenced by, their living descendants and, more loosely, the rituals associated with such claims.

Introduction

Anthropologists studying traditional kinship-based cultures have frequently, and perhaps universally (Steadman et al. 1996), encountered the claim that dead ancestors (i.e., deceased progenitors) can still influence, and/or be influenced by, their living descendants. In such cultures,

generation after generation of descendants not only communicates their acceptance of such claims, but they participate in traditional forms of sacrifice and other rituals to demonstrate their veneration of their dead ancestors and their willingness to accept the influence of those ancestors by following the traditional patterns of behavior they proscribed. This activity is typically labeled ancestor worship, and it is described as religious because the claims made about the actions of dead ancestors are supernatural in the sense of being beyond verification by the senses. Ancestor worship is potentially of extreme importance to evolutionary explanations of religion because its apparent ubiquity, including its presence among human foragers, suggests it might be a very early, if not original, form of religion.

Evolutionary explanations of ancestor worship, like essentially all explanations of all forms of religion, start with the assumption that the belief in the supernatural claims causes the religious behavior. In the case of ancestor worship, the typically unquestioned assumption is that ancestor worship is caused by the belief that dead ancestors really can influence, and/or be influenced by, their living descendants. This leads to attempts to explain why people hold this belief in the absence of empirical evidence. There is empirical evidence that *living* progenitors influence, and are influenced by, their living descendants, but there is no empirical evidence that this is also true of *dead* ancestors. Given that dead ancestors are kin to their living descendants (i.e., individuals related through birth links) and kin selection appears to have great explanatory power concerning behavior involving closely related kin, evolutionary explanations of ancestor worship have often considered the possibility that kin selection may have been involved in the evolution of ancestor worship.

Main Text

Evolutionary explanations of religion can be conceptually divided into those postulating that beliefs in the supernatural are adaptations favored by individual-level selection (Sosis and Alcorta

2003), adaptations favored by group-level selection (Wilson 2002), or are merely by-products of other adaptations (Boyer 2001). All of these hypotheses follow the orthodoxy of assuming belief and therefore ask why natural selection may have either favored the behavior caused by those beliefs (i.e., see religious behavior as an adaptation) or how such beliefs could be a side-effect of selection for other mental adaptations (i.e., see religious behavior as a by-product).

Perhaps the most obvious way kin selection could be involved in the evolution of ancestor worship is through the similarity of the venerated/worshipped ancestor and the respected living parent, a similarity so strong that Freud proposed it as the basis for all religion (Freud 1913). Further, just as parents are expected to have evolved to encourage altruism among their offspring (Trivers 1974), in ancestor worship, dead ancestors are claimed to greatly desire their descendants to exhibit altruism toward each other, producing what anthropologists refer to as the axiom of kinship amity (Fortes 1969). The psychological mechanisms producing these similarities could be either adaptations increasing the inclusive fitness of individuals engaging in religious behavior, or perhaps the survival of religious groups, or by-products of other adaptations.

There are, however, a number of challenges to the use of kin selection to explain ancestor worship. First, there is the difficulty, if not impossibility, inherent in attempts to explain any form of religion and of identifying if it is actually the religious belief that causes the behavior, or even who, and if anyone actually holds such a belief (Rappaport 1999; Steadman and Palmer 2008). This can be avoided by focusing on identifiable behavior and its identifiable effects. This means restricting explanations of ancestor worship to what the living descendants of dead ancestors *say* about those ancestors and the effects of this *talk* on the behavior of the other living co-descendants of those ancestors.

There are also challenges specific to explaining ancestor worship with kin selection. First, although some rituals focus on only the recently deceased ancestors, rituals also include a focus on ancestors deceased for many generations. This is

crucial because the individuals participating in, and most influenced by, these rituals are typically the descendants of the dead ancestor being named, venerated, or worshipped in the ritual. When that ancestor is a parent or grandparent, these descendants are limited to the very close kin (siblings, aunts, uncles, nieces, nephews, first cousins) whose interactions may have been subject to kin selection. However, in the typical forms of ancestor worship centered on an ancestor deceased for many generations, the ritual involves and influences the behavior of many descendants who are so distantly related that kin selection would have no influence on the evolutionary consequences of their interactions. This is particularly important because so much of the interaction occurring among these distantly related co-descendants involves sacrifice and other forms of altruism.

To explain the altruism exhibited toward these distantly related co-descendants, it is first necessary to account for how such distantly related co-descendants (e.g., members of the same clan) could come to be identified as kin. When, *and only when*, the transmission of a traditional clan name, or other marker of kinship, persists over many generations, do “large lineages or clans . . . grow up over time as the descendants of the original ancestor/ancestress accumulated” (Fox 1967, p.122). van den Berghe and Barash (1977) provide examples of huge numbers of individuals who share the same descent name, whose existence implies the traditional transmission of a descent name over many hundreds of generations: “large unilineal kin groups such as clans and lineages with memberships running into hundreds or thousands, or indeed in a few cases, millions” (p. 821). The same process of copying behavior from ancestor to descendant for many generations that allows the identification of huge numbers of co-descendants from one generation to the next is also responsible for transmitting the axiom of kinship amity to each subsequent generation.

Conclusion

The time and effort put into faithfully transmitting names from ancestor to descendant over many

generations may help decide whether religion is an adaptation or by-product. This is because the high cost of transmitting the tradition of ancestor worship suggests that there must have been some evolutionary advantage to such transmission that offset this cost. An explanation of how traditions causing altruism toward very distant kin could have evolved requires a concept of evolutionary success (i.e., fitness) that takes into consideration a multigenerational time scale compatible with the many generations required for large clans to form (Dawkins 1982). The concept of measuring evolutionary success by the number of descendants alive after many generations has been referred to as “descendant-leaving success” (Steadman and Palmer 2008), in contrast to the conventional use of “reproductive success” when measuring evolutionary success in the next generation, or at the most, counting grandchildren. At the very least, explanations ignoring traditions, and only focusing on evolved psychological mechanisms, cannot account for the talk about long-deceased common ancestors encouraging altruism toward distantly related co-descendants. Thus, evolutionary explanations ignoring traditions are unable to account for ancestor worship, nor religion in general.

Cross-References

- [Altruism in Kin Selection](#)
- [Cultural Inheritance](#)
- [Cultural Universals](#)
- [Increased Grandchild Survival](#)
- [Kin Recognition](#)
- [Kinship](#)
- [Religion](#)
- [Selectionist Models: Implications for Behavior](#)

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Ancestral Birth Spacing

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Synonyms

Interbirth interval (IBI)

Definition

Time elapsed between a birth and the previous birth.

Introduction

Variation in birth spacing can have substantial effects on lifetime reproductive success: spacing births too close together leads to maternal depletion and lowered infant survival, whereas spacing births too far apart results in the production of fewer offspring over the life-course than is optimal for maximizing reproductive success. In this entry, ancestral primate birth spacing

patterns are discussed, and how humans compare with nonhuman primates. This is followed by discussion of some of the evidence that birth spacing patterns have been shaped by evolution and addresses whether women in modern industrialized nations should adhere to ancestral birth spacing patterns.

A

Nonhuman Primate Birth Spacing

Our closest living genetic relatives, the great apes, have longer average birth intervals than humans. Birth spacing patterns in apes and humans are summarized in Table 1. There are a number of explanations for birth spacing differences between primate species; some evolutionary lineages contain species with similar birth intervals simply through lineage effects. Small body size and short lifespans are also associated with shorter birth spacing when comparing species (Mitani and Watts 1997). One social factor in primates which appears to be important is shared infant care between mothers and others in the social group (allocare or allomaternal care). Species which have allomaternal care have shorter birth intervals than species in which the mother alone provides all of the care for her offspring (Mitani and Watts 1997).

What Do We Know About Birth Spacing In Our Human Ancestors?

Our best insights into typical birth spacing in our ancestors come from studies of living hunter-gatherers or foragers. Forager birth intervals are typically between two and three years (see Table 1). These short intervals when compared with apes may be part of a broader life-history pattern in which humans, like many other primates with short average birth intervals, use allo-maternal helpers (especially grandmothers) to achieve short birth intervals and as a consequence higher fertility (Hawkes et al. 1998).

In both nonhuman primates and in human forager societies, birth intervals are shorter after an infant dies (e.g., Blurton Jones 2016). Much of this

Ancestral Birth Spacing, Table 1 Mean closed birth intervals, where a birth follows a previous birth in the period of time in which the study was carried out, in apes and humans

Group or species	Mean closed birth interval in years	Source
Ache foragers living on reservation (S. America)	2.6	Hill and Hurtado 1996, p. 257
Hadza foragers (Africa)	2.8	Blurton Jones 2016, p. 335
Yanomamo foragers (S. America)	2.9	Melancon 1982
Ache foragers (S. America)	3.1	Hill and Hurtado 1996, p. 254
United Kingdom (1970 British Birth Cohort)	3.4	Waynfirth 2015
Aka foragers (Africa)	3.5	Hewlett 1993
!Kung foragers (Africa)	3.7	Bentley 1985
Gorilla	3.9	Watts 1991
Chimpanzee	6.0	Nishida et al. 1990
Sumatran orangutans	9.3	Wich et al. 2004

effect is likely to be due to a more rapid return to ovulation with the cessation of breastfeeding and the other energetic demands of motherhood that suppress normal menstrual cycling and fertility in mothers of infants (Wood 1994).

Evolutionary Optimality Models of Birth Spacing

Birth spacing patterns have evolutionary selection pressure on them due to a trade-off between the number of offspring that can be produced in a reproductive lifespan and the survival of the offspring. This trade-off contains other potential compromises, such as between number of offspring produced and maternal survival. There have been several tests of whether observed birth spacing fits with the birth spacing pattern that would be evolutionarily optimal in forager societies. To carry out a test of optimality, it is necessary to know what effects different birth intervals have on child survival in the conditions that the society lives. This can be achieved by measuring survival both of the newborn child and their older sibling(s) who have been supplanted as the youngest child. With this information, it is then possible to calculate the average number of surviving children a woman will have over her reproductive career given different birth intervals. In Hadza foragers of Tanzania, there is evidence for a trade-off between timing and number of children produced; close birth intervals (less than 2 years) are associated with an increased risk of mortality

in both the supplanted older child and the younger child (Blurton Jones 2016). For the Hadza, optimality modelling of birth intervals suggested that intervals of between 2 and 3 years lead to the greatest number of surviving children. When applying this model back to observed birth intervals over a Hadza woman's reproductive life, Blurton Jones found that the overall pattern of birth intervals approximately fit what was predicted by the optimality model, except that there were more short intervals than predicted (Blurton Jones 2016). Hill and Hurtado (1996) used a similar optimality modelling approach to test whether birth spacing was optimal in Aché foragers living on an indigenous reservation in Paraguay. In contrast to the optimality model calculated for the Hadza data, for the Aché no intermediate optimum birth interval was found: women's reproductive success was maximized by having the shortest observed birth intervals and the most children possible.

The Hadza and Aché forager data were used to formulate mathematical optimality models of whether observed birth intervals were consistent with infant mortality levels as a function of birth intervals. This is because the amount of parental care provided influences a child's chances of survival. However, not all mortality can be influenced by giving more parental care or giving it exclusively to a child for longer. This type of mortality which is insensitive to energetic allocation to immune function or tissue repair is termed extrinsic mortality. Two situations in which there is increased extrinsic mortality are

famine and warfare. When these and other extrinsic causes of mortality are considered, the evolutionarily optimal birth interval is shorter under conditions of high extrinsic mortality (Quinlan 2007). This may be one reason why observed birth intervals are shorter than expected in studies of forager intervals.

In sum, if we assume that throughout recent human evolution resources were reasonably scarce and child mortality was common, intermediate birth spacing of between 2 and 3 years is likely to be the norm for our species and has been selected for by natural selection.

Proximate Mechanisms Underlying Birth Spacing

Although birth spacing decisions can be made consciously by parents, much of the variation in birth spacing is likely to result from the high energetic cost of reproduction. Lactation and caring for an infant are very energetically costly. The ovulatory cycle of well-fed breastfeeding mothers does not resume for around 10 months after the birth of a child on average due the metabolic burden of breastfeeding (Valeggia and Ellison 2009). This is likely to be longer in nutritionally stressed populations but would still not alone account for birth spacings of 2–3 years typically observed. Women can extend postpartum infertility by sucking their child more frequently and for longer durations (Vitzthum 2009). Culturally based factors also play roles; in the Hadza, men report that sexual access to women with young children is more difficult to achieve (Blurton Jones 2016, p. 346). In the absence of modern contraceptive methods, cultural practices and taboos which restrict male access to mothers of toddlers is a common way that mothers can achieve their desired birth spacing.

Differences Between Women and Between Births

Alloparental care, particularly from grandmothers, which is hypothesized to explain short

human birth intervals compared with other higher primates, also explains some of the differences between individual women in birth intervals. For example, in a noncontraceptive using population in India, the presence of a grandmother in the household was associated with shorter birth intervals (Nath et al. 2000). This is most likely because the grandmother is able to relieve the mother of some of the energetic burdens associated with having an infant.

If evolution has shaped birth spacing decisions, it is also expected that infant viability itself will predict birth spacing. Parents would be expected to parentally invest less in unviable offspring and to subsequently have a short birth interval. This was found to be the case in a British sample, where the birth of an infant with chronic health problems was associated with shorter following birth intervals (Waynfirth 2015). However, this pattern should only hold when parents are not able to substantially improve their infant's viability by increasing parental care.

An existing offspring would be expected to benefit from a longer birth interval than may be in the mother's reproductive interests, thus parent-offspring conflict is relevant to the evolution of birth spacing patterns (Trivers 1974). Extended nursing would serve to tax the maternal energy budget and extend the postpartum return of ovulation. Haig (2014) has proposed additional mechanisms which function due to the presence of cells from an embryo remaining in the mother's body long after birth (microchimerism). These cells may lengthen the next birth interval by affecting conception and implantation of subsequent potential sibling competitors for maternal resources.

Predictions Which Have Not Consistently Been Upheld in the Research Evidence

Male infants require more parental investment: boys are born larger than girls after a slightly longer gestation length and require more maternal resources as infants. The expectation would therefore be that birth intervals are likely to be longer after the birth of a son. The evidence in support of this in forager and other populations

living in nonindustrialized conditions is mixed; Mace and Sear (1997) found evidence for longer intervals after the birth of a boy, but Blurton Jones (2016) did not, and these mixed results are also reflected in the literature from other societies. Similarly, mothers in good physical condition or who live in good conditions would be expected to have shorter birth intervals. This is not the case in the Hadza (Blurton Jones 2016), but when Aché foragers moved to living an easier life on reservations, birth intervals became shorter (Hill and Hurtado 1996).

Do Ancestral Birth Spacing Patterns Remain in Modern Industrialized Societies?

As can be seen in Table 1, modern British birth intervals have a similar mean to forager intervals and do not appear to deviate from what optimality models predict for the Hadza, which is 2–3 years. Longer birth intervals are selected for by natural selection when infant and child mortality are raised by having to care for two young children simultaneously. Given very low infant and maternal mortality rates when compared with forager societies, reproductive success would likely be maximized by very short birth intervals in modern industrialized societies, and thus modern average birth intervals do not reflect or have not tracked the current optimum.

Some of the details of variation in birth intervals in modern industrialized societies differ from the Hadza and other forager societies. In Britain families with large completed family sizes tend to be characterized by longer birth intervals, and birth intervals are significantly shorter at higher parity in Europe and the United States (for fourth and later born babies) (Waynfirth 2015; Andersson 1999; Weinberg and McCarthy 1989). In Sweden and the United States, birth interval length has been declining in recent decades. In the United States, this decline has been the greatest in women with higher education levels (Weinberg and McCarthy 1989). This suggests that decreasing birth intervals in recent

decades are driven by women closely spacing births to minimize career disruption and maximize lifetime financial income.

Conclusion: Should Women in Modern Industrialized Societies Space Births More Than 2 Years Apart?

With the rise in application of evolutionary approaches to health-related behaviors in recent decades, many consider ancestral patterns of behavior to be the healthiest approach to apply to living in modern industrialized conditions; it is best to do what we were evolved to do. Nowhere is this type of view more common than in diet and exercise, for example, for followers of the paleo-diet. The World Health Organization and other public health bodies recommend spacing births more than 2 years apart. This is due to the weight of evidence that close birth spacing results in increasing infant morbidity and mortality. However, the most modern statistical approaches to studying birth intervals such as multilevel modelling suggest that public health organizations have overestimated the risks to children of close birth spacing in modern industrialized societies (Ball et al. 2014). In addition, the health risks of infant morbidity and mortality due to short birth spacing would need to be balanced against the health benefits associated with increased maternal income from minimizing career disruption; in modern industrialized societies, income remains positively associated with many child health outcomes. Thus although the World Health Organization urges families to space births at least 2 years apart, it is not clear that well-fed women living in societies with good access to healthcare should worry about close birth spacing.

Cross-References

- ▶ [Alloparenting and Grandparenting](#)
- ▶ [Birth Spacing and Birth Order](#)
- ▶ [Conflict Between Parents and Offspring](#)
- ▶ [Cooperative Breeding](#)

- [Extrinsic Mortality](#)
- [Genetic Conflict](#)
- [Helpers at the Nest](#)
- [Infant Survival](#)
- [Life History Theory](#)
- [Optimal Clutch Size](#)
- [Parental Investment](#)
- [Quantity Versus Quality of Offspring](#)

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Ancestral Environment

- [Climate and Habitat Diversity](#)

Ancestral Threats Versus Modern Threats

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Introduction

Survival threats posed by the environment have continuously tormented and challenged human

beings. From an evolutionary perspective, the brain mechanisms associated with fear were designed by natural selection to contend with these threats. The list of hazards likely faced by our ancestors included snakes, spiders, heights, darkness, and strangers. Our ancestors' concerns about dangerous stimuli such as these have been carried over to modern humans. In addition to evolutionary threats (e.g., predators and diseases), modern humans encounter a staggering array of novel threats (e.g., ionizing radiation, automobile accidents, and chain saws) that did not exist until very recently on an evolutionary time scale.

Ancestral Threats

Throughout human evolution, the ability to identify threatening situations has been a critical feature of our psychological structure. A failure to recognize and thwart a threat could have been fatal for our ancestors. The concept of biological preparedness – a theory about the psychology of fear and our reactions to threats – argues that the successful identification of environmental threats leads to a reproductive and survival advantage for the individual (Seligman 1971). In this view, children learn to fear some threats more quickly than others and, consequently, seem biologically prepared to avoid poisonous animals but less prepared to detect the difference between the sidewalk and street traffic.

The environment of evolutionary adaptedness (EEA) is the ancestral environment to which a species is adapted or the set of selection pressures that shaped an adaptation. A central premise of evolutionary science is that forces in our distant past helped make us who we are today. The EEA refers to a group of selection pressures occurring during an adaptation's period of evolution responsible for producing the adaptation (Tooby and Cosmides 1992). A selection pressure can be any factor in a population that impacts reproductive success. Physical, social, and intrapersonal pressures from our ancestral past help to shape our current human design because all animals have heritable variations that are selectively favored or disfavored in accordance with reproductive success (Buss 1995). Each adaptation has its own

EEA, or set of adaptive problems, that shaped it over evolutionary time.

Researchers have found that some of the threats present in the EEA (e.g., snakes and spiders) can induce stress responses to modern humans even at the very young age of 6 months (Hoehl et al. 2017). It is not even necessary for humans today to have had negative experiences with the creatures to fear them. They are likely embedded in us thanks to our ancestors' coexistence with them for 40 to 60 million years. More modern threats include knives, airplanes, and syringes, but they have not been around long enough to establish a threat response from birth.

Modern Threats

A modern threat is anything that poses a problem today that was not prevalent throughout human history. While snakes, spiders, and other predators are referred to as ancestral threats, today we must also be cautious of fast-moving automobile traffic, firearms, and razor blades. A brief list of deadly modern threats would include automatic weapons, electricity, weaponized nanotechnology, pollution, fried foods, alcohol, drug overdoses, decompression, power drills, and helicopters.

An adaptationist approach to studying behavior involves examining the environment in which the brain evolved; at the same time, the modern industrialized world of today differs in many important respects from the EEA. This mismatch serves as a useful starting point for understanding the function and design of current psychological mechanisms. The primary threats to most people today, especially in modern urban settings, are different than the environmental threats dominant up until a few centuries ago. We now increasingly face threats that are substantively different, more technical, and in some ways less tangible.

The list of novelties offered by our modern world but not present in the EEA includes agriculture, electricity, refrigeration, large-scale weapons, medicines, mass communication, effective contraceptive devices, and virtually unlimited access to all types of proteins and carbohydrates. We are navigating our current social and physical world with psychological mechanisms designed

to solve problems associated with survival and reproduction in an ancestral environment much different than the one we live in now.

Because adaptations evolved over many generations, they are said to be “in tune” with reliable features of the environment. It is possible for an adaptation to fail to perform properly (i.e., fall “out of tune”) if the environment changes. A behavior that is maladaptive in one environment may not be maladaptive in other environments. Returning to an earlier example, one could make the case that salt, fat, and sugar negatively impact health when consumed in large quantities over long periods of time. However, this is not an evidence of maladaptivity in the EEA. Moreover, the “lack of fit” to the current environment does not change the intense desire for those substances formed in the EEA.

Natural selection molded mechanisms into our ancestors’ brains that were specialized for focusing cognitive energy on humans and other animals. These adaptive traits were then passed on to us. According to some research, humans today are biased to pay attention to other people and animals much more so than nonliving things, even if inanimate objects are the primary hazards for modern, urbanized populations (New et al. 2007).

Globally, the top causes of death in 2016 according to the World Health Organization (WHO) were heart disease, stroke, pulmonary disease, respiratory disease, and Alzheimer’s and other dementias. Combined, these five issues are implicated in approximately 23 million deaths (World Health Organization 2016). If the danger detectors in our brains were perfectly in tune with our current industrialized world, we would focus our attention on threats that have a greater chance of bringing us down. Statistically speaking, you are much more likely to die from heart disease in our modern world than jet engine failure or a lion attack. Yet we seem to be overly anxious about airplane crashes and the odd death-by-tiger story and less panicked by cardiac health and lung infections.

Conclusion

Throughout human evolution, the ability to identify threatening situations has been a

critical feature of our psychological structure. A failure to recognize and thwart a threat could have been fatal for our ancestors. In contrast, the primary threats to most people today, especially in modern urban settings, are different than the environmental threats dominant up until a few centuries ago. We now increasingly face threats that are substantively different, more technical, and in some ways less tangible.

Cross-References

- [Gordon Orians](#)
- [Landscape Preferences: Climate and Weather](#)
- [Natural Versus Artificial Environments](#)
- [Savanna Hypothesis and Landscape Preferences, The](#)

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Ancestry

- [Birthrights and Bloodlines](#)

Ancient Homosexuality

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Synonyms

Sexual expression; Sexual orientation

Definition

Same-sex attraction in early recorded history.

Introduction

Despite recent attention to the issues surrounding gender identity and sexual orientation, human same-sex attraction is not a novel phenomenon. Historical, anthropological, cross-cultural, and archaeological evidence points to frequent same-sex attraction and sexual behavior in early recorded human history. The consistent instantiation of same-sex behavior throughout time and across disparate civilizations suggests the possibility that evolutionary processes have helped to shape human same-sex attraction (Bailey et al. 2016). This entry presents some interpretations of the evidence for same-sex attraction in early history, focusing on manifestations of same-sex attraction in antiquity.

The Multitude of Same-Sex Attraction

The earliest evidence for the existence of same-sex attraction dates back to pre-civilization. Archaeological records describe Mesolithic rock art depicting same-sex male sexual activity (Nash 2001) and tombs containing male skeletons accompanied by female-typical artifacts (Hollimon 1997). Scholars have interpreted this evidence as suggesting both same-sex attraction and the conceptualization of same-sex attraction via stereotypical gender roles, similar to views of

same-sex attraction common today (Kite and Deaux 1987; Tskhay and Rule 2015).

Additional written evidence of same-sex attraction exists within the New Kingdom period of ancient Egypt (1292–1069 BCE). These records describe sexual relations between pharaoh Neferkare and his general Sisene (Meskell 2001). Similar conclusions have been made from the ancient Greek writings of Sappho, who described romantic relations between women (Campbell 1982) and homosocial lifestyles (i.e., close bonds) between men (e.g., nude athletics; Scanlon 2005). Perhaps the best-known examples of same-sex attraction in antiquity come from Spartan Greece, where records suggest that mature Spartan men engaged in sexual relations with their younger trainees (Bertosa 2009). The variety of evidence thus suggests some degree of acceptance and understanding of same-sex relations in these societies.

Indeed, ancient writers, medical practitioners, and philosophers have developed multiple typologies of same-sex attraction that resemble contemporary understanding of the expression of sexual orientation and gender identity (Boswell 1982/1983). Furthermore, in Plato's *Symposium*, Aristophanes developed a theory of same-sex attraction proposing that all people seeking romantic relationships with other humans have a need to reunite with their primordial twin, regardless of whether this twin is male or female. Thus, similar to modern time, same-sex attraction in the ancient past was a subject of discussion and research, requiring theoretical interpretation.

Conclusion

In sum, evidence from early Western history highlights a pattern of same-sex attraction in multiple cultures and prehistory. Same-sex attraction and its multiple forms of expression therefore seem to have been recognized and studied in antiquity. Early definitions of same-sex attraction appear to have conceptualized it in terms of more common heterosexual gender roles that resemble those still active today.

Cross-References

- ▶ [Personality, Gender, and Culture](#)
- ▶ [Sexual Identity](#)
- ▶ [Sexual Orientation and Human Sexuality](#)

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Ancient Music

- ▶ [Music and Hormones](#)

Androgen

- ▶ [Testosterone](#)

Androgenic Hormone

- ▶ [Testosterone](#)

A

Anger Proneness

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Synonyms

[Angry personality](#); [Probability of anger](#); [Trait anger](#)

Definition

Anger proneness refers to individual differences in the frequency, intensity, and duration of anger across time and situations.

Introduction

Anger is conceptualized as a common emotional response to loss, goal thwarting, and frustration (Berkowitz 1989). Anger is observed cross culturally, and the behavioral referents of anger – threatening, aggressive, and dominant behaviors – are also observed across species. Although anger is often deemed a “negative” emotion, the ubiquity of anger across contexts coupled with observations of anger-related behaviors across species suggests that the emotion has resulted in some adaptive advantages over the course of human evolution.

Anger has been operationalized in many ways, and most definitions include a combination of cognitive, behavioral, and affective responses made in response to threat (Ronan et al. 2014).

Cognitive processes of anger include selective attention toward threatening stimuli, hostile attributions, rumination, and aggressive fantasies. At the behavioral level, anger may be accompanied by muscular tension, cardiovascular reactivity, verbal aggression, and physical violence. The affective and physiological change characteristics of anger were likely selected because they facilitate aggressive behaviors observed in freeze-flight-fight responding. The conditions that provoke anger also tend to alter the motivational functions of various stimuli, particularly those associated with threat and injury. For instance, under conditions of pain and frustration, the sights, sounds, and other sensations that arise from harm to others may be temporarily more motivating and reinforcing. The verbal and non-verbal expression of anger functions to signal to adversaries that the individual is more likely to aggress or retaliate.

Like other negative emotions including sadness and fear, anger itself may be experienced as an aversive state of being that individuals themselves prefer to avoid or escape. However, the motivational function of anger is distinct from other negative emotions because it tends to increase the likelihood that the individual will approach rather than flee the triggering stimulus. Within the framework of freeze-flight-fight responding, such attempts to approach the source of threat could be adaptive when the threat cannot be avoided, risk of harm from fighting is minimal, or if attacking the adversary may deter future attacks.

Contemporary models distinguish state or episodic anger triggered by momentary aversive conditions from anger proneness – the overall propensity for an individual to become angry (Alcazar and Deffenbecker 2013). Within the Five Factor Model (FFM) of personality traits (a dimensional model of openness, extraversion, agreeableness, conscientiousness, and neuroticism), anger-prone individuals are conceptualized as those with high levels of neuroticism coupled with low levels of agreeableness, presenting as more neurotic, emotionally labile, and less trusting of others. Individuals may adopt several strategies to regulate their anger.

Individuals may adopt styles where anger is directly expressed through verbal and physical aggression, inhibited and suppressed, or expressed assertively to others. Depending on the situation and other traits of the individual, anger-prone individuals may be quietly hostile, verbally aggressive, or physically violent. Angry behaviors may be reinforced and maintained to the extent that they yield instrumental gains, dominance, status, and power over others. Those prone toward suppressing anger may experience paradoxical increases in anger as these individuals must self-monitor whether they are engaging in angry thought processes. As a result, an ironic process occurs in which angry thoughts and emotions are kept longer in conscious awareness (Burns et al. 2012).

Evolutionary Models of Anger

Whereas episodic angry behaviors may serve important protective and communicative functions, relatively stable individual differences in anger proneness present interesting problems for evolutionary psychology because of the negative consequence of chronic anger. Evolutionary psychology assumes behaviors are more likely to be selected and persist if they increase the reproductive fitness of the individual. A high propensity toward anger could undermine reproductive fitness when anger-prone individuals indiscriminately generalize aggressive behaviors across many contexts and fail to attend to the long-term consequences. For instance, many current social contexts actively prohibit and punish aggressive behaviors, anger is linked to a number of health risks including pain (Burns et al. 2012) and cardiovascular disease (Iyer et al. 2010), and aggressive behaviors may increase exposure to injury and death. Whereas intermittent anger may signal others to attend to the needs and boundaries of an individual, chronic expression of anger may be viewed as off-putting by others and ultimately push others away particularly in family, work, and other social settings where cooperation is valued. Considerable loss of resources can also occur

through incarceration, job loss, and other social sanctions of angry and aggressive behaviors.

Several hypotheses have been proposed to explain the plausible evolutionary function of stable individual differences in anger and aggression. The polygynous human mating system coupled with relatively lengthy social and reproductive careers leads to a risk proneness in young males, such that competition for mates, resources, and even social status can lead to male-male confrontation as competition emerges (Fessler 2010). This risk-prone behavior can be generalized to physical risk taking and violence, including homicide, in male-male confrontation and competitions. In competition for mates, a single transgression by another male adversary could reduce one's reproductive fitness. Risks to reproductive fitness could also accumulate over time to the extent that other potential adversaries come to view the individual as weak or vulnerable. Individuals more prone to experiencing anger and expressing it through aggression, violence, and other risky behaviors could in some settings be more likely to deter competitors. Fessler and colleagues found that men who voluntarily participate in nonviolent/nonphysical risk-taking behavior are conceptualized as being larger and stronger by potential mates, enemies, and allies, despite actual physical characteristics. In addition to deterring adversaries, achieving such social status could also attract allies and potential mates. However, in some contexts physical risk-taking behavior (e.g., violence) leads men to be conceptualized as more violent which can cause others to view them as a threat and thus not someone with whom they wish to associate or mate.

Mechanisms of Selection

Aggressive and emotional behaviors have been observed throughout the animal kingdom, albeit humans appear unique in their abilities of self-awareness of their own behavior. Animal models of aggression are well-established paradigms of research. This suggests that variation and selection of angry or aggressive behaviors has existed throughout much of phylogenetic history.

Individual differences in irritable infant temperament – before substantial socialization has occurred – may be predictive of future aggressive behavior. Several areas of research suggest that the propensity toward anger may be selected at multiple levels including the genotype.

Emerging evidence suggests that anger has multiple genetic determinants, specifically in the realm of gene-environment interactions. The monoamine oxidase (MAOA) genotype moderates the effects of childhood maltreatment on male antisocial behaviors (Byrd and Manuck 2014). There is also a three-way interaction in which the serotonin transporter (5-HTT) gene, the MAOA gene, and childhood sexual abuse interact to predict aggressive behavior (Zhang et al. 2017). In each case, genetic components appear to moderate how individuals respond to trauma and adversity.

Based on the abovementioned work on gene-environment interactions that predict aggression, it is plausible that phylogenetic contingencies also have selected neurological structures that enabled animals including humans to adapt to unique characteristics of their environment. Given the physical tolls of chronic anger, a highly heritable and rigid anger-prone phenotype could undermine reproductive fitness if the biological and interpersonal costs outweigh the benefits of deterring adversaries. For instance, the anger-prone phenotype would be expected to be less adaptive in social environments marked by high levels of parental investment and low levels of competition from adversaries. Thus, it may be the case that genetic variation allows for some individuals to be more sensitive to threat and develop anger proneness through operant, respondent, and higher-order learning processes. The importance of individual development in the development of anger and aggression is well recognized in the practice of clinical and forensic psychology. For instance, in the clinical evaluation of aggression, a number of developmental events such as prior history of traumatization, exposure to aggressive models, and the individual's age at the time of their first significant episode of aggression are assessed in order to make classifications about future risk of aggression (Ronan et al. 2014).

Selection of angry and aggressive behaviors might also occur at the level of culture if such behaviors help groups overcome the problems that they face. As with selection of angry behaviors at the individual level, contexts may have existed and continue to exist in which aggression and anger proneness may facilitate the defense and preservation of resources such as food and shelter. In contexts where resources are scarce and competition and deceit is common, a greater sensitivity to threat and higher degree of anger proneness may deter potential adversaries from attacking the individual, their kin, or affiliates. Emerging evidence on the distribution of personality traits in the United States suggests that personality traits of neuroticism and agreeableness cluster in systematic ways, and this clustering may contribute to regional differences in culture (Rentfrow 2010; Rentfrow et al. 2013). Northeastern states tend to have higher aggregate levels of neuroticism and lower levels of agreeableness implying that this region may be more irritable and temperamental compared to other regions in the United States. One possible explanation is that people with similar interests tend to cluster together or land in the same region for similar reasons. Rentfrow uses the example that those high in agreeableness tend to stay in their hometown, while those high in extroversion and openness tend to move away, often clustering in areas that value diversity. Another theory is that people are influenced by those around them via socialization and reinforcement and thus become more similar. Finally, personality traits, including anger proneness, could be impacted by ecological influence.

Conclusion

Anger is often considered a momentary reaction to frustration or other sources of stress. Anger proneness refers to stable differences in how often and how strongly people experience anger across situations. Anger-prone individuals may be

at greater risk of injury and chronic health problems. However, anger may serve important functions for individuals and groups especially when it motivates individuals to persevere and defend themselves, their kin, their resources, and status.

Cross-References

- ▶ [Attractiveness and Anger-Proneness](#)
- ▶ [Sex Differences in Anger Proneness](#)
- ▶ [Strength and Anger-Proneness](#)

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Angry Personality

- ▶ Anger Proneness

Animal Behavior

- ▶ Field of Comparative Psychology, The

Animal Communication

- ▶ Animal Signalling

Animal Emotions

- ▶ Marc Bekoff

Animal Intelligence

- ▶ Nonhuman Intelligence

Animal Signaling

- ▶ Vocal Communication

Animal Signalling

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A

Synonyms

Animal communication; Signals

Definition

Signals are an important aspect of social behavior in the biological world, as they allow information and/or influence to be transmitted between organisms via intermediary signalling and response behaviors. This is often interpreted through an evolutionary lens, whereby the relevant behaviors are assumed to have co-evolved; however, alternative definitions and formalizations exist in the literature.

Introduction

The evolutionary science of animal signalling began with Charles Darwin's *The Expressions of the Emotions in Man and Animals*, published in 1872, and signalling has been central to the study of animal behavior (ethology) since then. In 1973, the Nobel Prize in Medicine was jointly awarded to three ethologists whose work was pioneering in this regard: Karl von Frisch, Konrad Lorenz, and Niko Tinbergen. This included work on the phenomena of imprinting by hatchling birds, and von Frisch's description of the complex, information-rich "waggle dance" of worker bees, by which the details of distant food sources are encoded and communicated to others in the hive. Since then, animal signalling has been the subject of laboratory and field studies on animals ranging from

microbial life to large vertebrates including primates and cetaceans. Several bodies of theoretical literature have also been spawned, with cross-over applications to the human sciences.

Forms of Animal Signalling

Animal signalling occurs in a wide variety of forms and contexts. Striking cases occur across species boundaries and in highly asymmetric relationships, for example, between prey animals and their predators as in the case of the leaping (stotting) behavior of Thompson's Gazelles during pursuit by predators, and vivid coloration of some amphibian or insect species to advertise their toxicity. However, most animal signalling takes place between conspecifics and functions to regulate social behavior. Most signals are also biologically fixed and involuntary, in the sense of either being expressed developmentally (such as coloration) or reactively, e.g., via visual or audible cues of aggression, fear, and sexual arousal, and nonvisual signals such as pheromones and physical contact. Such traits and behaviors are typically innate and robust across a species, though there are known cases, such as whale song, where signal variants propagate by cultural transmission and social learning.

Many vertebrates also engage in behaviorally complex signalling systems, such as the alarm calls of several monkey species and the gestural systems of great apes. Vervet monkeys emit alarm calls that discriminate between different types of predator (e.g., snake, eagle, leopard, baboon) which in turn elicit "best response" avoidance behaviors from alerted conspecifics (e.g., climb a tree, hide under a bush, etc.) (Seyfarth et al. 1980). Communicative behaviors of chimpanzees and other great apes have been extensively studied and include both reflexive signals (such as baring teeth to communicate aggression) and dozens of vocalizations and gestures (such as clapping and beckoning) which facilitate social interaction. These appear to be intentional in performance but are also innate and robust with respect to usage, with many gestural signals being common across the great ape clade, including human children (Byrne et al. 2017). However, there is

ongoing debate about the intentionality, ontogeny, and origins of these gestural systems, including the degree to which learning and ritualization plays a role, as well as the implications that can be drawn regarding the evolution and acquisition of human language (Tomasello and Call 2019).

Evolutionary Explanations

Several theoretical and formal approaches have been developed to explain the evolution of animal signalling. Amotz Zahavi famously proposed the "handicap principle," whereby costly or risky traits or behaviors can be interpreted as strategic signals of underlying qualities, for example, the spectacular tail of the peacock as a costly investment in advertising the male's quality as a mate. Though initially focused on sexual selection, Zahavi and others have argued that the handicap principle is broadly applicable to signalling throughout the biological world, and it has been formalized using evolutionary game theory as a signalling game by which "high-quality" senders can advertise themselves as such by sending a signal that is too costly for low-quality individuals (Grafen 1990; Zahavi and Zahavi 1997). The stotting behavior of Thompson's Gazelles during pursuit by predators is one putative illustration of this model: the high leaps are less risky if the animal already has a good chance of getting away, and can therefore serve as an honest signal for the predator to switch targets, to the benefit of both animals. If fitness benefits for receivers and high-quality senders align in this way, then conditional signals and responses can co-evolve.

However, there is disagreement about the degree to which the handicap principle and costly/strategic signalling underpins signalling ontogeny. An alternative proposal, especially in cases of sexual selection, is the "truth in advertising" principle (Kodric-Brown and Brown 1984), which states that some animal signalling takes place costlessly via traits which also serve the purpose they advertise. For example, an impressive set of antlers on a stag can both help their bearer compete for mating privileges but also deter weaker opponents from competing. In a seminal text on animal signalling, Maynard

Smith and Harper also draw the distinction between handicap signals and “index signals,” which are honest because of an intimate relationship between their method of generation and the trait being signalled for, such that they are difficult or impossible to fake. Their example is the roar of a stag, which is a costless-yet-honest signal of the stag’s size and strength, because these qualities are what determine the tone and volume of the roar (Maynard Smith and Harper 2003). Other theoreticians have emphasized game-theoretic models and interpretations which are more general and nuanced than the classic handicap formulation, including signalling games where senders and receivers have more common interest, and there is scope for richer communication (Skyrms 2010). Importantly, these different signalling models have different implications with respect to costs and benefits, and resulting evolutionary trajectories. Alternative frameworks have also been developed by theoretical biologists which are more closely linked to the specifics of ecological context (e.g., Hebets et al. 2016).

Information, Influence, and Evolution

Given the diversity of signalling forms and explanatory approaches, the scientific study of animal signals is spread across many disciplines. It can involve observational studies of animals (in the wild and in captivity) and experimental studies, but there is also a considerable body of theoretical and formal work on biological signalling, e.g., carried out via evolutionary game theory and other modelling approaches.

This means that working definitions of signalling do not always agree. One common criterion for a signal is that it encodes and transmits information, so any observable trait of an organism that is correlated with an unobservable trait could be a “signal” of it to some other organism. More commonly, however, as outlined by Maynard Smith and Harper (2003), signalling is seen by evolutionary biologists as an evolved *mutualistic* relationship, where the sharing of information improves the fitness of both senders and receivers. This definition is narrower and more precise: “any act or structure which alters the behaviour of other

organisms, which evolved because of that effect, and which is effective because the receiver’s response has also evolved” (Maynard Smith and Harper 2003, p. 3). For example, bleeding did not evolve to attract sharks, so blood in the water, while informative, is not a signal in this co-evolutionary sense and is instead a *cue*.

Cues are one way of breaking the co-evolutionary condition: receivers adapt to take advantage of information that the sender reveals in a way that was not itself selected for. Conversely, senders might adapt to take advantage of preexisting receiver responses in order to *manipulate* them. One cross-kingdom example is the *Ophrys speculum* orchid, which attracts male *Campsoscolia ciliata* wasps by mimicking the chemical signals of a sexually receptive female wasp so effectively that males preferentially copulate with the flower rather than with actual females (Ayasse et al. 2003). Cues and dishonest manipulation are both one-sided phenomena where an exploitative adaptation in either the sender or the receiver was not responded to by counter-adaption in the other. Given there is no selection for the cue or manipulable trait, its persistence therefore requires additional explanation particular to the case; e.g., for the wasp species, remaining vulnerable to the orchid’s manipulation is probably less costly than altering the relevant parts of its mating strategy.

However, the co-evolutionary definition is not universally accepted. In an early dissent, Dawkins and Krebs (1978) described it as the “classical ethological” approach to signalling and proposed their own definition of signalling as *influence*. On this view, what is essential to signalling is that the sender intervenes on the receiver’s behavior by triggering conditional responses. This bundles together as signals both co-evolved signals and dishonest manipulation, as in the orchid-wasp case. Notably, this fits with how the term is used by at least some biologists; for example, throughout the Ayasse et al. paper describing the orchid-wasp case, the authors describe the deceptive pheromones manufactured by the *Ophrys speculum* orchid as “chemical signals.”

Three distinct uses of “signal” can therefore be found in the literature: (i) a narrow sense where signals are both informative and influential,

contrasted against cues and manipulations, (ii) the signals-as-information sense which includes cues but not manipulation, and (iii) the signals-as-influence sense which includes manipulations but not cues. In many contexts, the differences are merely semantic, but in others, the three uses would imply different evolutionary narratives regarding which behaviors (sender and/or receiver) have been selected for and why.

Animal Signalling and Human Behavior

Other than language, many attempts have been made to explain distinctively human traits via applications of animal signalling theory. These are often speculative and controversial. Some early theorists and popularizers of sociobiology ascribed evolved, innate, non-intentional signalling functions to exaggerated morphological features such as turned-out lips and enlarged ear lobes, breasts, and penises. A range of signalling explanations have also been proposed for intentional behaviors as diverse as conspicuous consumption, generosity, suicide bombing, grief, regret, and religion. Many proposals state that the costliness of such behaviors can be explained via the handicap principle or other signalling mechanisms but few attempts to interpret and quantify the relevant costs and benefits in a way that plausibly fits the relevant game-theoretic models (Grose 2011). Evidence for testable predictions (where these exist) has also been mixed or difficult to obtain, compounded by the additional modes of selection and transmission which human enculturation enables.

Conclusions

Animal signals are a common object of study in the biological sciences, where there is a large body of both case studies and theoretical literature. However, there are disparate approaches to describing and explaining animal signalling, with ongoing debates at both the conceptual and empirical level. Evidence of evolutionary causation also becomes problematic outside of

cases where (i) innate sender and receiver behavior means there is a one-to-one mapping between stimulus and response and (ii) fitness differences are readily discernible. Signalling theory, as developed in the study of animal signals, is therefore an intriguing and potentially powerful tool for crafting evolutionary explanations, but moving beyond simple verbal models of signalling requires a challenging degree of engagement with the complexities of both the signalling explanations and their application.

Cross-References

- ▶ [Communication, Cues, and Signals](#)
- ▶ [Costly Signaling](#)
- ▶ [Costly Signaling and Altruism](#)
- ▶ [Costly Signaling Theory](#)
- ▶ [Evolution of Communication](#)
- ▶ [Manipulation and Dishonest Signals](#)
- ▶ [Sexual Signaling During Ovulation](#)
- ▶ [The Handicap Principle](#)

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Animism

- Ancestor Worship

Anisogamy

- Parental Investment and Sexual Selection (Trivers Foundational Theory)

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Synonyms/Keywords

Female gangs; Indirect aggression; Intrasexual aggression; Maternal investment; Urban gangs

Definition

Anne Campbell was a prominent evolutionary psychologist most noted for her work examining sex differences in aggression and her ethnographic studies of female gang members.

A

Introduction

Anne Campbell received her Doctorate in Experimental Psychology at Oxford in 1977. Two years later, Campbell began researching female gang members by living in New York City and talking with members of three gangs. She published her findings in her book *Girls in the Gang*. In February of 2017, Anne Campbell passed away, but her research on sex differences in aggression and on the intrasexual aggression of women continues to inspire others (Cross 2017).

Anne Campbell's work in the field of evolutionary psychology primarily focused on intrasexual aggression among women and female gang members. Campbell was one of the first evolutionary psychologists to articulate that women engage in less direct aggression than men, not only because there are fewer incentives for this behavior among women relative to men, but also because of women's vital role as a caregiver and the threat posed to that role by their involvement in direct aggression (Campbell 1999). This theoretical insight generated many empirical studies examining sex differences in aggression, competition, violence, and mating strategies. Campbell is also well known for her ethnographic work that she conducted while observing three different female gangs in New York. This work shed light on the motivations for women's involvement in gangs, which had previously been largely ignored by researchers whose primary focus was on male gang members (Campbell 1984). This entry provides an overview of the research accomplishments of Anne Campbell throughout her career.

Sex Differences in Aggression

A large literature in social and evolutionary psychology has documented marked sex differences

in aggression (e.g., Archer 2009; Campbell 1999). For example, research has shown that across cultures, males use more direct aggression than females from the age of two, onward. Early theorizing in evolutionary psychology explained these sex differences as the result of distinct mating strategies among males and females that incentivize aggressive and violent competition for access to mating opportunities among men, but not women (Archer 2009; Daly and Wilson 1988). A primary contribution made by Campbell was the theoretical argument that women's relatively lower levels of aggressive behavior could be attributed not only to reduced incentives relative to men, but additionally to an increased cost of aggressive behavior owing to women's primary and essential role as a caregiver.

Campbell used parental investment theory (Trivers 1972) as a foundation to explain why females are less likely to participate in direct aggression. She argued that women not only invest in their offspring more than men, but also that this investment is absolutely essential to the survival of her offspring. Studies have indicated that the death of the mother can increase the likelihood of her infant's death by a factor of five, whereas the death of the infant's father increases the offspring's mortality likelihood by a factor of three. Other studies report a child mortality of 100% following the death of the mother (Campbell 1999). Because females are vital to the survival of their offspring they must protect themselves in order to ensure that their offspring survive. As a result, engagement in physical aggression is often too risky for females, as their offspring's life depends on the mother's survival. Additionally, although intrasexual competition and aggression among women could allow women to compete for higher *quality* mates, the advantages of acquiring a greater *quantity* of mates is much reduced owing to women's large investment in each offspring and the reduced reproductive capacity that this investment constrains. However, for males, the benefits of intrasexual aggression typically outweigh the costs. This is owing to the fact that the costs of aggression are less steep (the survival of their young does not depend on their own survival)

and the benefits are greater because men's intrasexual aggression, if successful, can yield both a higher quality and quantity of mating opportunities. Additionally, a man's decision to opt out of aggressive competition with other men for mating opportunities could result in his complete exclusion from the mating market.

Campbell therefore argued that although there are benefits to be had for women engaging in intrasexual competition (e.g., increased quality of mates, stronger mate retention), competition involving direct aggression that would put women at risk of injury or death, would be avoided as a means of protecting oneself and one's offspring. Campbell supported this argument with evidence of sex differences in aggressive acts. For example, she noted that as the type of aggressive act increases in terms of direct violence, the gap in sex differences also increases, as women do not tend to participate in the riskier aggressive acts (Campbell 1999). Campbell also noted that women think more carefully about the potential consequences of impulsive actions (including aggressive acts), which may discourage them from participating in these actions. Women are less impulsive due to the necessity of their survival in order to take care of their young. Indeed, females must not only consider their own survival, but also the survival of their offspring (Cross et al. 2011).

These sex differences in aggression are not explained by sex differences in experienced anger. Indeed, research by Campbell (2006) illustrates that men and women experience similar levels of anger in response to physical danger. Rather, what appears to down-regulate women's aggressive behavior is their experience of fear. Campbell argues that fear may act as an emotional inhibitor of direct aggression by women, thereby reducing their risk of incurring serious injury. For example, females report more fear of physical harm than males. Women may be more fearful of physical harm due to their role in the survival of their young. These findings support Campbell's maternal investment theory (Campbell 1999, 2006). However, there are occurrences when the risks of nonaggression outweigh the benefits of nonaggressive actions.

For example, research suggests that oxytocin has a role in the reduction of fear in mothers during an attack on their young. In this instance, the overriding of the fear response is necessary, as the mother must put her life at risk by retaliating if she is to ensure the survival of her offspring. Oxytocin can also promote affiliative behavior in women. Instead of demonstrating a “fight or flight” response, females will often request help and protection from other females. By bonding with other females, mothers are able to protect themselves and, therefore, their offspring (Campbell 2008).

Although men tend to participate in more direct aggression than females, women and men have a similar age-assault curve, wherein violence is more prevalent during their teenage years (Campbell 1995). This research suggests that the motivation for aggression in both males and females is the same: the elimination of romantic rivals. During the teenage years, both males and females are entering their reproductive prime and are primarily motivated by the desire to secure potential mates. However, due to the maternal investment instinct that women possess, they are disinclined to use aggressive and violent behaviors to compete for those mating opportunities which may result in bodily harm, relative to men. Women, instead, are more likely to use indirect aggression, such as the verbal derogation of competitors in order to appear superior to their romantic rivals. This aggressive behavior is typically expressed indirectly, such as through gossip, rather than verbal derogation directed directly toward a romantic rival. This behavior is used in order to shield the aggressor’s identity, which will protect the aggressor from retaliation. This tactic is useful to women, who wish to protect themselves in order to care for their offspring. However, indirect aggression is less advantageous for men, as they must appeal to potential mates by demonstrating their dominance over other men in a more direct and public fashion (Campbell 1995, 1999, 2004). Campbell’s emphasis on the important role of maternal investment added much more depth and predictive power to the traditional evolutionary framework for explaining sex differences in intrasexual aggression. These insights

continue to play an important role in the work of many evolutionary psychologists.

A

Female Gang Members

Although there has been a fair amount of research on gangs and their members, very few researchers have systematically examined the role that women play in their involvement in gangs. When researchers did examine female gang members, it was often to explain the way in which male gang members viewed them. This research sorted female members into different categories, such as “Sex Objects” and “Tomboys,” but did not reduce male gang members to such labels. Campbell was one of the first researchers to directly examine the experiences and motivations of female gang members. In order to do so, Campbell spent 6 months in New York engaged in intensive observations of, and interviews with, three different gangs: The Sandman Ladies, The Sex Girls, and The Five Percent Nation.

Campbell applied the same evolutionary background when researching female gang members as she did when studying aggression in other females. She noted that most of the aggressive actions demonstrated by female gang members were performed in order to appeal to or guard mates. Additionally, although female gang members are more likely to use violence than other women, the pattern of aggression still fits that which was described above. That is, female gang members tend to use indirect aggression rather than direct aggression in order to shield their identity and protect themselves and their young. Seeking mates is especially important for female gang members, as most join gangs in order to escape poverty by finding a mate who will provide financial security and protection for the woman and any offspring she may have. Because these women depend so heavily on their partners, they engage in intense competition with other women in order to guard their mate from rivals. Female members enact these mate-guarding behaviors by using indirect aggression in order to derogate rivals. Indeed, most of the aggressive behaviors demonstrated by female members are directed

against romantic rivals. When direct aggression is used by females, the fights are less likely to include firearms than male gang fights, demonstrating the less violent nature of female intrasexual fights. One especially common reason for fighting is due to the female gang member's need to protect her reputation or integrity. These fights may also occur due to the member's desire to defend the honor of her child or her partner (Campbell 1984, 1991).

Conclusion

Anne Campbell made many contributions to the literature on gangs and to the field of evolutionary psychology, especially regarding sex differences in intrasexual aggression. In particular, Campbell's research gave voice to the female psychology of aggression— a topic that had been taken for granted as simply the inverse of men's psychology. This research was achieved through her ground-breaking theoretical advancements as well as her rigorous empirical and observational research. The research that she conducted continues to inspire researchers and provides fertile ground for the generation of new research ideas.

Cross-References

- [Intrasexual Rivalry Among Women](#)
- [Sex Differences in Same-Sex Aggression](#)
- [Urban Gangs](#)
- [Verbal Derogation Among Women](#)

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Anonymity

- [Deindividuation](#)

Anonymity of Cyberbullying

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Synonyms

Cyber/Internet/online harassment; Cyberstalking; E-bullying; Electronic aggression; Electronic bullying

Definition

Although cyberbullying shares certain categorical features synonymous with traditional types of bullying, cyberbullying itself is a unique

phenomenon that occurs through the use of technology (e.g., social media, email, chat rooms, instant messaging, text messaging, or websites) rather than through traditional face-to-face (e.g., physical fights, destruction of property, verbal insults) or in-person (e.g., gossiping, ostracism) modalities. Anonymity is often an essential component of cyberbullying and is used to refer to anonymous posts and interactions in which a person's identity cannot be determined through the computer IP address, usernames, or handles. Further, anonymity can also be used as a description when the actual name/identity of a person's offline presence is more difficult to determine even in the obvious existence of an online one (e.g., impersonating another individual, computer IP address, usernames, or handles).

Introduction

With rising technology use, more social interactions occur through the internet (e.g., social media, websites, chat rooms) or other electronic means (e.g., texting, messaging systems). An important facet of this online social communication is an applied or assumed anonymity within interactions (e.g., posting anonymous comments). In fact, people are often recognized online by their username or handle in which they establish an online persona as opposed to their actual one (e.g., GoTheDistance2016 vs. Joe Smith). However, in many cases people are not as anonymous as they perceive themselves to be as a result of computer IP addresses that are typically attached to online activity. Many electronic devices (e.g., cell phones) also track data and activity and link the information with specific users. The perceived anonymity of online and electronic social interactions is considered by many (though not all) researchers to be an important feature of cyberbullying. Researchers who do not consider anonymity to be an important distinguishing feature of cyberbullying note that other forms of bullying can also be characterized by anonymity (e.g., not knowing who started a rumor or who defaced someone's possessions). Cyberbullying can be perpetrated by a single person or a group of people

and is characterized as repetitive aggressive acts or messages that occur online or electronically with an intention to inflict suffering, harm, embarrassment, or discomfort to another person. Approximately 50% of youth have been estimated to have experienced and been involved in cyberbullying.

Recent research has been conducted to determine whether people who are involved in bullying at school (i.e., traditional forms of bullying including overt/physical, indirect/relational) as bullies, victims, or bully-victims are also involved in cyberbullying. The evidence to date is mixed with some researchers finding that over 80% of youth who bully others through cyber or electronic means also bully others at school through traditional forms of bullying; similarly, over 80% of victims of cyberbullying are also victimized at school (e.g., Raskauskas and Stoltz 2007; Juvonen and Gross 2008). In contrast, other researchers have found substantially less overlap; for example, approximately 70% of school bullies and victims and 50% of bully-victims were not involved in cyberbullying (Kowalski and Limber 2013). Regardless of the percentage of overlap, researchers do agree that certain environmental factors like being male, having friends involved in delinquent activities, and having non-trustworthy nonsupportive friends are predictive of being involved in cyberbullying. Additionally, engagement in cyberbullying is also predicted by frequent internet use and high levels of computer/internet abilities (e.g., Ybarra and Mitchell 2004). Given that a substantial amount of youth are involved in cyberbullying, it is important to consider whether the anonymity associated with cyberbullying leads to more negative outcomes than traditional forms of bullying.

Role of Anonymity

Although traditional forms of bullying can occur anonymously (e.g., uncertainty about who started a rumor or defaced possessions), the role of anonymity is considered a crucial predictor of the severity of cyberbullying (Barlett et al. 2016; Vanderbosch and Van Cleemput 2008). Perceived

anonymous online activity predicts crueler online behavior (i.e., the online disinhibition effect; Suler 2004) compared to nonanonymous online activity. The association between perceived anonymity and being a perpetrator of cyberbullying is mediated by positive attitudes toward cyberbullying. The online disinhibition effect (i.e., crueler online behavior compared to face-to-face behavior) has also been explained by perceived anonymity in online activity leading to reduced self-awareness and, in turn, increased deindividuation. There is also evidence that having anonymous interaction partners reduces the level of intimacy during online disclosures and feelings of closeness. Overall, anonymity appears to reduce anxiety levels for the perpetrator, perhaps because there's a perception of fewer negative consequences.

Negative Outcomes Associated with Cyberbullying

Cyberbullying is associated with a host of negative outcomes (e.g., Tokunaga 2010). Specifically, being the target of cyberbullying is robustly associated with increased internalizing problems such as anxiety, depression, loneliness, suicidal ideation, and suicide attempts/self-harm and externalizing problems such as increased substance use, alcohol use, rule-breaking behavior, and aggression. In addition, cyberbullying experienced during adolescence is associated with negative developmental outcomes including poor school performance and increased avoidance of school. There is also an association between low self-esteem and teens who seek out opportunities to interact online with strangers (Valkenburg and Peter 2011).

An important feature distinguishing cyberbullying from more traditional forms of bullying is that specific aggression acts are not isolated to a single area such as a school or park but rather can rapidly spread to multiple domains such as multiple social media sites, chat rooms, and text/picture messages. Moreover, many online interactions are asynchronous in nature. The negative outcomes associated with being bullied has been

hypothesized to be exacerbated in cyberbullying due to the wider group of people who see, and often respond to, the aggressive acts as well as the longevity and permanency of the aggressive acts. There is also evidence that youth with low levels of self-control are more likely to engage in cyberbullying than their peers with high self-control suggesting that youth engaging in cyberbullying are not carefully considering the ramifications of their online aggressive behavior; this lack of using self-control may be partially due to the perceived anonymity of their behaviors.

Conclusion

Although cyberbullying shares characteristics similar to traditional forms of bullying, the motives and desire to engage in cyberbullying over more traditional forms may differ. One component that sets cyberbullying apart is the presence of real or perceived anonymity in an online space. A child who is smaller in stature or lower on the social hierarchy may not have the "power" to induce fear in a traditional bully-victim interaction. However, size becomes irrelevant in the case of cyberbullying, and the power gained in the bully-victim relationship is now done so by anonymity. By virtue, certain characteristics that precluded an individual from being a traditional bully is not a concerning factor in becoming a cyber one. As a result, the anonymity of cyberbullying has been proposed by some researchers to increase the severity and negative outcomes associated with being the target of aggressive online and electronic acts compared with experiencing other forms of bullying. Other researchers, however, have noted that anonymity is not limited to cyberbullying and can also be a component in more traditional forms of bullying. Regardless, it does appear that anonymity in cyberbullying is more prominent and apparent to targets and bystanders and that the feeling of anonymity, perceived or in actuality, predicts more severe levels of cyberbullying.

More recently, the legal and ethical responsibilities of how to protect those experiencing cyberbullying in conjunction with the

safeguarding of an individual's constitutional rights has become heavily debated. The perceived anonymity of a perpetrator, coupled with a known constitutional protection, may actually further encourage the use of cyberbullying compared to a more traditional form. Clearly, the anonymity that can be achieved within cyberbullying does indeed make it a unique phenomenon worthy of continued study. With the rising use of technology for the foreseeable future, the greatest task we may be faced with is how to encourage positive uses of social interaction while simultaneously mitigating negative attributes like cyberbullying.

Cross-References

- [Child Abuse and Bullying](#)
- [Procedures for Dealing with Bullies](#)
- [Sex Differences in Cyber Bullying](#)

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Anorectic

- [Anorexia Nervosa](#)

Anorexia

- [Anorexia Nervosa](#)

Anorexia Nervosa

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Synonyms

AN; Anorectic; Anorexia; Eating disorders (EDs); Fear of weight gain; Food restriction; Low weight

Definition

According to APA.org (“Eating Disorders”, 2018), anorexia nervosa is defined as an eating disorder characterized by individuals (most commonly adolescent girls) who restrict their eating to the point of starvation due to the false belief that they are overweight or carrying too much weight (i.e., an obsessive drive for thinness).

Introduction

Eating disorders (EDs) are abnormal eating patterns and behaviors that can be detrimental to one's overall health (i.e., physical and psychological) and, in extreme cases, can result in death. EDs are most frequent in industrialized societies, and 95% affected are women. Symptoms of eating disorders are present in at least 10% of school-aged girls co-occurring with medical, dietary, and psychological issues. Anorexia nervosa is defined as an eating disorder characterized by individuals (most commonly adolescent girls) who restrict their eating to the point of starvation due to the false belief that they are overweight or carrying too much weight (i.e., an obsessive drive for thinness). On a similar note, bulimia is an eating disorder characterized by individuals who eat an excessive amount of food followed by purging through vomiting, laxatives, and/or excessive exercise ("Eating Disorders", APA.org, 2018).

Both anorexia and bulimia share three major characteristics: disturbed body image, an obsessive strive for thinness, and an almost identical geographical distribution.

Because of these similarities, many evolutionary theories conceptualize both anorexia and bulimia as having the same underlying etiology and thus are thought to both derive from the same general mechanism(s). According to a review by Kardum, Gracanin, and Hudek-Knezevic (2008), current evolutionary theories on the development of eating disorders (anorexia specifically) are adapted-to-flee-famine hypothesis (Guisinger 2003), kin selection theory (Hamilton 1964), the model of parental manipulation (Trivers 1974), reproductive suppression hypothesis (Wasser and Barash 1983), sexual competition hypothesis (Abed 1998), and social attention-holding power (Gatward 2007).

Adapted-to-Flee-Famine Hypothesis

The present theory posits that ED symptomologies (i.e., restricting food, denial of starvation, hyperactivity) are a result of an evolutionary adaptation to cope with times of famine. In ancestral

times, food was not readily available and migration was necessary to find food sources.

In support of this theory, it has been found that many species refuse food intake during times of migrating and breeding. Additionally, increased activity is elevated during times of limited food resources assumedly to increase chances of finding food resources. Anorexic-like syndromes are found in several low body weight species, and anorexia has been found to be highly heritable, suggesting that such symptoms were evolved to be advantageous in the ancestral environment.

The adapted-to-flee-famine hypothesis does not explain why those who suffer from anorexia refuse to eat when food is plentiful and why hyperactivity is not always a marker for anorexia.

Kin Selection Theory

The kin selection theory contends that anorexia is adaptive for favoring intra-familial prosocial behavior (i.e., caring, helping, self-sacrificing) over reproductive success. Common attributes of those who suffer from anorexia are overprotective attitudes regarding family members and incessant worrying about their well-being. Reproductive suppression elevates a female's inclusive fitness by assuring the reproductive success of her family members. In other words, a female becomes anorexic as a way to completely devote herself to taking care of her family members so that they are more likely to survive and have children of their own. By not bearing children, the female is not using up vital resources that her family may need to adequately function and thrive.

The Model of Parental Manipulation

The model of parental manipulation has three underlying hypotheses (note: these are all unconscious drives): (1) parents influence (e.g., dominant and overprotective mothers) the onset and maintenance of EDs by preventing the daughter from finding a partner and/or preventing detachment from the parent(s) to find a partner; (2) eating disorders elevate parental reproductive fitness by

allocating resources to children of higher reproductive value; and (3) EDs reduce fitness of those who suffer from them by evoking reproductive suppression. That is, parental fitness increases because reproductive suppression weakens or diminishes the reproductive value of the sufferer, which in turn preserves familial resources by not having to provide for possible additional offspring. Overall, the female experiences a switch from genetically based selfish behavior (i.e., reproducing) to selfless behavior (i.e., not reproducing) for the sake of preserving and optimally utilizing resources for her family.

Reproductive Suppression Hypothesis

The present theory suggests that females suppress their reproduction when the current conditions are not in favor of reproductive success or offspring survival. That is, the female believes that the benefits of suppressing reproduction (i.e., depleting fat stores to the extent of stopping the ovulatory cycle; amenorrhea) outweigh the costs and that resources will be more plentiful and readily available in the future to assure reproductive success. This reproductive suppression is done through extreme dietary behaviors, and preferring a thinner body ideal can be a way to manipulate the timing of reproduction.

A variant of this hypothesis was proposed by Surbey (1987). Females can become anorexic as a way to stunt development. If a female is predisposed to mature earlier in a modern day society that favors late maturers, anorexia is a way to change a female's natural developmental trajectory to one of a late maturer. Again, this is done by reducing fat through strict dietary behaviors. The benefit of late maturers in modern society is that it takes reproduction (i.e., reduces libido, attracts fewer males, induces amenorrhea) out of the equation when academic and professional success are more valued in the female's family.

The reproduction suppression hypothesis fails to address the symptoms of hyperactivity and distorted body image prevalent in those who suffer from anorexia and does not explain why an alternate and less costly method to suppressing

reproduction in women was not evolved, why anorexia exists in postmenopausal women, and why anorexia is most common in those who are white and wealthy.

Sexual Competition Hypothesis

The present hypothesis proposes that eating disorders are the product of "runaway" (spiraled out of control) intra-sexual competition in Westernized societies. As a result of decreased long-term mating strategies and increased female social and economic independence in the modern Westernized environment, intra-sexual competition among females for long-term mates has increased. Thinness has been related to youthfulness and the ideal "nubile shape" that was once a signal of fertility in ancestral times. The present hypothesis posits that eating disorders are an unconscious attempt for females to better match the nubile body shape that signals a longer period of fertility when competing with other females for a long-term mate in Westernized societies.

The sexual competition hypothesis does not account for proximate causal factors of eating disorders and does not provide an explanation for eating disorders among males.

Social Attention-Holding Power

The social attention-holding power hypothesis incorporates response to threat to evolutionary ideas to understand the onset of EDs.

The present hypothesis explains that ED symptoms are a result of social attention-holding power (i.e., the ability to gain and maintain attention and investment from members of a group) and the need to belong in a social context. This concept also ties into the degree a person feels in control in a social context: a dominant (i.e., high status or position) person feels more in control, and a submissive (i.e., lower status or position) person feels less in control. It is assumed that the need to belong has ancestral roots due to the idea that in the ancestral environment, it was likely that exploitation led to death. In other words, being

excluded meant less access to vital resources to assure survival.

Unlike ancestral times where being heavier meant having greater access to resources, modern day society favors thin individuals, as being thin is representative of status and control (i.e., the ability to afford healthy foods and gym memberships). In summation, this new drive for thinness can set off the threat of famine response, eliciting the onset of an eating disorder.

Conclusion

Eating disorders (EDs) are abnormal eating patterns and behaviors that can be detrimental to one's overall health and, in extreme cases, can result in death. EDs are most common in adolescent women in industrialized societies. There are several current evolutionary theories behind the onset of eating disorders that have yet to be extensively investigated.

Cross-Reference

► [Eating Disorders](#)

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Anorgasmia

► [Orgasmic Disorders](#)

Antagonizing

► [Child Abuse and Bullying](#)

Anterior Cerebral Cortex

► [Frontal Cortex](#)

Anthropological Universals

► [Cultural Universals](#)

Anthropologist

► [Brian Hare](#)
► [Michael Tomasello](#)

Anthropology

► [Towards Methodological Pluralism in Psychological Sciences](#)

Anthropomorphism

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Synonyms

Attribution of human traits; Imposing humanlike characteristics

Definition

The attribution of human traits, motivations, and persona-like qualities to nonhuman animals and/or inanimate objects.

Introduction

The perception that nonhuman animals and inanimate objects possess human characteristics, motivations, and personalities is described as anthropomorphism. Application of anthropomorphic interpretations may reflect both the conceptual nature of anthropomorphism and its use as a critical means of understanding phenomena and patterns of behavior. Anthropomorphic thinking may, at times, be imprecise in relation to real world phenomena, whereby human traits are projected in an exaggerated manner onto a nonhuman animal or object in order to predict or depict their internal states, desires, thoughts, and motivations. This kind of anthropomorphism is most often found in children's books, cartoons, films about animals, and even some nature documentaries. In contrast, another form of anthropomorphism involves applying psychological principles in very systematic and biologically accurate ways, providing unique insights into an animal's or species' life history.

In understanding the origins of anthropomorphism, we can ask why humans feel the need to

impose human-like qualities on other animate beings and inanimate objects? Are there psychological and evolutionary functions (adaptations) derived by anthropomorphizing that assist in problem solving in social and environmental milieus, in a cause-and-effect manner? Are humans the only species that anthropomorphize? Do domestic dogs, for example, anthropomorphize human behavior in relation to their own canine frame of reference? Given that so many behaviors are shared between closely related species (possibly stemming from common ancestors and similarities in nervous systems, physiology, and anatomy), are other species also prone to anthropomorphic tendencies?

Anthropomorphism and Perspective-Taking

Taking another species' perspective (or that of an inanimate object) is crucial to the process of anthropomorphism. The famous question posed by the philosopher, Nagel (1974), of "What does it feel like to be a bat?", is indicative that humans do process other species' experiences by attempting to take their perspectives, although it is not clear how effective we are at this task. It may be very difficult to project oneself within the mindset of an octopus whose body is so different from that of a human, or to truly imagine seeing with the compound eyes of a dragonfly (Dennett 1991). However, the process of anthropomorphizing may be a reflection of the capacity to empathize to some degree (Mitchell et al. 1996). Empathic processes might include thoughts projected onto others, such as, "If I were that dog, what would I feel in that situation?", and, "If I were that orangutan, what would I say if I could talk?".

It is noteworthy that humans tend to anthropomorphize animals that more closely resemble themselves and have a high "cuteness" factor (e.g., are reminiscent of babies in features and actions) as more human-like in their motivations and responses. For example, nonhuman primates are more likely to be anthropomorphized as child-

like or as surrogate humans, while an animal as distinct from humans as a cockroach, or an inanimate object such as a rock, may not be described as possessing the same extent of internal states and emotions. The foundation of these differences may lie in humans' ability to more easily empathize with creatures that are biologically more like them and are closer taxonomically.

Anthropomorphism of Nonhuman Animals

When humans infer that nonhuman animals are psychologically, cognitively, consciously, emotionally, and even spiritually like humans, they can be said to be imposing an anthropomorphic interpretation on the behaviors they observe and inferring human-like internal states (Mitchell et al. 1996). Fundamentally, the tendency towards anthropomorphism diverges into either a "subjective" and/or an "objective" interpretation of nonhuman animal behavior. Under some circumstances, the term "anthropomorphism" is applied pejoratively, referring to a highly subjective, inaccurate, and anthropocentric (human-centered) nature of referencing behaviors as human-like for explanation, but without regard to a realistic assessment of the animal's internal state(s).

Occurrences of inaccurate anthropomorphic inferences are often used for effect in children's books to create a sense of empathy with an animal character, particularly in illustrating a moral code (e.g., greed, kindness, sympathy, etc.). For example, Winnie-the-Pooh, as a children's book character, is highly personified and depicted entirely in anthropomorphic terms. He speaks and is friends with humans and other species with whom he interacts, not at all reflecting a wild bear's behavior or ecological requirements. Inaccurate anthropomorphic inferences may also occur in some nature documentaries: voice-overs provide a running commentary of the internal thoughts and motivations, feelings, and desires of animals, presenting a blurred, subjective version of the facts to explain events as they unfold visually. By personifying the animals in such a

subjective manner, the documentary becomes more story-like and possibly enhances its entertainment. Even so, the audiences may develop greater empathy and recall additional information about that species than if the documentary was presented in a drier, more objective style (Dolins et al. 2010).

Under some circumstances, however, it may be both accurate and acceptable to interpret other species' behaviors using a human-like frame of reference. This is because what we understand about human behavior, the psychological principles, may also be true for other species, particularly those closely related to humans, such as nonhuman primates and other large-brained, long-lived, highly social species, such as dolphins, elephants, parrots, etc. With these animals, an anthropomorphic interpretation may provide a biologically insightful explanation in an objective framework.

Anthropomorphism as a Critical Tool

In science in general, and in the scientific study of animal behavior, Ethology, it has long been a tradition to avoid the use of anthropomorphic interpretations of animal's internal states and motivations. The tendency is to explain behavior in the most objective, reductionist manner, so to avoid subjectivity, consistent with a Behaviorist framework. This is in contrast to a framework that posits higher order thinking and emotions in non-human animals, yet is still objective. In more recent years, it has become clear that the strength of evidence in support of the biological continuum (in cognition, emotions, and other internal states) between humans and other species should influence our interpretations of nonhuman animal behavior, and not surprisingly, our interpretations of human behavior as well (Darwin 1859; 2006). Much of this evidence is based on parallels among closely related species and even more distantly related species in anatomical features and consequent function and behaviors, as well as similarities in the neural connectivity (pathways) of the central nervous system and brain (e.g., Spocter et al. 2010).

An excellent example is Barbara Smuts' (1985) detailed study of wild olive baboons in Kenya and Tanzania over two years, which provided her with insights into the social relationships between males and females. Her observations lead to a significant understanding of baboons' patterns of sociality that were based on objective behavioral assessments using ethograms and operational definitions as proscribed by ethological methods. Smuts referred to these tightly bonded social relationships as "friendships" between baboons (1985), which from a reductionist viewpoint, could be viewed as consistent with an anthropomorphic explanation. However, applying the term, anthropomorphism in the positive sense, Smuts' framework summarized and described behavior patterns that parallel those occurring in human societies and between human males and females who develop close bonds lasting over many years. These "friendships" as we would define it for humans were between pairs of baboons and persisted over long periods of time. Smuts' close observations of these baboon friendships were based on empirical observations of the number and frequency of grooming bouts between individuals; proximity during feeding, resting, and travel; and for some friendships, the number and frequency of copulations between male and female friends, although some friendships remained platonic. Smuts' research further revealed that the choice of whom to copulate with in a baboon troop was not random. The patterns suggested that females more often chose to mate with males who were her friends. These male friends were individuals with whom she selectively spent significant amounts of time in close proximity without fear, groomed more often compared to others, and allowed them to play with her offspring (Smuts 1985).

Through Smuts' insight into another primate species' patterns of sociality, her detailed and empirical observations from within a theoretical framework of behavioral analysis, and anthropomorphic application of human psychological principles, her research substantially shifted the perception of nonhuman primate social behavior within the fields of primatology, animal behavior, and animal cognition.

Anthropomorphism and Anecdotes

Where do we draw the line between objective and subjective observations and interpretations of behavior? Is one observation sufficient (i.e., an anecdote) or is that deemed too subjective? If an observation of a behavior is made just once, is it a data point or an anecdote? Should it always be the requirement to have repeated observations of a behavior under controlled experimental conditions that are purely objective and empirical, and open to being tested statistically against the random probability of its occurrence? Ethological methods for studying animal behavior uses repeated observations of the same set or sets of behaviors to accumulate data for statistical analyses. It takes time to become an experienced observer who accurately assesses the frequency of each behavioral occurrence. However, there are types of behaviors that are rarely and/or only very briefly displayed, as occurs in highly effective types of problem solving and innovation. The existence and significance of these rare behaviors may be diluted, and/or lost, in pursuit of an empirically driven, repeated measures framework.

In his book, *Animal Intelligence* (1888), George Romanes used descriptive anecdotes that he deemed valid, received from individuals whom he considered to be experienced, reliable observers. From these anecdotes, he deduced patterns of insightful problem-solving abilities in animals. Later, Wolfgang Köhler (1925) in addition to assessing captive chimpanzees' cognitive abilities in controlled experiments, also used one-time observations of these apes' insightful problem-solving behaviors. Indeed, incredibly valuable insights have been derived from anecdotal evidence, often in the form of narratives, where an individual animal or animals demonstrate an isolated occurrence of an unusual behavior that can only or most easily be explained by attributing human-like cognition and/or motives. For example, Köhler's most referenced study of chimpanzee tool use in problem-solving involved providing the chimpanzees with sticks that if combined in the right order could create a longer stick to reach bunches of bananas that had been hung high up. Boxes for stacking were also

provided, to help reach the bananas with the elongated stick. One of the chimpanzees, Sultan, after repeated efforts to attach two shorter sticks together, eventually fitted them together into a longer stick. He also placed boxes on top of one another, and so was able to retrieve the bananas. This solution demonstrates insight into the problem and shows innovation by combining the elongated stick with the stacked boxes to achieve the height necessary to obtain the food. Not only are anecdotes such as this one useful for understanding behavior in a particular context, it also provides an avenue for theoretical investigations of broader behavioral patterns and for examining intelligence across species as an adaptation.

In their two book series, *Machiavellian Intelligence* (1989, 1997), Byrne and Whiten accrued anecdotes of accurately observed single instances of primates' innovative problem solving and/or cases of deception. It would be very difficult to create controlled experiments to collect these kinds of empirical data on a repeated basis. When combined, these large numbers of accurately observed events by reliable observers (primatologists) formed a significant database and paralleled that of repeated measures and observations. Through this method and the insights derived, Byrne and Whiten were able to generate new hypotheses and questions about the evolution of primate intelligence, to postulate differences in social intelligence across phylogeny, and to identify potential selective pressures on intentional manipulation of social partners (e.g., as occurs in deception).

Another example is the comprehensive avian IQ index that was created by Louis Lefebvre (Lefebvre et al. 2004) based on "the reported frequency of behavioral innovation as an operational measure of cognition" (p. 233). Lefebvre stated that he and his team look for patterns in reported anecdotes that help explain and validate innovative and intelligent behavior in birds that otherwise appear as individual occurrences. When assembled into a cohesive set of independent and individual observations, it becomes clear that the patterns of intelligent behaviors occur would not have been predicted from

previous theoretical positions on avian behavior and innovative problem solving. Moreover, the behavioral flexibility displayed by some individual birds and species was found to be an essential adaptation for survival compared to others who did not demonstrate this adaptive capacity. Based on the combined anecdotal evidence, Lefebvre et al. (2004) writes that, "In birds, innovation rate is associated with the ability of species to deal with seasonal changes in the environment and to establish themselves in new regions, and it also appears to be related to the rate at which lineages diversify. Innovation rate provides a useful tool to quantify inter-taxon differences in cognition and to test classic hypotheses regarding the evolution of the brain." (p. 233). Thus, summarized anecdotes and the process of anthropomorphic identifiers of intelligent behaviors in birds (and other species) provide opportunities to expand theoretical boundaries of our understanding of the evolution of problem-solving functions correlated with changes and/or differences in the brain, across species.

Anthropomorphism of Animal-Human Chimeras

Human-made artifacts in the archeological record were often wrought to resemble extraordinary nonhuman animals or chimeric creatures composed of a nonhuman animal morphed with a human. It is likely that the cultures that were responsible for these artifacts placed a value on animals as other than just as a means of survival (e.g., as food). Animals may have served as stand-in humans or human surrogates with special powers that superseded nature, potentially in a religious or spiritual context (Passariello 1999). Shamanistic powers, for example, are thought to derive partially from animal spirits that confer some of the animal characteristics and the special powers emanating from that animal to the human. This mixing of human and animal, as exemplified in the Lion Man Figurine (Smithsonian, <http://humanorigins.si.edu/evidence/3d-collection/>

[artifact/lion-man-figurine](#)), may have conferred the animal's powers in a kind of symbolic projection into the human psyche and social-religious-spiritual sphere (Passariello 1999).

Conclusion

Accuracy in understanding and predicting the behaviors of others, including nonhuman animals, requires both observational data and a conceptual framework in which to interpret those data. The conceptual framework most often involves the consideration of human intentions, thoughts, desires, emotions, and motivations. When these attributes are imposed, in exaggerated form, on nonhuman animals or even inanimate objects, it is labeled "anthropomorphic" in the pejorative sense. However, when we apply our understanding of psychological principles to nonhuman animals (e.g., in research), it can also be described as "anthropomorphism" in a positive sense, and may lead to important insights and assist in generating novel theoretical frameworks and hypotheses to better understand other species' behaviors. Thus, anthropomorphism can take two main forms, one that inaccurately applies exaggerated human characteristics to nonhuman animals and inanimate objects, and another where it is used as a critical tool to investigate and construct a framework in which to explain/understand the behavior of other humans and non-human animal species. The division between subjectivity and objectivity largely parallels the division of an inaccurate application of anthropocentric qualities compared to an insightful projection into understanding behavior.

In summary, we are left with more questions than answers about the function of human's ability and desire to use anthropomorphism to explain their world: Is it possible to form truly objective representations of another species' behavior without using insight that we would apply in understanding another human or human society; insight that when applied to another species is referred to as anthropomorphism? And, is the anthropomorphic process necessary for survival, acting as a

filter through which individuals perceive and navigate their social and physical world?

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Anti-cuckoldry

► [Prevention of Infidelity](#)

Anti-cuckoldry Adaptations

- ▶ Psychological Evidence for Human Sperm Competition

Anti-cuckoldry Tactics

- ▶ Solution to Paternity Uncertainty
- ▶ Sperm Competition Tactics

Antigay Bullying

- ▶ Homophobic Bullying

Antimicrobial Hypothesis

- ▶ Antimicrobial Hypothesis, The

Antimicrobial Hypothesis, The

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Synonyms

Antimicrobial hypothesis; Cultural transmission;
Pathogens; Taste preferences

Definition

Drawing from the insights that bacterial growth is promoted by higher temperatures and spices

can inhibit or kill bacteria, the antimicrobial hypothesis of spices argues that cultures in warmer regions of the world are more likely to include spices in their recipes (and benefit from the antimicrobial properties of spices) relative to cultures in cooler regions.

Introduction

Pathogenic microbes, such as disease-causing bacteria and viruses, have posed a threat to the health and reproduction of many organisms for as long as microbes have existed, thereby constituting a significant recurring adaptive problem (Thomas et al. 2012). In turn, the selection pressure imposed by pathogenic microbes gives rise to various physiological and behavioral adaptations that facilitate the prevention of microbial infections, such as the immune system, feelings of disgust, and avoidance instincts (e.g., Curtis and Biran 2001; Tybur et al. 2016). The cultural transmission of practices that may help to ward off pathogenic microbes (as well as a corresponding favorability toward those practices) also constitutes another important line of defense. The current entry discusses one such cultural practice – the use of and taste for spices (Billing and Sherman 1998) – as an important accompaniment to humans’ array of antimicrobial defenses.

Spice Use Through the Ages and Across Regions

Spices refer to dried and aromatic plant substances whose primary food function is for seasoning and flavor rather than nutrition. These include seeds (e.g., cardamom), fruits (e.g., chilli pepper), leaves (e.g., cilantro), and roots (e.g., garlic). Spices derive their distinctive flavors from chemicals that are produced in order to fend against pathogens and parasites. Food spicing may have originated from early hunter-gatherers who unwittingly improved the flavor of their game by encasing the meat in certain types of leaves. Over time, early

civilizations began realizing the useful properties of spice plants (Rosengarten 1981; Tapsell et al. 2006). For example, the Ancient Indians (approximately second to fourth century BC) documented their discoveries of the antiseptic and digestion-aiding properties of spices such as sesame and cloves, while the Ancient Egyptians (~1500 BC) initiated a classification that grouped spices such as garlic, onion, and thyme as health boosters. The antimicrobial prowess of spices was also well recognized as can be seen from their extensive use in the embalming and preservation of bodies. Spices progressively became high in demand. When the Goths besieged Rome in 408 AD, they demanded a ransom of 5,000 pounds of gold and 3,000 pounds of pepper. Marco Polo, Christopher Columbus, and Hernando Cortes count among the famous explorers who changed history while seeking faster routes to the spice-rich Indies.

Although spices have been used in food preparation throughout the world for centuries, patterns of spice use differ considerably across regions. More specifically, spice use varies as a function of regional temperature such that countries with higher average temperatures tend to incorporate more spices into their recipes (Billing and Sherman 1998). This pattern paints a puzzling picture. First, it is not clear why spices would be popular only in some cuisines despite their health benefits and usefulness as a preservative (Tapsell et al. 2006). Second, given that spices can make people feel hot and perspire, it seems counterintuitive that cultures in warmer regions would exhibit a stronger preference for spices. Third, although the use of spices is most often attributed to their role as a flavor enhancer, this does not address the ultimate, evolutionary question of why people would find foods tastier when flavored with spices. In light of these puzzles, and drawing from the insight that higher ambient temperatures are more conducive to bacterial growth (Genigeorgis 1981), Billing and Sherman (1998) hypothesized that the use of spices arose as protection from food-borne bacteria that are more likely to thrive in warmer climates.

Antimicrobial Hypothesis of Spices

Recipes containing meat products that have been kept for some time at room temperature in hotter, tropical climates exhibit a substantial hike in bacterial concentration (Genigeorgis 1981). Noting both the tendency for bacteria to proliferate at higher temperatures and the antimicrobial properties of spices, Billing and Sherman (1998) argued that spices are popular in warmer regions because they help to kill or inhibit food-spoiling bacteria, thereby contributing to the health and reproductive success of people who find their flavors enjoyable. To test the hypothesis, they examined 4,578 traditional meat recipes from a sample of 36 countries for the number of spices used out of 43 spices. Meat recipes were selected for analysis over nonmeat recipes (e.g., vegetable recipes) because of their greater likelihood of breeding bacteria and carrying food-borne illnesses. The number of spices used in the recipes was then compared between countries with varying average temperatures.

The results supported the prediction that countries with higher average temperatures add more spices to their recipes relative to countries with lower average temperatures. The researchers found that in ten of the hot-climate countries, namely, Ethiopia, Kenya, Greece, India, Indonesia, Iran, Malaysia, Morocco, Nigeria, and Thailand, every meat-based recipe included at least one spice. By contrast, in cold countries such as Finland and Norway, respectively, 19 of 62 and 25 of 77 meat-based recipes did not use any spices. The results also showed that higher average temperatures (such that food-borne pathogens would be most prolific) were associated with the use of spices with stronger antimicrobial effects. A follow-up study found that, on average, vegetable-only recipes called for significantly fewer spices than meat-based recipes (Sherman and Hash 2001), thus lending further support to the argument that spice use is aimed specifically at treating food that is more prone to spoilage.

Billing and Sherman (1998) examined the alternative hypothesis that inhabitants of warmer tropical regions eat more spices simply because

more spice plants are grown there. They analyzed the distribution of spice plant growth within countries and found no correlation between average temperature and the number of spices grown in a country. This suggests that some warmer regions appear to favor the use of spices even though the inhabitants of those areas do not necessarily have a larger proportion of local spice plants to select from.

The antimicrobial hypothesis can be extended beyond temperature and spice use to other factors that influence the risk of food-borne illnesses, such as raw or undercooked recipes, and the use of other types of seasoning with similar antimicrobial effects, such as olive oil and vinegar (Medina et al. 2007). For example, a study by Ohtsubo (2009) showed that recipes containing uncooked products, such as Japanese dishes consisting of raw fish or meat (e.g., sashimi), are more likely to incorporate the use of vinegar than recipes containing cooked or heated food. Likewise, meat dishes made from raw ground meat, such as the European steak tartare dish, also tend to include more seasoning in their preparation.

Another important contribution of the antimicrobial hypothesis is its ability to account for why humans would have a taste for spices in the first place. Chilli peppers, for example, produce chemicals that create a painful burning sensation when exposed to bodily tissue and are typically avoided by herbivorous animals. Despite the aversive effects of contact with chilli peppers, people can enjoy eating them. From an evolutionary perspective, humans may have adapted a taste for such flavors to motivate the consumption of spices and reap the associated health benefits. That said, considerable variation exists in people's liking of spicy food. For example, Indian dishes feature strong flavors contributed by the wide variety of spices used, whereas Scandinavian cuisine tends to be bland. Correspondingly, Scandinavians may be less tolerant of spices while Indians enjoy them. This facultative proclivity for spices therefore reflects our ability to adaptively calibrate preferences in response to environmental conditions.

Conclusion

Humans have, for centuries and arguably longer, exploited the chemicals designed to safeguard plants to season food and prevent food-borne illnesses. The antimicrobial hypothesis of spices provides an important evolutionary account for the peculiar correlation between spice usage and regional temperature. Examples of other antimicrobial food preparation practices that extend beyond the use of spices in hot climates, such as the treatment of raw recipes with vinegar, attest to the general validity of the hypothesis. These examples show that under the veneer of cultural differences in taste preferences, which are undoubtedly an important proximate reason for the different varieties of cuisines on offer, lies key survival and reproductive concerns at a fundamental level.

Cross-References

- ▶ Cultural Differences
- ▶ Cultural Transmission
- ▶ Cultural Variation
- ▶ Ecological Influences
- ▶ Ecology
- ▶ Pathogen Protection
- ▶ Pathogen Resistance
- ▶ Pathogen Risk

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essay *On the Suffering of the World*, Schopenhauer said that the general rule of life is misfortune and suffering (1851). Because people are aware of the impending threat of death, they must struggle against both pressure from time and, in other moments, boredom or despair. As a result, Schopenhauer considered humans to not just be sentenced to death but also to life. He considered the state of nonexistence to be a blessed calm of nothingness, a stark contrast to the disturbance of life. In fact, Schopenhauer questioned whether the human race would still exist if the decision whether or not to have children was completely free of sexual impulses. He thought that if people were thinking rationally, they would choose to forgo having children in order to spare new people from being burdened with life (Schopenhauer 1851).

Antinatalism

- Debating Procreation (With David Benatar)
- Permissibility of Reproduction

Anti-natalism

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Definition

Anti-natalism is the ethical view that it is immoral for people to have children. This principle has been supported and defined in various ways, and this entry summarizes what the construct is, some reasons for why anti-natalism may not be a popular idea, and why some people might choose to postpone or forgo procreation.

Introduction

While the origins of the term anti-natalism are unsure, much of the ideas found in anti-natalism were expressed historically by the nineteenth-century philosopher Arthur Schopenhauer. In his

The Philosophy of Anti-natalism

In the twenty-first century, anti-natalism has been popularized by South African philosopher David Benatar. According to Benatar (2006), people should not reproduce because being brought into existence is always a grave harm; in his view, existence affords more cost than benefits. While life contains some good, much of life is bad, and everyone that comes into existence suffers in some way. Many people live in poverty or with disability; most people will experience a slow decline and various diseases later in their life, and everyone will eventually die. Benatar (2017) compared everyday life to a hamster on a wheel; much of people's time is spent doing mundane tasks in order to keep them alive and comfortable, such as sleeping, going to work, and eating.

The only way for someone to not experience suffering is to not be born at all (Benatar 2006). Those who do not exist cannot suffer from any loss of the good because they cannot experience its absence; furthermore, it is good that they miss out on the suffering that they would have experienced if they had been born. Any amount of suffering is a net bad, because that suffering could have been avoided by never existing (Benatar 2006). Even if there were much less suffering than there currently is, procreation

would still be wrong as all people would still be guaranteed to suffer some, which they would have avoided if they were never brought into existence. So why do individuals continue to reproduce and pass on their genes, continuing this cycle of human misery?

The Human Bias Toward Optimism

According to Benatar (2006), people are not reliable at assessing the quality of their own lives, and this is because humans have a bias toward optimism about the human condition. The optimism bias is a common phenomenon where people overestimate how likely they are to experience positive events and underestimate how likely they are to experience negative events (Sharot 2011). A moderate level of optimism can be beneficial in motivating people to adapt their behaviors in order to reach a future goal, and optimism has been shown to promote physical and mental health. A bias toward optimism has been shown to motivate people to persevere toward goals that, though they are unlikely to be achieved, would be beneficial to the person if they were achieved (Sharot et al. 2007). Haselton and Nettle (2006) argued that it is better to be optimistic so long as the cost of the false alarm for a positive event is relatively low compared to the cost of missing out on an opportunity that would enhance the individual's fitness.

Humans Choosing to Delay and Forgo Reproduction

For the most part, research has not been conducted on what influences people's opinions on whether or not others have a moral responsibility not to reproduce, though some factors cause individuals to accelerate or delay (and sometimes forgo) their own reproduction. For example, reminders of personal mortality cause people from a higher SES (socioeconomic status) background to report a desire to postpone reproduction until later in life and, conversely, cause people from a lower SES background to report a desire to accelerate reproduction (Griskevicius et al. 2011). People that

desired to postpone reproduction, likely having fewer children in the process, reported wanting to achieve a better position to care for any children they may eventually have by attaining more education and work experience (Griskevicius et al. 2011). Women with higher levels of education desired to delay reproduction longer than women with lower levels of education (Tavares 2016). Additionally, that research found that women who were higher in openness to experience desired to delay reproduction longer.

Certain personal factors are also linked to people choosing to forgo reproduction entirely. Early in life both more intelligent young adult men and women, as measured by childhood intelligence, were more likely to desire to remain childless (Kanazawa 2014). Though, later in life, only more intelligent women were more likely to have remained childless, more intelligent men were not more likely to remain childless for life (Kanazawa 2014). This sex difference in desire for children has been shown elsewhere. Fritzsche et al. (2007) found that reminders of death led men to report desiring to have more children than they desired to have when not being reminded of death, but reminders of death did not cause a difference in the number of children women desired having.

Conclusion

This entry has covered the philosophical thought of anti-natalism and some factors that can cause people to delay or forgo reproduction. Anti-natalism was covered using the work of philosophers Arthur Schopenhauer and David Benatar. People's proclivity to see their lives as being better than they really are was described using research conducted on people's bias toward optimism, which can work to increase their fitness. The desire of some people to delay having children was described using research conducted on childhood SES level and amount of education. And sex differences in people's desire to have less children and forgo reproduction entirely were explored using research conducted on intelligence level and reminders of mortality. Though

research has been conducted on why people might choose to delay or forgo reproduction, thus defying an evolutionary drive to reproduce, more investigation needs to be done to examine why people might hold anti-natalist beliefs.

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Antinatalism Key Text

- ▶ Better Never to Have Been

Antinatalist Philosophy of David Benatar

- ▶ Better Never to Have Been

Anting

A

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Synonyms

Einemsen (German)

Definition

The deliberate application of ants and ant secretions (or other pungent substances) by birds to their plumage and skin.

Introduction

Anting (or *Einemsen*) is a term originally used by ornithologists in the 1930s to describe the application of ants by birds to their plumage (Whitaker 1957; Chisholm 1959). Birds perform anting behavior presumably to apply to their feathers or skin some substance produced by the ants (formic acid or other secretions). With the passage of time, the term has been used more broadly to include application to the plumage of objects or substances other than ants (e.g., citrus fruits, mothballs, burning cigarettes), because the postures and movements performed by actively anting birds are similar regardless of the object used. This prompted Simmons (1966) to distinguish “true anting” (the use of ants during the activity) and “anting with substitutes.” Regardless, anting is a more or less stereotypical form of anointing behavior. It is often categorized with other forms of avian maintenance behavior, such as sunning, bathing, and dusting (Simmons 1966), although not all researchers consider anting’s primary function to be for plumage maintenance.

Forms of Anting and Its Global Prevalence

Anting by birds occurs in two forms (Simmons 1957, 1966; Whitaker 1957). During active

anting, birds pick up ants (or other organic and inorganic objects) with their bill, often crushing the ants in the process, and dab or sweep them through the plumage of the wings and tail, particularly the undersurfaces; some species also sweep ants through other parts of the body plumage (breast, rump). During *passive anting*, birds stand, settle, or wallow on an aggregation of ants (an ant mound or other locations where ants are concentrated) with their wings and tails partly spread, sometimes provoking the ants to attack by poking at them with the bill or making stirring motions with the wings, and allow the ants to crawl through the plumage. The two forms of anting have also been termed, respectively, “ant-application behavior” and “ant-exposure behavior” (Simmons 1966). During active anting, birds may blink and use the nictitating membrane, shake and scratch the head, rub the eye on the shoulder, stamp the feet, lose balance, and tumble over. Passive anting birds may stand several times and resettle in new locations. Anting birds are often easier to approach than when engaged in other activities, suggesting that anting serves some kind of adaptive function that favors the behavior despite the increased risk to predation.

More than 210 bird species worldwide have been reported to ant (Simmons 1957; Whitaker 1957; Chisholm 1959; Craig 1999). It is particularly widespread among the Passeriformes (perching birds), perhaps not surprisingly as most extant bird species are members of this order. It has also been reported for a few species of at least nine other avian orders, although Simmons (1966) questioned whether reports for non-passerines represent true anting. Active anting is the form most often reported for the majority of passerines, although passive anting appears prevalent in some families comprised of larger species, such as Turdidae (thrushes) and Corvidae (jays, crows, and ravens). Most birds appear to practice only one form of anting, but both forms have been reported for a small number of genera and species (Simmons 1957, 1966), a pattern that may result from the difficulty of studying anting in wild birds and the unpredictability of the behavior.

Anting behavior probably evolved in relation to ants rather than any of the reported ant substitutes (Simmons 1966), such as citrus fruits. Ants favored by birds for use in anting typically are worker castes of species that do not sting but exude or spray chemicals for attack and defense (Groskin 1950; Whitaker 1957; Simmons 1966) and often involve ant genera in two subfamilies with global distributions: Formicinae (e.g., *Camponotus*, *Formica*, *Lasius*) and Dolichoderinae (e.g., *Iridomyrmex*, *Dorymyrmex*, *Tapinoma*).

Hypotheses for the Function of Anting

At least three broad hypotheses have been proposed as explanations for why birds ant:

1. *Food Preparation*: anting serves to remove distasteful chemicals from ants (specifically formic acid) before they are eaten. This hypothesis was favored by several early investigators (see Chisholm 1959). Recently, Eisner and Aneshansley (2008) showed that captive blue jays (*Cyanocitta cristata*) performed anting at a much higher rate prior to ingesting ants when presented with ants whose acid sacs were intact. Anting caused the ants to discharge their formic acid spray and empty the acid sac before they were eaten. When the same jays were presented with ants whose acid sacs were surgically removed, the birds almost invariably ate them without anting first. This research, when combined with prior studies cited in their paper, led Eisner and Aneshansley to conclude that anting is essentially a food preparation activity. However, this conclusion does not account for many other observations and controlled studies where birds failed to eat the ants after actively anting (Simmons 1957; Whitaker 1957; Chisholm 1959), nor does it address passive anting, where ants are allowed to discharge their chemical defenses and rarely get eaten.
2. *Feather Care*: anting serves some sort of feather maintenance function, such as
 - (a) suppression of arthropod ectoparasites

(feather lice, ticks, and mites), (b) suppression of feather-degrading bacteria and fungi, (c) removal of stale lipids from skin and feathers, or (d) decreasing skin irritation associated with feather molt. Formic acid is known to kill bird arthropod ectoparasites and suppress feather microbial growth under controlled conditions (Simmons 1966; Craig 1999; Revis and Waller 2004), but does not appear to be effective against either when applied in concentrations released by ants as a component of their secretions. Nor does the seasonal peak in anting by wild birds correspond to peaks in ectoparasite loads (Potter 1970). Thus anting to control ectoparasite and microbial infestations is not clearly supported by available evidence. Simmons (1966) proposed that anting may increase the flow of saliva for use in preening and that it would help in removing stale preen oil and other lipids. This possibility awaits experimental investigation, but anting often occurs during new feather growth, presumably a time when feathers are relatively free of stale preen oils and other lipids. Finally, there is evidence that peaks in anting by wild birds in some regions correspond to timing of molt (Potter 1970; Potter and Hauser 1974). Wild birds tend to ant while replacing feathers of the wings, tail, and belly, all of which are accessible to the bill, and they tend to sunbathe (sun) while replacing feathers of the head, neck, and back, which are less accessible to the bill. Wild birds also tend to ant during periods of high summer humidity shortly after heavy precipitation, which can induce simultaneous loss and replacement of feathers. Anting and sunning are thus considered by Potter and Hauser to be complementary comfort-motivated behaviors for applying heat (the thermogenic effect of formic acid or other ant substances, solar radiation) to soothe irritated skin. This remains a viable explanation for the function of anting, but a challenging one to test under natural conditions. Also, it is not clear how effective anting always is (particularly active anting) for exposing irritated skin to ant secretions, as birds sometimes apply ants to areas other than the base of

feathers (Whitaker 1957; Simmons 1966), where skin irritation should be located.

3. *Self-Stimulation:* anting serves to provide a purely pleasurable sensation. This hypothesis is the least favored by most investigators. Whitaker (1957) suggested that anting birds appeared to derive sensual pleasure during anting, possibly even sexual stimulation, as a result of the thermogenic effect of the ants. She noted that her captive oriole preferentially directed anting to the underparts of the tail and possibly the cloaca, and these body regions are also mentioned in other reports of anting (Simmons 1957; Potter 1970; Potter and Hauser 1974). The idea of a skin-stimulus function was also promoted by Chisholm (1959). Simmons (1966) argued against this hypothesis on evolutionary grounds, observing that selection would act against birds performing just for pleasure a stereotyped behavior in a place and manner which makes them much more vulnerable to predator attack. While it may be questioned whether or not birds derive (in a purely aesthetic sense) sensual or even sexual pleasure from anting, the central thesis of this argument is similar to that promoted by Potter and Hauser (1974) that anting serves to soothe irritated skin and thereby provides a pleasurable sensation to the anting individual.

Conclusion

The function of anting remains unclear. Studies under natural conditions are hampered by the (as yet) unpredictability of the behavior, so most close observational and experimental studies have been undertaken with captive or tame birds. Examination of accumulated opportunistic observations made under natural conditions reveals some patterns in anting activity, such as the relationship with feather replacement (Potter and Hauser 1974), but rarely are details available which might help clarify all circumstances promoting the behavior, and the suite of environmental variables associated with anting in the wild remains poorly documented.

Nevertheless, it seems from the accumulated observational and experimental data that anting probably serves more than one function, perhaps dependent on each individual bird and a proper combination of psychological and environmental conditions.

Cross-References

- ▶ Adaptation
- ▶ Bird Tool Use
- ▶ Corvids
- ▶ Nonhuman Tool Use
- ▶ What Makes a Tool

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Antipathy

- ▶ Prejudice

Antipredator Behavior

- ▶ Vigilance, Sentinels, and Alarms

Antipredator Calling

- ▶ Alarm Calling

Antipredator Vocalization

- ▶ Predator Confusion Hypothesis

Anti-predator Vocalization

- ▶ Alarm Calling upon Predator Detection

Antipredatory Behavior

- ▶ Alarm Calling Predicted by Inclusive Fitness

Antisocial

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Synonyms

Delinquent; Deviant; Dyssocial

Definition

Violation of societal standards, social norms, and/or established rules of behavior and action.

Introduction

The term antisocial describes actions that violate laws, social norms, and established standards of appropriate behavior, including destructive, violent, and aggressive behavior toward others. Personality characteristics of individuals who engage in antisocial behavior include impulsivity, a lack of empathy, and a lack of morality. The development of antisocial behaviors has been shown to be due to a complex interaction of genetic heritability, environmental, and contextual factors.

Antisocial

The term antisocial is generally used to describe actions that violate societal standards and laws or activities that do not adhere to established social norms. Saddock and Saddock (2007) describe antisocial behavior as actions that are “illegal, immoral, or both” (p. 891), adding that the presentation of antisocial behaviors vary in frequency and severity. Tuvblad and Beaver (2013) describe antisocial behavior as encompassing various possibilities of destructive behavior including behavior that causes harm to others, involves property damage or destruction, violates the rights of others, as well as violent and aggressive actions toward others. Historically, the term antisocial has been used to replace broad labels such as psychopathic and sociopathic (Silverstein 2007).

Specific personality characteristics have been identified in individuals who engage in antisocial behavior. Rasmussen (2005) outlined a number of characteristics that comprise the antisocial personality style, including a limited response to punishment; impulsive decision-making that does not involve a consideration of possible negative consequences; high activity level in the pursuit of a desired goal with a great deal of attention focused on personal gain; an inclination to act aggressively and unethically as a means to get their way; a disregard for the effect their actions have on others; and a willingness to

manipulate and lie to avoid negative consequences or obligations. Silverstein (2007) identified the key characteristics of the antisocial personality style as an “absence of guilt, lack of remorse, incapacity to form intimate or lasting relationships, an engaging or charming manner, shallow or insincere affective experience, and lack of concern about or empathy for other people” (p. 158). The core aspect of the diagnosis of antisocial personality disorder is represented by “a pervasive pattern of disregard for, and violation of, the rights of others” (American Psychiatric Association 2013, p. 659). This pattern may include a variety of features including a lack of conformity to social norms of lawful behavior, dishonesty, impulsivity, aggression and irritability, disregard for the safety of self or others, irresponsibility, and a lack of remorse (American Psychiatric Association 2013).

A variety of etiologies and risk factors have been proposed to explain antisocial behavior. These suggested causes and risk factors fall into individual, environmental, and social categories. The prevailing belief is that these factors interact to influence the expression of antisocial behaviors and personality characteristics. Although numerous studies have demonstrated a significant genetic influence on antisocial behavior, a more complete explanation highlights the interaction between genetic predisposition and environmental factors (Niv and Baker 2013). A dysfunctional family environment, which has also been identified as a prominent risk factor, “may also reflect common heritable vulnerabilities in both parents and children” (Paris 2015, p. 69). Contextual factors including living in violent and economically disadvantaged communities have also been found to contribute to the development of antisocial behavior (Chamberlain 2003).

Conclusion

The term antisocial has been utilized to label actions that violate the rights of others, involve damage or destruction of property, or represent

a deviation from established laws and societal norms. Empirical research has identified characteristics that comprise an antisocial personality style including a lack of response to punishment, cognitive and behavioral impulsivity, and a lack of empathy. Numerous risk factors have been identified as contributing to the development of antisocial behavior, with significant research supporting an interaction of genetic, environmental, and social factors.

Cross-References

- ▶ [Antisocial Personality Disorder](#)
- ▶ [Criminal Behavior](#)

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Antisocial Behavior

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Synonyms

Dysfunctional; Maladaptive; Undesirable

Definition

Antisocial behavior is a description for all behaviors, attitudes, and personality traits that people engage in that appear to be dysfunctional, in that they often have negative interpersonal and societal outcomes.

Introduction

Antisocial personality traits like psychopathy, narcissism, and Machiavellianism are correlated with sexual coercion (Figueiredo et al. 2015), criminality (Hare 1985), and deception (Azizli et al. 2016). Antisocial behavior can be presented alone or in the context of antisocial personality disorder (see Hashmani 2018a). Unsurprisingly, traits, like these, and the behaviors that may manifest from them have led professionals to strive to reduce these traits and their behaviors to relatively little avail. It may be that attempts to reduce antisocial behaviors and traits have generally failed because efforts to do so are based on a faulty premise. This premise is the often implicit, but dominant, cultural and academic epistemology known as the standard social science model. This model is built on philosophical “insights” from Rousseau who considered people to be “noble savages” corrupted by society and can be seen in modern clinical and social psychology in the form of “environmental determinism.” Environmental determinism is a philosophical position that

places contextual, cultural, and circumstantial factors as the primary and immediate cause of behaviors and values (including antisocial ones) and attempts to dismiss or downplay the role of genetics, biology, or physiology in accounting for human (but generally not nonhuman animal) behavior. Much of this work in psychology and the social sciences has been fueled by explicit and implicit blank slate thinking, which has been portrayed as flawed (Pinker 2003). In essence, when people who adopt this framework are asked why there is “evil” in the world, they reply: because of conditioning, bad childhood experiences, or modeling “bad” behavior.

Over the last 30 years, a challenge has been brought to this type of thinking in the form of evolutionary psychology (Confer et al. 2010), referred to as an interactionist paradigm (Crawford and Anderson 1989). That is, evolved and genetically rooted psychological adaptations interact with contextual factors to drive behaviors (i.e., solutions) that over evolutionary time have resulted in positive fitness benefits on average (populations evolve, not individuals, and in each generation variation is born). Therefore, the presence of individual differences in antisocial behavior does not challenge this model in a serious way.). These solutions may not fit modern concepts of “good” or “evil” as they can come at the cost of the group, which is implicitly treated as more important than the individual (Jonason et al. 2012). From this perspective, “bad” behavior or “evil” (There is an implicit rejection of religious notions of the origins of evil.) – antisocial behavior – might be considered pseudopathologies (Crawford and Anderson 1989) whereby they benefit the individual at the cost of the group. For example, deception, a common antisocial trait, often involves an individual engaging in a selfish act, without the concern of another’s well-being (Gneezy 2005). Although socially frowned upon, agentic pursuits and their motivations are of utmost importance to evolutionary researchers. In essence, this model makes one question what is meant by “evil” and suggests defining evil as anything that does not fit our group’s interest, even when such actions might serve the individual’s adaptive or social goals.

Evolutionary Models of Antisocial Behavior

This entry aims to detail modern thinking on evolutionary models of antisocial behavior. The authors will review how life history theory redresses the (relative) theoretical vacuum in classic and most modern research on antisocial behavior and traits. We will also attempt to review research on antisocial behavior (broadly construed) and highlight that while such behaviors might have undesirable consequences, they also have potentially “positive” outcomes as well.

A characteristic limitation of work on antisocial behavior has been its rather atheoretical, descriptive nature. Only recently have authors made attempts to understand antisocial traits and behaviors using a strong theoretical framework in the shape of life history theory (see Del Giudice 2014). This theory – taken from evolutionary biology – holds that organisms make trade-offs between efforts dedicated to mating and survival. The idea is that life is a zero-sum game whereby any energetic resources dedicated toward one task (e.g., mate searching) cannot be reallocated to other tasks (e.g., finding food). Researchers using a life history paradigm to understand antisocial traits and behaviors suggest that what is really reflected in these traits is trade-offs for short-term, mating (i.e., *r*-selected) decisions at the cost of long-term, survival (i.e., *K*-selected). This can explain some of the apparent illogical behaviors associated with antisociality. For instance, when presented with a smaller sum of money today or a larger sum of money in 1 year, those high on antisocial traits choose the former over the latter (Jonason et al. 2010). From a life history perspective, it is possible that people high on these traits have cognitive biases that nudge them to take smaller, immediate outcomes, because they are trading off “mating” needs against “survival” needs.

Informed by life history theory, there are a number of potential reasons for the emergence of apparently antisocial traits and behaviors. For instance, life history theorists (Frankenhuis and Del Giudice 2012) have identified three key dimensions to modulate how organisms allocate

their resources: *resource availability*, *extrinsic mortality-morbidity*, and *unpredictability*. Higher mortality-morbidity and unpredictability shift organisms toward *fast* life history strategies (e.g., a focus on reproduction, reduced investment in long-term bonding, and increased investment in short-term mating), which thereby promote risk taking, aggression, and other forms of antisocial behavior. Additionally, from an evolutionary perspective, natural selection favors mechanisms that produce risk taking when the fitness benefits outweigh the costs, even if these may be deemed socially unacceptable. Though these behavioral strategies may have unfavorable consequences to a subset of individuals, natural selection will still favor the traits if they increase fitness adaptability on average. Additionally, developmental mismatch contributes to the development of antisocial behaviors. An evolutionary developmental mismatch approach (rather than a developmental psychopathology model) suggests that children's negative stressors increase the adaptive fit between organisms and their environment. This perspective suggests that environmental mismatch in either direction (i.e., moving from a supportive to harsh environment and vice versa) evokes fitness costs (Cameron et al. 2005). More specifically, individuals who develop in harsh environments may on average achieve lower fitness than individuals in flourishing environments; nonetheless the former group should be better adapted to environmental harshness than the latter group (Frankenhuis and Del Giudice 2012). These aforementioned reasons are based on the premise that heritable tendencies interact with environmental contingencies in an adaptive heuristic framework to produce some output or response that attempts to maximize one's fitness given contextual limitations (Crawford and Anderson 1989).

Take, for instance, the commonly used distinction of "externalizing" and "internalizing" disorders (Del Giudice 2014). Externalizing disorders (e.g., oppositional defiant disorder, conduct disorder, and antisocial disorder) may represent *fast* life history trade-offs that result in impulsiveness, aggressiveness, and antisocial behaviors (Krueger et al. 2002). Moreover, these fast life strategies are correlated with numerous

pathological antisocial traits, such as negative affectivity, detachment, antagonism, and psychoticism (Jonason et al. 2017). Such traits may stem from harsh and unpredictable environments in childhood (Clark 2005). Conversely, slow life history strategies entail restricted sociosexuality, planning, responsibility, and altruism, with a tendency toward long-term romantic relationships. Rather than the externalizing spectrum, slow spectrum disorders often consist of obsessive-compulsive pathological traits (i.e., dysfunctional protective responses and hypersensitivity; Del Giudice 2014), anorexia nervosa, and depression (e.g., chronic guilt and hyperactive altruistic concerns; O'Connor et al. 2002).

The life history model also provides a priori reasons for sex differences in these types of behaviors. Ancestral men and women faced asymmetrical costs and benefits for how they solved adaptive problems. The benefits (e.g., more offspring) are greater for men who engage in exploitative social/sexual behavior (Jonason et al. 2009), whereas women who engaged in such behavior pay for reproductive costs (Jonason and Lavertu 2017). Unsurprisingly, men (compared to women) are more competitive, tend to seek dominance over others, and use physical aggression (Archer 2009), whereas women tend to be better characterized by antisocial behavior that acts to upregulate women's protective defensives (McGuire and Troisi 1998), as seen in obsessive-compulsive disorders, eating disorders, and depression (Del Giudice 2014).

The most fundamental implication of this model for antisocial traits is that even the most abhorrent behaviors can have adaptive benefits and adaptive costs (see Table 1). For instance, interpersonal aggression (e.g., Jones and Neria 2015) may have costs to both the victim (e.g., potential physical harm) and the perpetrator (e.g., punishment and possible jail time) but can result in increased reproductive fitness by protecting one's fitness interdependence partners and improving survival with the accrual of resources (Archer 2009). On the other hand, coalitionary aggression in chimpanzees can lead to numerous benefits to one's fitness including increased social bond strength, health, and

Antisocial Behavior, Table 1 A summary of ten common antisocial behaviors and their hypothetical adaptive costs and benefits

	Costs	Benefits
1. Aggression	Possibility of death from injury. Possibility of incarceration leads to being relinquished from society and, thus, reproductive opportunities	Increases attention from the opposite sex – seen as “competent.” Means of gaining power and having increased access to resources and potential mates
2. Bullying	Lack of mutual relationships formed – loss of protection/support if in danger or need of resources	Rising to the top of social hierarchies by gaining popularity. Reduces competition from others for desired resources. Develops physical self-protection from one’s “tough” appearance
3. Casual/exploitative sex	Increased risk of disease. Passing on poor/unwanted genes	Increased reproductive outlets. More offspring
4. Deception	If discovered as a liar, one may be socially shunned and ostracized by society	Self-deception: we deceive ourselves to protect against attacks to our happiness and well-being. Deceiving others is a means to achieving one’s goals, at the expense of others’ success
5. Domestic violence	Possible repercussions or attacks by other members of society. Possible physical injury from victim	Means of keeping one’s reproductive partner, rather than spending resources looking for another mate
6. Future discounting/impulsivity	Long-term needs and desires possibly ignored. May have chosen a smaller reward, rather than waiting for a larger reward (i.e., less gain if ignoring future discounting)	Short-term/immediate gains. If limited quantities of resources (e.g., scarce food), the impulsive individual will obtain the reward, while others fail
7. Psychopathy	Lacks ability to create close connections with others – can be viewed as an outcast by society. Can scare off potential mates	Lack of “normal” emotions (guilt and shame) can assist in selfish advantage. For example, these emotions can be disabling and mentally exhausting. Lack of empathy depersonalizes the victim and facilitates crime
8. Prejudice/racism	Limits reproductive outlets to one’s own race/social group. Limited options lead to less success and less possibilities to spread genes	In social living, one must respond functionally to the affordances of others. In order to obtain cooperative groups, one must recognize outsiders with potential threats
9. Substance use	Increased risk of death by substance abuse. Can lead to addiction, and, thus, one must allocate financial resources for more substances	Substances lower one’s inhibitions and fears. Can lower and mask physical or emotional pain
10. Theft	Possible risk of attack by victim. Risk of incarceration	Increased accumulation of resources and assets

number of offspring (Gilby et al. 2013). Moreover, psychopathy (see Table 1) can bring about numerous benefits, such as a reduction of *primary emotions* (e.g., guilt, shame, remorse), which may be emotionally exhausting and disabling, while also facilitating crime through depersonalizing the victim (Hashmani 2018b).

While it is easy to fixate on the costs, a more balanced model of antisocial traits and behaviors must include the benefits as well. Such a full understanding – while often unpalatable – has implications for theory and treatment. Understanding the function of the behavior and its

correlated traits should give better insight to “fixing” or reducing such tendencies in societies/individuals. For instance, although antisocial behavior can lead to negative consequences such as social rejection and criminality, there are also adaptive qualities that provide clarity on why these behaviors still persist in today’s society. For example, engaging in physical fights carries the potential to cause harm and the possibility of death; however, men who do not participate in fights increase the likelihood of being shunned from reproduction and, therefore, decrease reproductive success (Del Giudice 2014).

Alternatively, by exploiting and deceiving others in order to obtain a high social status, one can increase their own reproductive success, thereby providing evidence for these adaptive yet socially unwanted traits. These traits, in the eyes of society and clinicians, are deemed as dysfunctional and abnormal, yet from an evolutionary standpoint, they provide a way of maximizing reproductive success (Brüne 2014).

Conclusion

This entry approached the topic of antisocial behavior from an evolutionary perspective in order to accentuate the adaptiveness of these socially undesirable traits. We briefly discussed life history theory, where organisms must allocate their time to either mating or survival, and how these actions correlate with fast and slow life strategies. While highlighting numerous insights provided by an evolutionary approach (e.g., pseudopathology, externalizing disorders, and heritability), we discussed the adaptive costs and benefits of antisocial traits. The hope of this entry is to facilitate awareness to evolutionary psychologists in exploring the adaptive benefits of antisocial traits while also facilitating a framework for clinicians to understand the ancestral sex differences when treating men and women.

Cross-References

- ▶ [Personality Disorders](#)
- ▶ [Psychopathy \(Mealey\)](#)
- ▶ [Strength and Anger-Proneness](#)

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Antisocial Personalities

- ▶ [Psychopathy \(Mealey\)](#)

Antisocial Personality

- ▶ [Psychopathy](#)

Antisocial Personality Disorder

- ▶ [Psychopathy \(Mealey\)](#)

Antisocial Personality Disorder (ASPD)

- ▶ [Psychopathy](#)

Anxiety

A

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Synonyms

[Apprehension](#); [Nervousness](#); [Worry](#)

Definition

Distress or uneasiness of mind caused by fear of danger or misfortune

Introduction

Anxiety is a normal human emotion that is experienced by all in different situations and in different measures. Anxiety is often confused with fear, but the two are not synonyms. Fear is an alarm response to present or imminent danger, whereas anxiety is a future-oriented mood state associated with preparation for possible, upcoming negative events (Barlow 2002). Anxiety evokes fight-or-flight response and energizes a human being both psychologically and physiologically to deal with a situation or challenge. However, excessive or continued anxiety, which is disproportionate to the threat, presents in absence of any threat, or persists even when the threat has waned, is unhealthy and can become a troublesome problem for many. Such anxiety states could be acute as well as chronic and could lead to impairment in social, occupational, and other important areas of functioning.

Anxiety Disorders

Among psychiatric disorders, anxiety disorders are most prevalent (Kessler et al. 2010). As per estimates made in the year 2013, it is believed that

one in nine people all over the world has suffered from an anxiety disorder during previous year (Baxter et al. 2013). Common symptoms of anxiety disorders are:

- Psychological: worry, excessive thinking, feeling of being at the edge
- Physiological: headache, tremors, dry mouth, nausea, diarrhea, shortness of breath, palpitations, sweating (especially in palms), frequent urination

The symptoms could vary in frequency, intensity, and chronicity from person to person and also among different anxiety disorders. Detailed discussion about anxiety disorders is beyond the scope of this chapter; however, a brief description is provided in Table 1.

Diagnosis of anxiety disorder is reached after taking a detailed history that covers important aspects of onset and chronology of symptoms, triggers (if any), childhood and developmental history, and personality and coping mechanisms. Several self-report questionnaires are also available that can help in screening for anxiety disorders. Symptoms of anxiety could also be present along with other psychiatric disorders like depression, bipolar disorder, alcohol and other substance use disorders, etc. Also, many a times, such symptoms could indicate toward physical illnesses like thyroid diseases (more common in hyperthyroidism), heart diseases, respiratory diseases, seizures, and tumors of the endocrine system. Therefore, a complete assessment including check-up for physical illnesses is a must before declaring an

anxiety problem as a psychiatric disorder (Craske and Stein 2016).

Treatment of Anxiety Disorders

Anxiety disorders could be treated with drugs as well as through psychotherapy. Many a times, combined approach needs to be used to help a patient. Among drugs, antidepressants belonging to the class of selective serotonin reuptake inhibitors and serotonin-noradrenaline reuptake inhibitors are first line of treatment. Benzodiazepines though carrying some risk of abuse and dependence have robust efficacy for treating anxiety and work wonderfully when used under proper clinical advice and guidance (Craske and Stein 2016). Psychotherapy is carried out by trained psychiatrists, psychologists, psychiatric social workers, and psychiatric nurses. Commonly employed psychotherapies used to treat anxiety disorders include (Bandelow et al. 2015):

- Mindfulness-based therapy: This therapy uses a blend of Eastern Buddhist philosophy-based education and meditation to help the subject focus on the present instead of worrying about either the past or future.
- Behavior therapy: This involves gradual exposure of person to cause of anxiety and, thus, getting used to the same without getting anxious.
- Cognitive behavioral therapy (CBT): In CBT, patient is taught to recognize pathological

Anxiety, Table 1 Common anxiety disorders (American Psychiatric Association 2013)

Panic disorder	Characterized by recurrent, unexpected episodes of intense anxiety, palpitations, and fear of imminent death
Generalized anxiety disorder	Characterized by anxiety and worries in almost all situations (home, work, school, etc.)
Social anxiety disorder	Characterized by anxiety and/or avoidance of social interactions/situations and fear of negative judgment and embarrassment in social situations
Agoraphobia	Characterized by anxiety and/or avoidance of open spaces, closed spaces, crowds, or being alone outside home
Specific phobia	Characterized by anxiety attached with specific objects (which are otherwise not dangerous) like certain animals/insects, blood/medical procedures, height, etc.
Separation anxiety disorder	Characterized by anxiety about separation from attachment figures that is inappropriate to age

feelings, thoughts, and behaviors and to replace those with positive and helpful thinking.

- Family therapy: This treatment helps family members to communicate and deal with conflict in healthy ways.
- Biofeedback: This is done with help of bio-feedback machine which provides feedback of body functions and helps the patient to achieve control over the same.

Along with specific therapeutic measures, many general activities can also help in managing anxiety disorders. These include deep breathing exercises; muscle relaxation exercises; balanced healthy diet; life changes to reduce stress; avoiding overuse of alcohol, caffeine, and nicotine; and participating in support groups.

Conclusion

Anxiety is a normal emotion and, when excessive, could develop in pathological states, i.e., anxiety disorders. Anxiety disorders could be disabling and dysfunctional for many but are treatable. Treatment includes drugs and psychotherapy.

Cross-References

- [Anxiety Disorders](#)
- [Correlates of Fear](#)
- [Fears and Phobias](#)
- [Social Anxiety](#)
- [Stranger Anxiety](#)
- [Stress Reduction and Mental Health](#)

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Anxiety (Randolph Nesse)

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Synonyms

Anxiety disorders; Evolutionary psychiatry;
Threat detection systems

Definition

From an evolutionary perspective, anxiety can be considered as a psychological hazard-detection system. In uncertain environments, the costs of responding to false cues of danger are often minuscule as compared to those resulting from undetected threats. Therefore, the anxiety response has evolved a bias toward false alarms under conditions of uncertainty. We discuss general and specific types of anxiety responses, underlining how the nature of these are often determined by the particular types of threats in the environment.

Introduction

Anxiety disorders are among the most common psychiatric disorders, with the global point prevalence estimated at 7.3% and lifetime prevalence reported as high as 33% in some countries (Baxter et al. 2013; Bandelow and Michaelis 2015). They refer to a series of DSM (*Diagnostic and Statistical Manual of Mental Disorders*) recognized mental disorders such as generalized anxiety, social anxiety, phobias, and obsessive-compulsive disorders. In clinical cases, anxiety tends to be unnecessary, excessively frequent, and severe; nevertheless, in certain circumstances, an anxiety response is expected and non-pathological. To fully understand pathological anxiety, it is essential to first consider the evolutionary function of the normal anxiety response, from which the vulnerability to mental illness stems. While the field of psychiatry has considerably advanced in deciphering the physiological mechanisms underpinning anxiety, ultimate explanations remain relatively unexplored in modern medicine.

Nesse rightly notes, “One hundred and fifty years after publication of *The Origin of Species*, new advances demonstrate the utility of evolutionary biology in medicine, but few physicians and medical researchers have taken a course on evolutionary biology, and no medical school teaches evolutionary biology as a basic science for medicine. It is as if engineering students never learned physics” (Nesse et al. 2010). He has developed an evolutionary checklist of the reasons for our susceptibility to illness, with three overarching explanations: selection is

too slow, there are trade-offs and constraints on selection, and apparent defects are in fact useful (see Table 1, Nesse 2004).

The principal evolutionary explanation for anxiety rests on the last point, which stresses that anxiety is a useful defense; and under conditions of uncertainty, excessive anxiety is usually less costly to fitness than insufficient anxiety. This entry introduces error management theory to explain how certain cognitive biases can be favored by natural selection. This is then applied to the domain of hazard-detection anxiety response, illustrated by Nesse’s smoke detector principle. Finally, the other two aspects of the checklist – time lags and constraints on selection – are briefly considered to illustrate the potential for dysregulation and misfiring of the anxiety response.

Anxiety as a Useful Defense

Error Management Theory and Cognitive Biases

Though the set of heuristic procedures constituting our cognitive function have been fine-tuned over millions of years, conditions of uncertainty make errors unavoidable. Signal detection theory (Green and Swets 1966) notes that in our perception of a situation, we can form four kinds of beliefs: two being accurate representations of the situation, a signal being present in reality and the organism detecting it (hit), there being no signal (just noise) and the organism detecting none (correct rejection); and two being errors in our judgment, a signal being present but the

Anxiety (Randolph Nesse), Table 1 Nesse’s six reasons framework for why our bodies aren’t better designed against anxiety disorders. (Adapted and modified from Nesse 2004)

Selection is too slow

The body is poorly adapted to modern environments
Older threats might not exist, but defenses against them do

Selection cannot do everything

Trade-offs between better-equipped defenses and aversive mental states
Constraints on cognitive design

What appears to be a defect is actually useful

Defenses are useful even if aversive
Defensive traits can increase reproduction, even if not health

organism not detecting it (miss), there being no signal present but the organism detecting one (false alarm; Table 2).

Cognitive biases refer to systematic errors in our judgment that are domain-specific. These biases, as understood by the error management theory, have evolved to promote behavioral responses that will, on an average, maximize fitness under conditions of uncertainty (Haselton and Nettle 2006). More specifically, in scenarios where the costs of false-positive and false-negative errors have been asymmetric over evolutionary history, natural selection has favored those biases which lead to making the least costly error. Nesse has applied this framework to the domain of hazard-detection and the anxiety response (Nesse 2005).

Biases in Anxiety and Hazard-Detection

In the case of hazard-detection systems, misses (false negatives) are often much more costly than false alarms (false positives). Hence these systems, whether designed by human engineering (e.g., smoke detectors) or natural selection (e.g., cough, immune responses, anxiety), tend to systematically overestimate the presence of a hazard, as illustrated by Nesse's *smoke detector principle* (Nesse 2005). Owners of a "paranoid" smoke detector pay the cost of having to respond to false alarms, but with the benefit that they are unlikely to incur the financial and health costs associated with not responding to a real fire. In the case of an "optimistic" smoke detector, these costs and benefits are reversed. The cost-benefit ratio in this case is far more favorable in the first situation ($B_{\text{paranoid}} : C_{\text{paranoid}} > B_{\text{optimistic}} : C_{\text{optimistic}}$), explaining

why it is useful to design smoke detectors as "paranoid," i.e., overcautious. The optimal sensitivity is achieved at the point where the marginal protective benefit is equal to the marginal cost of responding to more false alarms.

Emotions are psychological adaptations that function to motivate fitness-maximizing behavior in a flexible context-specific manner. In the context of hazard-detection, anxiety is the relevant emotion, which can be expressed in different forms. Each subtype of anxiety can be protective against a specific type of threat, for example, escape/avoidance in response to predators in the environment or submission/ appeasement in cases of social anxiety where an individual fears ostracism (Nesse 1994). In much the same way that a smoke detector is a human-engineered device designed to encourage a defensive behavioral response to a fire (leaving the building), anxiety can be thought of as a biological hazard-detector stimulating defenses (such as vigilance and physiological arousal) in response to potential threats in the environment. Therefore, it too has been selected to systematically make false positive rather than false negative errors, making us susceptible to disorders where anxiety at the mere hint of danger is common (Nesse 2004).

Given the emphasis of psychiatry on mental well-being, there is a tendency to focus on the benefits of positive affect and costs of negative affect. However, given that the currency of natural selection is genetic fitness, some traits which harm our well-being can still evolve if they enhance our reproductive success (Nesse 2015). So even though the cost of protective responses can be high in individual instances and even entail associated suffering, the mechanisms serve us in

Anxiety (Randolph Nesse), Table 2 Signal detection theory – four types of belief

Situation Signal Detection	Signal Present (Signal + Noise)	Signal Absent (Noise Only)
YES	True positive (Hit)	False Positive (False Alarm)
NO	False Negative (Miss)	True Negative (Correct Rejection)

survival. It is, thus, important to consider the overlooked (fitness) benefits of negative affect and costs of positive affect (see Nesse 2004 on diagonal psychology). The smoke detector principle illustrates the survival value of false alarms, explaining why some occurrence of unnecessary anxiety, although unpleasant, is to be expected from an adaptationist stance. Indeed, epidemiologic evidence suggests that long-term survival in people with low anxiety proneness is lower than those with medium levels (Bateson et al. 2011). From this perspective anxiety can begin to be regarded as a design *feature* rather than design *flaw* (Haselton and Nettle 2006).

Selection Is Slow and Subject to Constraints

Natural selection is unguided and slow, and there is usually a time lag between environmental change and biological adaptation. Given the stark differences between modern environments and those encountered by our ancestors for the majority of our evolutionary history, the anxiety response is prone to misfiring. This can result in extreme anxiety responses to stimuli that now carry little risk or are rarely encountered, as well as acceptance of some evolutionarily recent dangers with too much equanimity. The objects of phobias clearly demonstrate this – we have too much fear of spiders and snakes but too little fear of driving fast, saturated fat, and cigarettes (Nesse 1994).

Even plastic features of our psychology are subject to cognitive constraints, and exposure to environmental threats during critical periods in development can have long-lasting psychological effects, even if the threat is absent in later life. Though this early life environmental calibration is energetically more economical than lifelong plasticity, it can also provoke unnecessary and excessive anxiety if individual circumstances change substantially. It is well established that psychosocial stressors such as violence and neglect in childhood are strong predictors of anxiety disorders in adulthood, irrespective of later life improvements in social environment (Heim and Nemeroff 2001).

Conclusion

Anxiety helps in preparing an organism for dealing with threats at the physiological, cognitive, and behavioral levels, and from an adaptationist stance, false alarms are to be expected. If a drug were created that abolished all anxiety, it could be as harmful as a drug that induced anxiety of crippling degree (Nesse 1994). An evolutionary approach considers the functional benefit of psychological processes, acknowledging that they have evolved to maximize fitness rather than well-being and are subject to the constraints and time lags of natural selection. Thus, the utilization of evolutionary psychology and cognitive-affective theories can positively further the field of psychiatry in understanding threat detection, precautionary responses, and “why diseases exist” (Stein and Nesse 2011). Though classical psychiatry generally tags intense or prolonged negative affect to be abnormal, irrespective of the situation, deficits in negative affect and excesses of positive affect are rarely recognized as disorders. An evolutionary perspective provides a more balanced view (Nesse 1994).

Cross-References

- [Anxiety Disorders](#)
- [Evolutionary Psychiatry](#)
- [Social Anxiety](#)

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Anxiety Disorders

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Synonyms

Anxiety; Defense regulation; Fear; Threat detection

Definition

Anxiety disorders are a class of mental health conditions that include persistent and excessive feelings of anxiety or fear as a core feature (American Psychiatric Association [APA], 2013). Anxiety is typically associated with feelings of unease, restlessness, or concern about a future threat (APA 2013). Fear is typically associated

with a state of arousal in response to an immediate threat, either real or perceived (APA 2013).

A

Introduction

Anxiety is typically associated with unease, restlessness, or concern about the possibility of a future threat (APA 2013). In some instances the threat may be vague, unknown, or unidentifiable (Ranchman 2009). Fear is a response to an immediate object or situation that is threatening, or that an individual perceives to be threatening (APA 2013). Although the two are connected, fear is roused in response to an imminent threat and wanes once the threat is removed, whereas anxiety can be diffuse and may persist in the absence of any identifiable threat (Ranchman 2009). These emotional states are usually felt as something negative and unwanted. While most people experience appropriate levels of anxiety, some people experience very little anxiety while others experience debilitating anxiety.

If someone presents with anxiety or fear that is so severe or persistent that it causes considerable distress or functional impairments, then he or she may meet the clinical criteria for a diagnosis of an anxiety disorder (APA 2013). Evolutionary psychology contributes to the study of anxiety disorders by suggesting that their core features, anxiety and fear, are expressed because they provide an adaptive function when elicited in contexts in which an individual's fitness, or success contributing genes to the subsequent generations, is at risk (e.g., Marks and Nesse 1994). Additionally, evolutionary theory has provided a basis for models that describe optimal anxiety regulation and that explain why humans are prone to experiencing excessive anxiety.

The Anxiety Disorders

Anxiety disorders are characterized by distress or functional impairments caused by anxiety or fear that is immoderate or unwarranted given the circumstance or that persist beyond an appropriate period of time (APA 2013). Several disorders are

subsumed under the class of anxiety disorders, including separation anxiety disorder, selective mutism, specific phobias, social anxiety disorder, panic disorder, agoraphobia, generalized anxiety disorder, and substance- or medication-induced anxiety disorder (APA 2013). The 12-month prevalence of anxiety disorders in the United States is estimated to be 18.1% (Kessler et al. 2005). The majority of cases are classified as being relatively mild, but a considerable portion of the US population experiences moderate or serious symptoms (Kessler et al. 2005).

Treatments for anxiety include pharmacological and therapeutic interventions. Drugs commonly used to treat anxiety target neurotransmitters that mediate the expression of anxiety symptoms (Shah and Han 2015). Cognitive-behavioral therapy is the recommended nonpharmacological treatment method (Shah and Han 2015). Cognitive-behavioral therapy is more effective than current alternative therapies and has been widely adopted by clinicians (Ranchman 2009). Clinicians may recommend that both treatments be administered concurrently to help alleviate symptoms. In other instances, however, clinicians may decide that only one course of treatment is necessary. While evolutionary theory has provided a framework for understanding the function of anxiety and fear and has contributed to models that help account for humans' proneness to excessive anxiety, it has, at present, done little by way of advancing treatments for anxiety disorders.

Anxiety and Fear

Anxiety and fear, both negative emotions, are component parts of a cognitive and behavioral repertoire that motivates organisms to avoid incurring fitness costs (e.g., loss of life, injury, loss of social networks, loss of reproductive partners) and to mitigate fitness costs in circumstances when danger is unavoidable (Nesse and Ellsworth 2009). Although the two are often taken to be synonymous, they are distinguished by the presence or absence of a threat. Anxiety is a state of anticipation of danger that is yet to be encountered and is potentially unknown, whereas fear is an

emotional arousal response to a threatening being, object, or situation (APA 2013; Ranchman 2009). The behavioral patterns associated with fear and with anxiety are distinguishable. While fear readies an individual to cope with an imminent threat (e.g., fight or flee), anxiety prepares an individual to circumvent danger (e.g., remain vigilant, cautious, or avoidant) (APA 2013). Additionally, the neural activation associated with each emotional state is somewhat distinct (Öhman 2008). Anxiety can be seen as taking the principal role in anxiety disorders because, whereas fear responses are generally more time and location specific, much of the distress or functional impairment involved in these disorders is caused by a preoccupation with avoiding the feared being, object, or situation.

During periods of anxiety, people tend to exhibit heightened vigilance, they may be irritable, pace, experience difficulty sleeping, and be highly attentive to, or avoidant of, things that they believe to be related to their anxiety. Anxious individuals may ruminate on thoughts that something is wrong and may experience difficulty concentrating. Further, when faced with ambiguous indicators of threat (i.e., something that could be perceived either as threatening or nonthreatening), individuals who are in a state of heightened anxiety are biased towards perceiving a threat compared to nonanxious controls (Eysenck et al. 1991; Richards et al. 2002). Physical symptoms associated with anxiety can include changes in heart rate and in breathing, perspiration, muscle tension, and feelings of nausea.

Some researchers and clinicians emphasize a difference between trait anxiety and state anxiety (Spielberger 1966). Trait anxiety refers to the level of anxiety that an individual generally feels. State anxiety refers to the level of anxiety that an individual experiences at a particular moment and is potentially aligned with fear.

Fear is typically experienced only when a threat is perceived to be imminent. During periods of fear, people tend to experience intense arousal, tension, and feelings of dread. This arousal and muscular tension facilitates the escape from, or the defense against, danger; this is known as the fight or flight response (Cannon 1929). Fear is

usually localized to a time and place at which danger is present. Fear typically subsides once the danger is no longer present. However, anxiety may take the place of fear once the perceived danger is removed.

The Function of Anxiety and Fear

Evolutionary theorists have proposed that emotions are cognitive and behavioral patterns that have been shaped by selective forces because they increase fitness when elicited in appropriate contexts (Marks 1987). Emotional responses, such as anxiety and fear, have been described using the metaphor of computer programs (Nesse 1990). In the same way that computer programs are designed to achieve specific tasks, emotions adjust behaviors and cognitions to achieve specific goals. Anxiety and fear adjust one's behavior and cognition to prevent or reduce incurring fitness costs (Marks and Nesse 1994).

Anxiety and fear responses are advantageous in situations that threaten physical harm, death, social exclusion, damage to one's reputation or status, the loss of a sexual or romantic partner, or the loss of anything else connected to one's fitness (Marks and Nesse 1994). Specifically, anxiety affords the opportunity to avoid threatening situations. Fear provides the arousal necessary to escape or defend against danger and, in doing so, avoid or lessen associated fitness costs. It has been noted that, at times, fear causes immobility, which can reduce damage when an injury has occurred (Bracha 2004) and can prevent harm when faced with heights or predation (Marks and Nesse 1994). Fears and anxieties tend to be more pronounced when individuals sense that they are vulnerable to danger, or if humans have been vulnerable to a specific threat throughout evolutionary history (e.g., snakes, heights, separation from a social group) (Boyer and Bergstrom 2011; Neuberg et al. 2011).

When dealing with a potential threat, not all responses will yield equally desirable outcomes. Fortunately, humans are flexible, basing their responses on the nature of the perceived threat (Marks and Nesse 1994; Neuberg et al. 2011).

For example, an individual who is alone in an unknown area will vigilantly monitor the area for general signs of danger and may prepare to flee or fight if a threat is detected. A fight or flight reaction would be completely inappropriate, however, in a situation in which a socially subordinate person must continue to work closely with a socially dominant person. Instead, it is likely that the subordinate person will continually monitor the dominant's facial expression for signs of disapproval and may prepare to engage in submissive or appeasing behaviors to protect against negative social or professional ramifications (Trower and Gilbert 1989). Individuals who are keenly attuned to threats, and respond appropriately, will outcompete individuals who are less vigilant or respond inappropriately to threats.

Anxiety-Like Responses in Non-Human Species

Non-human animals commonly display defensive behaviors that are similar to those displayed by anxious humans. Non-human animals display signs of heightened vigilance when they perceive cues of danger (e.g., they will cease feeding, scan their environment, and remain still), they attend to threat cues, avoid perceived threats, and they will either attack or attempt to flee when faced with danger. Additionally, non-human animals that are in this anxiety-like state are more likely to respond to ambiguous threat signals as though they are threatening (Burman et al. 2009). Furthermore, drugs that effectively reduce symptoms of anxiety in humans similarly attenuate defensive behaviors in non-human species (Blanchard et al. 2011). Thus, the commonality between anxiety and defensive behaviors suggests that the two are related and are evoked to accomplish similar fitness goals.

Anxiety and Defense Response to Individual Threat Cues

It has been proposed that defenses are regulated via a response system that inclines animals to

assess and respond to threat cues in the environment, the so-called security motivation system (Szechtman and Woody 2004; Woody and Szechtman 2011). The authors proposed that animals continuously assess their environment and are sensitive to cues that, even subtly or indirectly, indicate danger. Once a threat cue is detected the security motivational system is activated. When the system is activated, animals will experience apprehension. This apprehension will evoke precautionary surveying of the area to acquire information about the potential threat. The security motivational system will deactivate only when animals engage in threat reduction behaviors, such as leaving the area, checking that no threat is present, or washing to remove a suspected contaminant. When a threat cannot be mitigated through behavioral means, humans may engage in ritual behavior (e.g., prayer, performance of superstitious practices) to regain feelings of control over their situation (Eilam et al. 2011).

Consistent with this model, individuals who believed that they were exposed to a contaminant reported elevated anxiety and demonstrated a change in heart rate, both of which persisted until they were able to engage in appropriate threat reduction behaviors (Hinds et al. 2010). It has been suggested that symptoms of obsessive-compulsive disorder (which was previously considered an anxiety disorder) are caused by an inability to feel satisfied that one's threat reduction behaviors have sufficiently removed the risk of danger (Szechtman and Woody 2006).

Optimal Threshold of Response to Cues of Threat

If someone were to respond to every cue that could possibly signal danger, he or she would have time and energy for little else. However, if someone fails to respond to real danger he or she may incur severe fitness costs. Consequently, threat response systems are under the influence of opposing selection pressures. If threat detection could operate perfectly, all stimuli would be accurately identified as either threatening or non-threatening, and no unnecessary costs would be

incurred. Such perfection cannot be achieved, however, because cues of the presence and severity of threats are often ambiguous. Signal detection theory has been used to describe how threat detection should be designed to optimally respond to threat (Nesse 2001). Signal detection theory is a mathematical technique designed to differentiate between a true signal and random background information in the face of uncertainty (e.g., Green and Swets 1966).

The general logic for signal detection theory, as it applies to threat detection, follows from the understanding that individuals are continuously receiving information (i.e., sensory stimuli) from their environments but much of this information is nonessential "noise." Individuals must make judgments about what information is important and requires a response and what information is unimportant. Making such judgments proves challenging because signals of threat are often ambiguous. Consequently, individuals must establish a threshold at which a signal will elicit a defense response. Below this threshold, stimuli will be considered noise and will be ignored.

If the cost of failing to respond to a threat and the energetic cost of responding to a threat were equal, signals that could indicate threat should elicit a defense response at approximately chance level (in the same way that one would guess the outcome of a coin flip). However, although individuals waste resources when they unnecessarily engage in defensive behavior, the cost of failing to engage in necessary defense behavior, even once, could result in fitness losses (e.g., injury, loss of life, loss of social networks, loss of reproductive partners). Nesse (2001) mathematically demonstrated that, if the cost of failing to respond to a threat cue were greater than the energetic cost of defense, selection would favor a system that errs on the side of excessive responding.

Nesse (2001) suggested that this principle could be understood using the metaphor of a smoke detector and has, thus, been called the smoke detector principle. If a smoke detector sounds whenever someone is cooking, a lot of time will be wasted attending to these false alarms. Yet, it is essential that a smoke detector sounds each time there is a real fire. An optimal

smoke detector should reliably catch every fire and will, thus, permit false alarms in the interest of achieving this level of sensitivity. Similarly, it is essential that an individual detects real threats, but, to achieve this sensitivity, false or unnecessary responses will occur. As a consequence, an optimally working defense regulation system permits vulnerability to excessive expressions of anxiety.

Exactly where this threshold needs to be set to optimally detect threats will vary based on an individual's circumstance. Individuals in dangerous environments, and individuals who are particularly vulnerable to certain threats, should have relatively low response thresholds and, therefore, will respond to a greater number of false alarms (Bateson et al. 2011). As such, these individuals are expected to frequently experience excessive or unwarranted anxiety. This reasoning may help account for some of the seemingly unrelated correlations between anxiety disorders and individual or demographic characteristics (e.g., correlations between anxiety symptoms and status as a discriminated minority member, an individual who has been victim to domestic violence, or a citizen of a war-torn region) (Bateson et al. 2011).

Optimal Levels of Trait Anxiety

Across the lifetime it is generally preferable to experience low to modest levels of anxiety. Research examining the association between trait anxiety and death by non-natural causes (i.e., death that was not caused by illness, physical condition, or age; e.g., accidental death or death by suicide) suggests that both low and high levels of trait anxiety are associated with higher mortality. High anxiety is associated with a greater risk of non-natural, non-accidental death, such as death by suicide, following the age of 25 (Lee et al. 2006). People with low levels of anxiety do not frequently seek professional care because they do not experience distress due to their lack of anxiety. However, individuals with low anxiety are at greater risk of accidental death, (Lee et al. 2006; Neeleman et al. 1998) particularly before the age of 25 (Lee et al. 2006). When

considering the relationship between anxiety and general mortality the association appears to be U-shaped – higher mortality rates are found among individuals with low anxiety and individuals with high anxiety compared to individuals with mid-range levels (Mykletun et al. 2009). As such, individuals who fall on both extremes of the anxiety continuum may be said to suffer impairments caused by excessive or insufficient anxiety, respectively.

Conclusion

Anxiety and fear responses are advantageous in situations that threaten one's fitness. Nevertheless, anxiety is often experienced superfluously, resulting in energetic cost with no benefit. This cost is outweighed by the exorbitant cost that could ensue if someone is unprepared for a situation that could result in loss of life, social ties, resource holdings, or reproductive partners. It is not always clear what signs may indicate threats to fitness. As such, it is advantageous to over respond to ambiguous signs of threat so that dangerous events can be avoided. Yet, for some people, anxiety may present in a manner that causes considerable distress and may be sufficient for a clinical diagnosis of an anxiety disorder. Evolutionary theory affords important insights into anxiety's function and regulation, but this thought has not generally been incorporated into clinical treatment.

Cross-References

- [Anxiety](#)
- [Anxiety \(Randolph Nesse\)](#)
- [Correlates of Fear](#)
- [Darwinian Medicine and Survival Problems](#)
- [Defending Against Attack](#)
- [Defending Against Predator](#)
- [Emotions](#)
- [Evolutionary Clinical Psychology](#)
- [Fears](#)
- [Fears and Phobias](#)
- [Phobias](#)

- Social Anxiety
- Stress Reduction and Mental Health

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Anxiety of Strangers

► Stranger Anxiety

Aplysia

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Synonyms

Mollusk; Sea slug; Snail

Definition

Aplysia is a species of sea snail, commonly referred to as sea hares because of their posterior tentacles that protrude like ears do in hares.

Introduction

Aplysia became known to the scientific world through the published work of Eric Kandel, a well-known neuroscientist for his research on memory and learning for which he shared the

Nobel Prize in Physiology or Medicine in 2000. Kandel's breakthrough came through his pioneering work with *Aplysia*, which provided a wealth of information regarding non-associative learning and its forms (habituation and sensitization).

A

Habituation and Sensitization in *Aplysia*

Among low-level organisms, *Aplysia* has become a fitting model for studies of how neurons and neural circuits regulate behaviors. What attracts scientists into studying them is their simplicity and the huge size of their neurons, which are easy to manipulate and work with. Also, *Aplysia* exhibits abilities on learning establishing thus its appropriateness for applying cell biological approaches to the investigation of learning and memory mechanisms Moroz (2011). Of particular interest to Kandel and colleagues was the gill and siphon withdrawal defensive reflex of *Aplysia*. *Aplysia* has a mantle cavity on its dorsal surface that protects the gill. The gill lies beneath the mantle shelf, which terminates at the back of the cavity in a fleshy, funnel-shaped spout, the siphon, which contracts to eject water from the gill. A two-component reflex is triggered when stimulation is applied to the siphon (mantle shelf) causing both the siphon and the gill to be retracted, protecting the organism from potential threat. These two components consist of two involuntary reflexes, the so-called siphon withdrawal reflex (SWR) and the gill withdrawal reflex (GWR). The *gill- and siphon withdrawal reflex* (GSWR) is mediated by distinct neuronal pathways, enabling scientists to record activities on the synaptic and neuronal level and to directly link synaptic plasticity to behavioral plasticity. The neural circuits of these reflexes are comprised of monosynaptic connections from sensory neurons to motor neurons, as well as polysynaptic connections containing excitatory and inhibitory interneurons. Kandel's and associates' work on this invertebrate animal regarding the cellular mechanisms underlying habituation and sensitization observed that while light siphon stimulation would naturally cause retraction, repetitive siphon

stimulation produced short-term habituation lasting for a few hours. On the other hand, long-term habituation was demonstrated by repeating multiple training sessions across several days. A single habituation training session consisting of regular trials separated with a time interval of 30 s produced typical reductions in response of the siphon withdrawal reflex. The replication of these training sessions once per day for 4 days produced a progressive buildup of habituation within each session. Habituation preservation was tested the next day and weeks 1 and 3 after training, and when compared to group, the experimental group exhibited greater habituation. The gill withdrawal component of the reflex was also tested for long-term habituation with the same procedures showing that siphon training produces long-term habituation in both components of the reflex Castellucci et al. (1970). Furthermore, in another series of experiments, noxious shocks at the rear produced an increase in the siphon withdrawal reflex and in the gill withdrawal reflex. A single shock increased the reflex for 15 min to an hour. After repeated shocks sensitization seemed to last up to several weeks. Four brief noxious electrical shocks were applied daily for 4 consecutive days. Sensitization retaining was measured again at day 1 and weeks 1 and 3. Also greater sensitization was observed with the addition of more shocks and by spacing the training sessions (two daily shocks within 10 days) Pinsker et al. (1973).

Generally it was indicated that short-term and long-term habituation results from homosynaptic depression of excitatory neurotransmission, while heterosynaptic facilitation of the sensorimotor connection caused sensitization. Habituation was not brought up by changes in the activity of sensory or motor neurons. Specifically sensory neurons release less neurotransmitter because of changes in calcium channels regulating neurotransmitter release, leading to the functional inactivation of the synapse in the long term. Nevertheless habituation still occurs after direct electrical stimulation of the motor nerve, avoiding that way the sensory receptors. This is essential as it reveals that the reduction in response is not due

to sensory adaptation. Furthermore, motor fatigue is also eliminated by showing that direct stimulation of the motor neurons can still provoke a normal reaction after habituation has occurred. Carew (1984) provides more detailed description of the work with *Aplysia*.

Conclusion

The physiological modification of the neural circuits that underlie behavioral plasticity in *Aplysia* has yielded fundamental information that can be extended to all animals providing valuable information on non-associative learning processes.

Cross-References

- [Habituation](#)
- [Non-associative Learning](#)
- [Sensitization](#)

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Apoptosis

- [Cell Death as an Adaptation Against Cancer](#)
- [Early Stage of Brain Development at Birth](#)

Aposematism

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Synonyms

Warning coloration; Warning display; Warning signal

Definition

Anti-predator strategy in which prey exhibit warning signals coupled with some form of secondary defense.

Introduction

Among the many strategies that animals have evolved to deter predators, aposematism is one of the most intriguing. Already in 1877, Sir Alfred Russell Wallace provided thoughts about how distasteful butterflies would benefit from displaying “showy” colors that made them stand out among other butterflies. This, Wallace suggested, helped them being easily seen and recognized, and, consequently, avoided by their enemies (Wallace 1877). The term aposematism, first used by Sir Edward Poulton in 1890, is composed of two words of Greek origin, *apo* (away) and *sema* (sign) and refers to an anti-predator strategy that consists of the display of warning signals by prey in order to inform predators about their unprofitability (Poulton 1890). The warning signal, often a conspicuous color or pattern, a characteristic odor, or a distinctive sound, functions as a primary defense. This means that it operates *before* the predator attacks the prey. Prey

unprofitability is in turn conveyed by any physical, chemical, or morphological attribute that deters the predator *after* the attack. These attributes are considered a secondary defense. Once the predator attacks the prey, it goes through an unpleasant experience that will evoke an aversive reaction to that particular kind of prey in future encounters. Thus, the predator learns the association between the warning signal and the secondary defense, which leads to aversion (Ruxton et al. 2004). Although aposematic organisms are frequently conspicuous, not all conspicuous animals are aposematic and, indeed, not all aposematic species are obviously conspicuous (Endler and Mappes 2004).

What Makes Warning Signals Efficient?

Warning signals are often distinctive and conspicuous, because they must be easy to recognize, learn, and remember for predators (Ruxton et al. 2004). For example, it has been suggested that red, yellow, and black are efficient warning signals because they endow a high contrast against most vegetation, but also because their appearance is relatively constant regardless the light environment (Stevens and Ruxton 2012). Furthermore, red and yellow are simply colors that undefended prey do not often bear, as they clearly increase prey detectability. A few studies have shown there is an innate bias toward these colors, but there is still evidence that, in most cases, this aversion is learnt. Colors such as red, yellow, and black (Fig. 1) combined with odors such as pyrazine are thus common features among aposematic prey.

Theoretical Expectations and Cognitive Aspects

Previous studies have shown that there can be some extent of innate aversion to certain colors and color patterns. However, there is also a wide consensus supporting the idea that learning is an important process involved in the eventual



Aposematism, Fig. 1. Examples of aposematism in nature. (a) *Arctia plantaginis*, the wood tiger moth; (b) Amazonian caterpillar (c) *Dendrobates tinctorius*, the

dyeing poison frog; (d) a butterfly of the genus *Heliconius*. Note the prevalence of yellow and red in combination with black

avoidance of aposematic prey by their predators. In that respect, a basic assumption of aposematism theory is that predators find easier to learn one signal to be avoided rather than several (Mappes et al. 2005). Therefore, natural selection is expected to exert a powerful pressure against warning signal variation. Despite this expectation, there are several aposematic organisms displaying variable warning signals even within the same population (polymorphism), spanning from insects and arachnids to amphibians and reptiles (Rojas et al. 2015). One among several non-mutually exclusive explanations for the maintenance of this variation is related to another cognitive process, *generalization*, which occurs when a predator transfers its learned avoidance from an aposematic prey to another one bearing a similar

appearance. Aposematism, however, is not an all-or-none strategy (Mappes et al. 2005). Some aposematic prey are not overtly noxious but only have an unpleasant taste that does not represent a major risk for the predator. This illustrates how secondary defense is about relative profitability, as high toxicity is not required. Accordingly, predators in search of food are capable to assess the toxin content of some prey and decide whether or not to eat it depending on their hunger level and their previous toxic load.

Secondary Defenses Can Vary Too

In the same way that primary defenses are expected not to vary in order to enhance predator

learning, secondary defenses are predicted to exhibit little or no variation within a population of individuals bearing the same warning signal. This variation is, however, more common than previously assumed (Speed et al. 2012). In fact, its implications are far from trivial for the dynamics of aposematism because individuals with weaker than average defenses may delay or obstruct predator learning, with negative consequences for the prey population. In several cases the production or sequestration of secondary defenses can be costly, as can be the production of the primary defense, and thus their effectiveness might depend on the availability of resources in the animal's environment. The variation in secondary defenses can be linked to a corresponding variation in the primary defense, such that stronger warning signals are coupled to more efficient secondary defenses. In these cases the warning signal might be considered an *honest* indicator of the quality of the secondary defense (Summers et al. 2015).

Variation in Secondary Defenses Can Lead to Cheating

Once a predator has learned to avoid prey bearing a particular warning signal, other prey sharing their appearance can gain protection too (Ruxton et al. 2004). This has given rise to the imitation of the warning signal by individuals of a different species who lack the secondary defenses. Thus, the non-defended species gets protection from predators without having to incur the expenses that the secondary defenses entail. This phenomenon is known as *Batesian mimicry*, and it works only if the number of "cheaters" (i.e., the non-defended individuals) is kept under a threshold where predators have still enough encounters with defended prey to maintain the aversion. Textbook examples of Batesian mimicry include the coral snakes, which serve as models to species of brightly colored, non-defended, or mildly defended colubrid snakes, and the swallowtail butterflies in the genus *Papilio*, whose coloration mimics that of several different species of unpalatable butterflies. But Batesian mimicry can also occur between animals of completely different groups,

such as the nestling of the Cinereous Mourner bird whose coloration and behavior resemble an aposematic caterpillar. It can also be the case that two or more defended species share a common warning signal, in a phenomenon known as *Müllerian mimicry*. This results in a benefit for all species involved because they share the costs of predator education, decreasing the per capita risk. Among Müllerian mimics, probably the best well-known cases are the *Heliconius* butterflies and the frogs in the *Ranitomeya imitator complex*, both of which occur in the Neotropics.

How Does Aposematism Originate and Evolve?

One central question in evolutionary biology is how the first aposematic individuals appeared and, most importantly, managed to multiply and spread (Mappes et al. 2005). This is puzzling because presumably the first individuals showing, for instance, conspicuous coloration would have been easy to detect for predators (Alatalo and Mappes 1996). Thus, those prey would have been injured or killed without being able to reproduce and reach the numbers required in order to elicit avoidance learning in predators. Likewise, the first defended prey that did not display a memorable signal, such as conspicuous coloration, would have been eaten without offering learning possibilities to the predator, who would have found more difficult to associate dull-colored prey with their unprofitability. This paradox has been under active debate and is still partly unresolved. However, some explanations have been proposed. For example, it has been suggested that both the primary and secondary defenses may have increased gradually or that both defenses may have first been associated with a selective pressure other than predation. In addition to these, there is some empirical evidence that predators such as birds are often reluctant to attack unfamiliar prey items for either short (neophobia) or prolonged periods of time (dietary conservatism). In this context, especially if familiar prey are available and abundant, these biases may favor the rise and

spread of novel color morphs and would have thus allowed for the spread of the first aposematic individuals. Other studies suggest that aposematism might have first appeared, and been favored, in aggregations of defended prey (Alatalo and Mappes 1996). This is because processes of learning and memorization of a signal will work better the more common the signal is. In other words, a predator is more likely to learn about the unprofitability of certain prey, if it encounters it frequently (Endler and Mappes 2004). Thus, the success of aposematism relies on “strength in numbers.”

Aposematism and Multimodality

Aposematic organisms can have warning displays that stimulate two or more sensory channels in the receiver, the predator, in this case. For instance, they can stimulate their visual system when detected and then their taste receptors when attacked. For this reason, warning displays are thought to be multimodal (Rowe and Guilford 1999). Multimodal warning displays are assumed to improve associative learning, the type of learning that predators go through, because they supply more information than displays consisting of just one sensory modality. Consequently, the interaction between two types of signals (say visual (color) and chemical (taste)) is predicted to be more effective than each signal separately. Relatively recently researchers have started to redirect their attention to the role of multimodality in the dynamics of aposematism.

Conclusion

Aposematism is a strategy by which prey deter predators combining an easy-to-recognize and memorable warning signal with some type of secondary defense. As a result of coevolution between predators and prey, aposematic species are often conspicuous. Yet, not all conspicuous

organisms are aposematic, just like not all aposematic individuals are conspicuous. For this reason, aposematism should be deemed as a continuum of warning signal conspicuousness and secondary defense efficiency rather than as an all-or-none anti-predator strategy. There is still much that warrants in depth investigation about the underpinnings of aposematism. For instance, it is essential to investigate in depth the role(s) of variation in predator community composition, as well as of interindividual differences in cognitive abilities among predators, in the evolution of warning signals, and the rise and maintenance of warning signal variation. Likewise, more attention should be given to the existing variation in secondary defenses and its function(s) in the interactions between predators and prey. Also, more studies are needed to gain a better understanding of the costs of both primary and secondary defenses and whether the resources for their production or sequestration are antagonist or synergistic. Finally, it is necessary to increase current knowledge on the link(s) between warning signals and secondary defenses, and life-history, behavioral, and ecological traits.

Cross-References

► [Müllerian Mimicry](#)

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Apparel

- ▶ [Clothing](#)
- ▶ [To Afford Protection Against Climate and Weather](#)

Appeal to Nature Fallacy

- ▶ [Naturalistic Fallacy, The](#)

Appearance

- ▶ [Appearance/Beauty in Girls](#)

Appearance Enhancement Effort

- ▶ [Desire to Be Included Among Desirable Women](#)

Appearance/Beauty in Girls

A

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Synonyms

[Appearance](#); [Attractiveness](#); [Dominance](#); [Youth](#)

Definition

Physical attractiveness in prepubescent females.

Introduction

Attractiveness is more important to females, as males weigh female attractiveness much more than females weigh male attractiveness, and beauty plays a role in social evaluations from infancy in girls. Physical appearance might represent a female's youth and reproductive value, leading to intrasexual (same-sex) competition among girls with attractiveness as a primary target.

Cultural Differences in Beauty

In all human societies, physical characteristics are an important factor in determining whom one finds attractive. Individuals across all cultures appear to have the same basic range of internal states, emotions, and external signals, but humans demonstrate plasticity of emotional response regarding what is physically attractive. Characteristics considered to be attractive vary considerably across cultures, and there is a fair degree of malleability in responses to external stimuli (Hyde and DeLamater 2008). In some cultures, for example, scars, tattoos, or piercings can be considered to be very attractive, while in others, they

are seen as ugly disfigurements (Workman and Reader 2014). Additionally, what a given culture finds attractive may change over time, and generations and may even differ between subsections of a society, such as emotional response to tattoos for younger members of society. The details of physical beauty can be diverse; however, there are cross-cultural agreements in what is judged to be beautiful. For example, bad complexion is considered to be unattractive in just about every human society (Hyde and DeLamater 2008). Additionally, many diverse cultures have a consensus regarding which individual faces are deemed attractive (Buss 2015).

Attractiveness

Psychological factors that affect attraction include similarity, familiarity, proximity, reinforcement (attraction associated with rewards or positive feelings), self-evaluation maintenance (individuals strive to maintain or improve their self-esteem through desirable or popular others), and attachment (attraction based on relationships early in development) (Clark and Pataki 1995). However, people are most attracted to good-looking others. Infants as young as 3 months old will gaze longer at attractive faces, compared to less attractive ones, indicating a very early-emerging bias (Buss 2015). Additionally, the more attractive an individual is rated, the more positive personality traits and life outcomes are ascribed to that individual (Eagly et al. 1991).

Individuals tend to focus on two major domains of attractiveness: facial and physical. For facial features, averageness is one characteristic; the more average a face is to a general population, the more attractive its rating. For example, if different individual faces are blended together, blended faces are rated as more attractive than individual faces, and the more blended or average they become, the higher they are rated on attractiveness (Buss 2015). Another major factor that affects both facial and physical attractiveness is symmetry. The more symmetrical a face or body is, the more attractive it is rated. The appeal of symmetry is found even in infants who prefer to

look longer at symmetrical patterns than asymmetrical ones (Etcoff 1999).

Physical Attractiveness in Females

Even though there are many cross-cultural differences in the details of what is attractive, one consistent universal finding is that males overall place greater importance on physical attributes when selecting a potential mate (Buss 2015). Attractiveness is significantly more important to males evaluating females than vice versa. Males are still evaluated based on physical appearance, with the ideal in many cultures, being tall, trim, narrow hips, broad shoulders, and square jaw (Hyde and DeLamater 2008). However, physical appearance in males only appears to be of increased importance for females in short-term mating contexts. For long-term relationships, the actions and achievements of men are primary considerations for women when considering a stable romantic partner. Males are valued predominantly for ambition, stability, maturity, economic resources, financial prospects, and high social status for long-term relationships (Buss 2015; Langlois et al. 2000). For females, it is the appearance that males primarily consider when evaluating a potential romantic partner, not just in short-term relationships but in long-term contexts as well. For heterosexual men, brain reward centers (particularly the *nucleus accumbens*) are activated simply by viewing attractive female faces (Buss 2015). Highly attractive women are significantly more likely than less attractive women to marry a wealthy man, while men who have the highest education and occupational status actually tend to be rated on lower ends of attractiveness scales (Udry and Eckland 1984).

Regarding physical features of females, there are a few general measurements that have emerged as strongly influential on attractiveness and beauty ratings. Physical attractiveness in women is based primarily on secondary sexual characteristics, such as breast size, hip size, and fatty deposits on buttocks. For example, waist-to-hip ratio (WHR), which is calculated by dividing the circumference of the waist (at the narrowest

point around the torso, under the iliac crest) by the circumference of the hips (at the greatest protrusion of the buttocks); body mass index (BMI), which is calculated by dividing body weight by height squared; and curvaceousness, which refers to the degree of the “hourglass shape,” such as the bust-to-waist ratio, have all been identified as important physical attractiveness factors (Buss 2015). Secondary sexual characteristics important to physical attractiveness measurements in females all appear after sexual maturation; however, attractiveness does not just begin to have an effect at puberty. Attractiveness plays a role in social evaluations from infancy.

Beauty Before Puberty

One of the defining aspects of physical immaturity is cuteness. Cuteness in babies is generally dependent on protruding cheeks, a large forehead, and large eyes below the horizontal midline of the skull (Etcoff 1999). Neonatal features of cuteness are thought to trigger parental care. For example, babies with higher ratings of attractiveness are more likely to have mothers who spend a greater amount of time holding them close, making eye contact, and making more vocalizations (Etcoff 2011). During childhood, attractive children (compared to unattractive children) are judged more positively and treated more positively and exhibit more positive behaviors and traits (Langlois et al. 2000). Similar to adults, appearance cues appear to be more important for females than males, with girls providing more appearance stereotypes than boys and both sexes providing more appearance stereotypes when describing girls than when describing boys (Miller et al. 2009).

Culturally, the importance of attractiveness has increased dramatically in the United States in the twentieth century, and this is reflected particularly in young girls. Prior to WWI, girls rarely mentioned their bodies in terms of strategies for self-improvement or struggles for personal identity, but in contemporary societies, girls are concerned with the shape and appearance of their bodies as a primary expression of their individual identity

(Brumberg 2010). Part of the shift from “good works” to “good looks” can be attributed to modern cultural acceptance and promotion of sexualization in young girls. For example, the modern child beauty pageant emerged in the early 1960s and currently includes approximately 250,000 pageants for girls in the United States with age categories as early as 0–11 months. Toy and clothing manufacturers regularly market items to young girls that feature sexualized content. The increase in sexualization of young girls has become so pervasive that the American Psychological Association, in 2008, assembled a task force to address public concern. While sexualization of young girls continues to be an issue, beauty does factor into social relationships, particularly dominance in intersex hierarchies, among girls in childhood.

Beauty and Dominance in Girls

Beauty does not just have advantages for females in direct mating contexts; attractiveness has many intersexual (same-sex) advantages in childhood. A strong relationship between attractiveness and popularity is found in girls, beginning in childhood as young as 3 years of age (Hyde and DeLamater 2008). Meta-analyses have demonstrated that children rated as attractive, compared to unattractive, were more popular, were better adjusted, and even had higher intelligence and performance competence, with no other moderating variables found (Langlois et al. 2000). Beauty is an especially strong contributor to young girls’ popularity in school, along with social skills and family socioeconomic status, which girls also use in intrasexual competition (Buss 2015).

Beauty is thought to be a path to social dominance for girls, leading to a higher status that is then maintained by derogating other girls about their physical appearance in particular, along with their sexual fidelity (Buss 2015). For example, girls (particularly more-attractive girls) commonly use words like “ugly” and “slutty” to insult other female peers, calling into question for boys (potential future mates) their attractiveness and sexual purity. Further, hearing an appearance-

related derogation about a specific woman, such as “fat and ugly,” can actually influence men’s ratings of attractiveness of that woman (Buss 2015).

Girls generally employ indirect (relational) aggression to establish dominance over same-sex peers, compared to boys who use direct (physical) aggression (Buss 2015). Relational aggression includes gossiping, shunning another person, spreading vicious rumors, breaking contact with the person as revenge, or befriending someone else as revenge. Bullying in girls typically includes derogation specifically related to another girl’s physical experience or sexual fidelity, theoretically to inflict costs in intrasexual rivals as intrasexual competition increases from childhood to middle adolescence. Moreover, female aggression often originates in motives such as jealous rivalries, competition over boys, and the desire to be included among the “desirable” group of other women (Buss 2015).

Evolutionary Benefits of Beauty in Females

There are many social advantages to being attractive. People are more likely to offer help to an attractive person (even if they do not like them) and to let an attractive person win an argument (Ectoff 1999). Compared to unattractive individuals, attractive individuals tend to be more confident and at ease socially, less likely to fear negative opinions, and more likely to demonstrate more entitlement (Ectoff 1999). Considering how cross-culturally ubiquitous the effects of attractiveness are and how early in development it begins to shape behavior, beauty seems to have played a major role in evolutionary history.

A dominant evolutionary theory as to why females are disproportionately evaluated on physical attributes is youth. Females’ reproductive capacity declines as she ages, dropping to essentially zero around age 50 (Buss 2015). Women have a relatively narrow window of opportunity to successfully reproduce during their entire lifespans. Males eager to reproduce

would have to selectively target those females that would be most likely to produce healthy, viable offspring. Any physical signals that would indicate a female’s reproductive value would have been desirable to males throughout human’s phylogenetic history. The physical cues to health, such as symmetry and averageness which would indicate a lack of infections, parasites, or disease, are still preferred by contemporary males. Faces that show a high degree of asymmetry have been linked to negative health indicators and may reflect psychological, emotional, and physiological distress (Buss 2015).

Younger females have higher reproductive value, because their future reproduction is expected to be higher, so features that indicate youth are expected to be particularly desirable in males. Research has indicated that males do prefer females that are younger than themselves, with the difference in age preference increasing as males get older (Buss 2015). Signs of youth, such as smooth and clear skin, would indicate reproductive value and therefore be desirable traits for males. Males demonstrate a strong predisposition for youth overall, as homosexual men are just as interested in youth and beauty in their partners as heterosexual males (Ectoff 1999). Females also demonstrate a predisposition to use their physical features to facilitate attractiveness. For example, flirtation is similar across many cultures, with women smiling, lifting eyebrows, display eyes, and looking away, which suggests a biological predisposition for a sexual behavior pattern (Hyde and DeLamater 2008).

Conclusion

What constitutes attractiveness varies considerably among cultures, but there are several universal factors that influence whether or not an individual is deemed attractive. Characteristics include good complexion, facial averageness, facial and physical symmetry, WHR ratio, BMI, and curvaceousness, which have all been theorized as displaying reproductive value. While

attractiveness in males is important in short-term mating contexts, attractiveness in females is much more important overall, as males primarily select mates based on physical appearance and beauty. Preferences for attractive faces begin in infancy, and young girls associate attractiveness with popularity and social dominance, from as young as 3 years old to middle adolescence. Early developmental emergence and cross-cultural universality of importance, along with the many social benefits, demonstrate the adaptive functions of beauty in girls.

Cross-References

- ▶ Opposite-Sex Relationships
- ▶ Sex Differences in Cognitive Development
- ▶ Sex Differences in Sexual Socialization
- ▶ Sex Differences in Social Development

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Appearance-Reality Task

- ▶ Smarties Task, The

Appeasement

- ▶ Reconciliation

Applications of Evolutionary Psychology

- ▶ How Evolutionary Psychology Can Still Explain Behavior

Applied Behavior Analysis

- ▶ Methods and Enduring Impact of Behaviorism

Appraisals: Construals

- ▶ Changes in Self-Esteem Motivate Behavioral Changes

Appraised Helplessness and Self-Slaughter

- ▶ Perceived Control and Suicide from an Evolutionary Mismatch Perspective

Apprehension

- ▶ Anxiety

Apprenticeship

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Synonyms

Training

Definition

A system of training a new generation of practitioners of a trade or profession with on-the-job training and often accompanying study.

As discussed elsewhere in this work (Peedicayil 2018), cultural inheritance involves the storage and transmission of information by communication, imitation, teaching, and learning. In this context, there is evidence that complex social behaviors like human altruism and mate choice (Rushton et al. 1986), social attitudes (Martin et al. 1986), personality (Eaves et al. 1999), and the human sex ratio (Lipatov et al. 2008) are culturally transmitted. The cultural transmission of such behaviors, for obvious reasons, will occur effectively only in an animal species that is social, i.e., where the members live in groups and interact freely with one another. Human beings are the archetype of that type of animal species and the groups they live in are termed societies (Wilson 2000). Indeed, the famous Greek philosopher Aristotle had stated “Man is by nature a social animal” (Aristotle 2015). All of man’s unique social behavior is pivoted around the use of language (Wilson 2000).

Regarding apprenticeship, it is found in humans because of the advanced level of cultural inheritance found in humans when compared to other animals. Apprenticeship refers to a system of training a new generation of practitioners of a trade or profession with on-the-job training, and often accompanying study (Wikipedia 2018). Apprenticeship also allows the practitioners to gain a license to practice in a regulated profession. Most of the training of those being trained is done while working for an employer who helps

the apprentices learn their trade or profession in exchange for their continued labor for an agreed period during which the apprentices achieve adequate capabilities. The system of apprenticeship is thought to have first developed in the late middle ages (the period of European history lasting from about 1250–1550 AD) and to have been supervised by craft guilds and town governments (Wikipedia 2018). Apprentices usually began at 10–15 years of age and would live in their teacher’s house. The modern concept of internship is similar to apprenticeship but not as rigorous. Also similar to apprenticeships are the professional development arrangements for new graduates in the accountancy, engineering, management consultancy, and law professions (Wikipedia 2018).

Cross-References

► Cultural Inheritance

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Approximate Number System

- ▶ [Quantity Estimation](#)

Aptation

- ▶ [By-Products of Adaptations](#)
- ▶ [Evolutionary By-Products](#)

Aquatic

- ▶ [Fish, Amphibian, and Reptile Tool Use](#)

Arbitrary

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Synonyms

[Conventional form-meaning mapping](#); [Noniconic form-meaning mapping](#); [Symbolic signs](#)

Definition

Arbitrary signs are signs where the relation between signifier and signified is solely a matter of convention and there is no natural connection between them. Words are considered arbitrary in the sense that the sound pattern of the word does not resemble its meaning and there is no intrinsic relation between the two. Thus, meaning cannot be inferred from a word's sound, and the same meaning can be expressed through different sound patterns.

Introduction

The nature of the relation between words and referents has long been a topic of discussion. Plato's *Cratylus* is an early testimony of the debate between a conventionalist stance that views this relation as purely a matter of convention and a naturalist stance that views this relation as stemming from a natural, nonarbitrary, connection. In the past century, ever since de Saussure (1916), the arbitrariness of the linguistic sign has become a central tenet of linguistic theories. Words are considered symbols, conventionally related to their referents; the form of the word does not resemble its meaning. For example, the word *big* is smaller than the word *small*. This is in contrast to motivated signs such as icons, whose form corresponds to their meaning (e.g., children crossing sign), or indices, causally related to their referents (e.g., footprints in the sand) (Peirce 1932).

Arbitrariness in Language

The arbitrary relation between form and meaning has even been designated a design feature of language by Hockett (1960), thus defining it as a necessary requirement distinguishing language from other communication systems. For example, posture can convey information, but its form is not arbitrary with respect to its meaning or function. Similarly in honeybees, the speed of the dance and its direction are not arbitrary with respect to the distance and location of the food. However, some animal communication systems, for example vervet monkeys alarm calls, are considered arbitrary. Although these alarm calls contain acoustic features that are not arbitrary with respect to their function (e.g., high amplitude, abrupt onset), the acoustic distinction between the alarm calls for different predators appears arbitrary (see Seyfarth and Cheney 2003). This design feature has also been used to distinguish spoken language from spontaneous gestures that typically accompany speech. While both speech and gesture convey meaning, they do so in fundamentally different ways. Whereas in speech meaning is

represented by discrete arbitrary symbolic units, gesture represents meaning through a nonarbitrary mapping of meaning onto continuously varied form (McNeill 1992). The arbitrary nature of the sign alleviates the need to rely on a circumscribed rigid set of form-meaning mappings, thereby enhancing the power of language to convey a richer more complex array of meanings.

The arbitrariness of the sign seems evident when one considers the range of expressions used to refer to the same object across different languages. To take a familiar example, the same animal is called *dog* in English, *kalb* in Arabic, and *perro* in Spanish. Not only do these words differ from each other, there is no way of knowing a word's meaning save for knowing language-specific linguistic conventions. In the absence of an intrinsic relation between word and referent, there is no way of inferring the meaning of the word from the sound alone. Although there are onomatopoeic words that phonetically imitate the sound they represent (e.g., buzz), these typically constitute a very limited class. Furthermore, even onomatopoeic words are not universal and vary cross-linguistically; for example a dog bark sound is *woof* in English, *guau* in Spanish, and *wan* in Japanese, suggesting they are conventionalized to some degree.

Iconicity in Language

Onomatopoeias represent one example of sound symbolic words exhibiting a nonarbitrary iconic relation between form and meaning, and there are several other instances of sound symbolism in language. One example comes from ideophones (also termed mimetics or expressives) which are words that depict sensory imagery (Dingemanse 2012) but are not confined to the auditory modality. That is, they can represent sound impressions, but they may also represent sensory impressions of color, shape, or even movement; for example *gorogoro* in Japanese for a large object rolling. Though relatively uncommon in Indo-European languages, ideophones are ubiquitous in many African, East Asian, and indigenous South American languages (see Dingemanse 2012). Even

speakers of languages in which ideophones are scarce show sensitivity to sound symbolic mappings between phonemes and specific meanings, as evidenced by laboratory experiments using invented or foreign vocabulary. Sapir (1929) was the first to document sound symbolic mapping between phonemes and object size. For example, high front vowels (e.g., /i/) are associated with smallness, whereas low back vowels (e.g., /a/) are associated with largeness. As high front vowels have higher frequency, Ohala, Hinton, and Nichols (1997) claim this mapping reflects a cross-linguistic cross-species "frequency code" associating high frequency sounds with smallness and low frequency sounds with largeness. This code is grounded in the biological inverse relation between vocalizer size and frequency of the vocalization. According to Ohala et al., the frequency code is also apparent in the use of rising intonation to express politeness or uncertainty and in non human agonistic vocalizations.

In addition to vowel sounds being related to size, there is also evidence for sound symbolism in the iconic mapping between phonemes and object shape. This relationship was first described by Köhler (1929), who found that the pseudo-word *maluma* was associated with a rounded shape and *takete* with an angular shape (subsequently termed the kiki-bubba effect by Ramachandran and Hubbard 2001). Phonological sound symbolism has since been found for various additional meanings (e.g., brightness, speed, taste). It has also been found cross-linguistically and in prelinguistic infants (see Perniss et al. 2010 for a review), further supporting the idea that it is not based on arbitrary linguistic conventions. Findings of such cross-modal associations in language have led Ramachandran and Hubbard (2001) to suggest that cross-modal correspondences between visual object properties and sounds provided the underpinnings for the development of a proto-language and played a key role in language evolution. Despite this line of research showing sound symbolic biases in interpretation of pseudo-words, the small inventory of actual sound symbolic words in Indo-European languages contributed to the relegation of phonological iconicity to a marginal role in language.

Yet the role of cross-modal correspondences in language is not limited to sound symbolic words. Moving from segmental units like phonemes to suprasegmental prosodic properties of speech reveals another source of information that does not act in accordance with the principle of arbitrariness. Although most research has focused on the role of prosody in conveying emotion, recent research has shown that prosody can also convey semantic-referential information. Language users can capitalize on existing cross-modal correspondences and convey information about object properties by modulating their pitch, loudness, and speech rate; for example, the modulation of pitch can convey information regarding object vertical location, motion, and size (see Perniss et al. 2010, for a review). This nonarbitrary gradual mapping between form and meaning in prosody can be seen as a form of spoken gesture (Shintel et al. 2006).

Conclusion

Taken together, these findings suggest a role of iconicity at different levels of language, from the level of the phoneme to suprasegmental prosodic structures. Other findings have also documented the role of iconicity in syntax (see Perniss et al. 2010). Thus, while not denying the fundamental role of arbitrariness in language, the assumption that the relationship between words and meaning is essentially arbitrary (e.g., Hockett 1960) needs some reconsideration. Iconic nonarbitrary form-meaning mappings may play a larger role in language than previously realized, and future research should clarify the extent to which they affects language comprehension and production.

Cross-References

- ▶ [Alarm Calls](#)
- ▶ [Language](#)
- ▶ [Linguistic Evolution](#)
- ▶ [Sign Language](#)

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Archaeological Records

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Definition

Archaeology is the study of the material remains of human activity, and an archaeological record is the evidence that informs such studies.

Introduction

The components of the archaeological record can include artifacts, which are objects that have been

moved or altered through human activity (i.e., stone tools, plant remains, or bones from a butchered animal), or features, which are immobile alterations to a site (i.e., burial pits or fireplaces). Archaeological records are often ancient but may also include objects or activities that are quite recent. Prehistoric archaeology is the study of human societies that are typically pre-urban, without surviving written records. Historical archaeology is the study of sites where either oral or written records or accounts can be accessed to inform the interpretations of those sites. It should be noted that these written or oral accounts may either correspond with or conflict with the evidence obtained from the site through archaeological investigations.

Archaeological Records

Archaeological records are typically revealed through the excavation of a site, which is a place that contains evidence of human activity. While evidence may be found on the surface, such surface finds can be difficult to interpret because they lack temporal context within the site. Temporal context or control of a site's contents is typically gained through the understanding of stratigraphy at a site. Stratigraphy is the layering of sediments within the ground. The interpretation of stratigraphy is dictated by the law of superposition, which states that in an unaltered sequence of sediments the oldest layers will be at the bottom and younger layers toward the top. Artifacts or features found within these layers can be placed within the timeframe of the formation of that site, with objects found in the deeper layers likely to be older than those found closer to the surface. A precise understanding of the spatial patterning of artifacts and features, both horizontally and vertically, within the context of a site's stratigraphy is crucial to the interpretation of the site. Artifacts that are believed to be in an original, undisturbed context within the site are referred to as *in situ*. Because archaeological excavations remove sediments, which permanently alters the site and may destroy contextual evidence, accurate

record keeping is very important for the preservation of information contained in the site's contents.

Stratigraphy within a site provides only very broad temporal context to these artifacts. Stratigraphic position can only tell which artifacts or features are likely to be older than other objects found at that site, a type of context known as relative dating. Relative dating is unlikely to be able to provide numerical ages for artifacts because of this fairly imprecise and site-specific level of interpretation. Numerical ages, known as absolute dates, can be obtained when there are materials deposited within the stratigraphy of the site that are suitable for a variety of dating techniques, such as radiocarbon or potassium-argon dating, that can measure the length of time that those materials have been buried at the site. Sometimes, these absolute dates can be obtained directly from artifacts of interest, such as bones, teeth, or charcoal, while other times these dates can be useful for providing ages for layers within the stratigraphic profile of a site. These dates provide crucial context for the artifacts found within the site, which enables broader interpretations of the site's functions.

Taphonomy is the study of the processes that result in fossilization of organisms, and a knowledge of these processes and the biasing outcomes they may introduce are useful for understanding and interpreting the archaeological record. Archaeological sites are imperfect for a variety of reasons, which must be acknowledged in any analysis or interpretation of a site's significance. A number of different phenomena can affect which materials are present in a site and how those materials may have been preserved. One such biasing effect can be the soils within the site itself. Highly acidic soils will damage or destroy many organic materials, which can significantly impact interpretations of a site and its contents. Burrowing animals or insects may also disturb a site's contents over time, a process known as bioturbation. Erosion by wind and water could have disturbed or even removed small artifacts and degraded details of features. Fast-moving water, such as rivers or floods, may even remove and

redeposit artifacts in different locations. Archaeologists must be aware of these processes and consider their potential effects in rendering conservative interpretations of a site.

Materials recovered from an archaeological investigation are typically described and classified during the process of analysis. This process often involves the artifacts or features from a site being separated into various “kinds” or “types” and placed into various typologies. Typologies are based upon the various physical characteristics of artifacts or features and are used to place various sites or artifacts within the broader context of cultural or behavioral change. Stone tools provide several examples of these typologies in recognized complexes such as the Oldowan or Acheulean. Typologies can be useful for facilitating conversation and study of the complexities of the archaeological record but are often the subject of discussion and debate within the archaeological literature.

A variety of theoretical perspectives within archaeology have had a profound impact on the interpretations of sites (see Praetzelis 2015 for further discussion). These perspectives question that idea that anything can be known with certainty and acknowledge that human beings are inherently biased by our individual experiences. These theoretical approaches to data analysis provide means to mitigate these biases. It should be noted that there is no single dominant theory of archaeology but instead a variety of theories used by archaeologists to provide the framework through which they interpret artifacts and sites. These different theoretical approaches allow archaeologists to treat evidence from sites in different ways and may lead them to come to different conclusions about that evidence. For example, Marxist theory examines archaeological residues through the lens of class hierarchies within economic systems. Alternatively, Structuralism proposes that underlying, sometimes unconscious structures inherent to human thought shape various cultural constructions. Feminist theory emphasizes the interpretation of gender roles as evidenced in archaeological residues as a means of understanding past cultures.

Conclusion

Ultimately, the goal of the archaeologist is to use the evidence from a site to reconstruct details of land use, behavior, culture, economy, and subsistence of local human groups and place those activities within a temporal context. This collection of evidence comprises the archaeological record.

Cross-References

- [Burials](#)
- [Olduvai Gorge, The](#)
- [Paleoanthropology](#)
- [Tool Use](#)

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Archaic Adaptive Introgression

- [Neanderthals and Humans](#)
-

Archeology

- [Evolution of Tool Use](#)
-

Architectural Acoustics

- [Cathedral Acoustics](#)
-

Archival Research

- [Census Data](#)

Ardipithecus Group

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Synonyms

Ardipithes; *Orrorin*; *Sahelanthropus*

Definition

One or more genera of fossil hominoids, including some probable hominids, dating from the late Miocene to the middle Pliocene (~ 7.0–3.4 Ma, millions of years ago) of East and Central Africa; the name *Ardipithecus* is derived from the Afar for “ground” or “floor” (*ardi*) and the Latinized Greek for “monkey” or “ape” (*pithecus*, Greek *pithekos*).

Introduction

The *Ardipithecus* group consists of, to date, three proposed genera and four proposed species of fossil hominoids (the group that includes apes and humans) and further unclassified materials varyingly considered as representing the earliest members of the human lineage (hominids or hominins; hereafter, hominids) after the split with the chimpanzee and bonobo lineage approximately 8 Ma. *Sahelanthropus tchadensis*, *Orrorin tugenensis*, and *Ardipithecus kadabba* are known from a relatively small number of fossils; *Ardipithecus ramidus*, the most recent form, is represented by a partial skeleton (“Ardi”) and considerable associated materials. The distinction between members of the *Ardipithecus* group, and their relationships to fossil and living apes, as well as later hominids such as *Australopithecus* and *Homo*, are matters of considerable discussion.

Discoveries and Initial Arguments

The *Ardipithecus* group, quite appropriately, began its history with an air of mystery – an air that, in truth, has never fully dissipated. In 1994 the new species *Australopithecus ramidus* was named to house some craniodental and arm elements from the Middle Awash, Ethiopia, dated to a then-ancient (for a hominid) 4.4 Ma (White et al. 1994). Great apes, especially male ones, are characterized by large canines that project beyond those of other teeth, with long upper eyeteeth that sharpen (hone) against the premolars beneath them. That *Australopithecus ramidus* lacked this canine/P₃ complex, as in *Homo*, was at the time the predominate evidence to classify it a hominid. Little could be said about whether it was bipedal, another flagship hominid characteristic. The following year, a pithy correction elevated the find to the novel genus *Ardipithecus* (White et al. 1995). Meanwhile, word spread that the Aramis group had discovered a partial skeleton of *Ardipithecus ramidus*, one which could potentially answer the critical question of how it moved about in life. Thus began what popularly became known as the “Manhattan project of paleoanthropology,” as others waited while the Middle Awash group meticulously, and quietly, analyzed the find.

The wait would be occupied by even more ancient fossils. The first, dubbed the “Millenium Ancestor,” involves a small collection of craniodental and postcranial elements from the Lukeino formation of Kenya, dated to around 6 Ma, and which were assigned to a novel genus and species *Orrorin tugenensis* (Senut et al. 2001). Arguments for the hominid status of *Orrorin* include its rather diminutive upper canine but center especially on several femur fragments argued to have bipedality-related features. These included an elongated femoral neck, contrasting with great apes, and an obturator externus groove – found on the back of the femoral neck, it has long been associated with frequent extension of the hip in erect, human-like posture and movement (Pickford et al. 2002). Associated fauna and other evidence suggests a general environment of woodland with varying degrees of open space, and lake margin.

This was immediately followed by the announcement of more ancient (5.2–5.8 Ma) *Ardipithecus* specimens from the Middle Awash, which after several years were placed in a new species *Ardipithecus kadabba* (Haile-Selassie 2001; Haile-Selassie et al. 2004). The key hominid features are an incipiently incisor-like canine, and a proximal foot phalanx with a “dorsally canted” joint surface, similar to later hominids and thought to be indicative of marked dorsiflexion of the toes during the “push-off” phase of bipedal locomotion (Latimer and Lovejoy 1990). The paleoenvironment of *Ardipithecus kadabba* has been characterized in detail and described as ranging from heavily closed to grassy woodland; any habitat preferences for *kadabba* within such a menagerie are at present difficult to determine (Su et al. 2009).

Perhaps the most enigmatic of the early proposed hominids is *Sahelanthropus tchadensis*, described from a very old (6–7 Ma) cranium, along with a partial mandible and some isolated teeth, from Chad (Brunet et al. 2002). Small canine teeth with tips worn flat (rather than pointed) and a relatively anterior foramen magnum placement, both suggested to its discoverers hominid, rather than ape, affinities. The estimated cranial capacity is within the range of adult chimpanzees and bonobos (320–380 cm³); the face, on the other hand, is far less projecting than in living apes or australopithecines. At the same time, the cranium exhibits unusually large brow ridges – a feature present in living apes but absent or only moderately developed in later hominids until Asian *Homo erectus* some five million years later. Paleoenvironmental work suggests a range of potential habitats from lake-edge forest to grassland. Along with an australopithecine mandible found in the same region and dating to roughly 3.5 Ma, *Sahelanthropus*, whatever it might represent, evidences that central Africa, in addition to the traditional early hominid-bearing locales of southern and eastern Africa, is vital to interpreting earliest human evolution.

The year 2009 brought the description of the *Ardipithecus ramidus* partial skeleton (ARA-VP-6/500, nicknamed “Ardi”) and other specimens from this form, along with a detailed examination

of its habitat. As outlined below, much of what is known on the *Ardipithecus* group comes from this work – which does much to clarify their taxonomy and, further, challenges several widespread assumptions about human origins.

Classification and Hominid Status

The various taxonomic names given to members of the *Ardipithecus* group might be considered, at present, more akin to convenient or confusing (depending on perspective) metaphors than actual species which lived in the ancient natural world. Their placement into three genera, by extension, is especially nonconservative. While they are found from differing times and places, there is too little overlapping fossil evidence to clearly differentiate them, and generalist forms (such as most or all hominids, see below) by nature inhabit broad geographic regions, often over extended periods. The ecologically pliable Virginia opossum (*Didelphis virginiana*), for example, is widely distributed from Central to North America with a range that is seemingly ever-increasing. With expected variation, it probably existed in relatively modern form over half a million years ago, and its genus dates back at least to the Late Miocene (6.8–9 Ma) of South America (Cozzuol et al. 2006). Such ecological considerations offer abundant cause for constraint in paleoanthropological classification.

Whether the various members of the *Ardipithecus* group represent hominids is perhaps the most important matter of controversy. In general, the older the fossils, the greater the disagreement. Historically, one sticking point was that some specimens dated from earlier than certain biomolecular estimates for the time of the *Pan-Homo* divergence. With improved methods, however, it is now thought likely that this event occurred earlier than 7 Ma (Langergraber et al. 2012); in other words, before any of the fossils under consideration were deposited. With this concern removed, the known morphology of the earliest potential hominids is the predominate evidence that can be brought to bear on the issue.

Sahelanthropus, for example, has been suggested to represent a non-hominid ape on several grounds, including that the canine measurements, and foramen magnum position, are potentially less differentiated from living African apes than originally suggested. Responses have focused on the seemingly derived characters of the skull – closer to later *Australopithecus* and *Homo* than living African apes – especially of the cranial base (Guy et al. 2005). The bipedality-related features of *Orrorin* and *Ardipithecus kadabba* have similarly been questioned, although current consensus, concerning taxonomic placement at least, trends towards those of the original describers (e.g., Richmond and Jungers 2008). Given the totality of the evidence, these forms can at present be considered probable hominids, with their more specific affinities to be determined by future fossil evidence.

The materials from *Ardipithecus ramidus* are more copious and conclusive. Over 100 specimens, from a minimum of 36 individuals including the female “Ardi,” have been described (White et al. 2009). This comparatively large sample confirms that both *Ardipithecus ramidus* males and females possessed small canine teeth lacking the aforementioned honing complex, with very little canine size differentiation (dimorphism) between sexes (Suwa et al. 2009). This is a very humanlike characteristic. Other aspects of the dentition, as well as limb proportions and features of the pelvis, hand, and foot are also derived in the direction of *Australopithecus* and *Homo* (Lovejoy et al. 2009a, b, c). While some initial reactions to *Ardipithecus ramidus* were critical, a holistic consideration of the materials available, including a detailed consideration of the cranial base, strongly tie *Ardipithecus ramidus* to later hominids (Kimbrel et al. 2014; Sayers et al. 2012). Whether *Ardipithecus* or another member of its group was directly ancestral to *Australopithecus* is an open question, although at present there are no other viable alternative candidates.

Locomotion

Locomotor behavior plays an important role in how a vertebrate explores its world. That humans

and our immediate forerunners walk (or walked) obligately on two legs is particularly intriguing, given not only that it is unique among primates, but that it makes us slower, more injury-prone, and much less capable of climbing than our non-human primate relatives.

The remains of *Ardipithecus ramidus*, with respect to movement, are an interesting mix of the primitive, perhaps very primitive, and the derived. The foot retains the divergent, grasping big toe of other primates, and indeed has been argued to be, in some respects, more similar to an Old World monkey than that of an ape. At the same time, it shows the dorsal cant of the proximal foot phalanges common to all later hominids (Lovejoy et al. 2009a). The pelvis in outline is short top-to-bottom and wide side-to-side – although this is more apparent in the humanlike upper pelvis than the ape-like lower – and its rotated ilium indicates a reorientation of the gluteal muscles that would have helped prevent “pelvic-tilt” during two-footed, upright movement (Lovejoy et al. 2009d). The legs were likely somewhat longer than the arms, trending in the later hominid direction; the hands evince no evidence of the knuckle-walking seen in extant African apes (Lovejoy et al. 2009b, c). A partial foot skeleton from 3.4 Ma, from the central Afar of Ethiopia, indicates an animal with an *Ardipithecus*-like foot living contemporaneously with australopithecines that possessed a more human-like lower appendage (Haile-Selassie et al. 2012).

Taken together, *Ardipithecus ramidus* has been characterized as a “careful climber” in the trees and a “facultative biped” on the ground. Unlike living apes and monkeys, which can and often do walk bipedally for at least short distances, *Ardipithecus ramidus* appears to exhibit skeletal adaptations for this strange mode of progression. The most likely interpretation is that of a transitional biped with only a subset of the distinctive locomotion-related characteristics found in *Australopithecus* and *Homo*. The limited sample from earlier suspected hominids is consistent with a similar diagnosis, although a fuller appreciation of their locomotor repertoire can only come with further fossil discoveries.

Ecology and Behavior

Finding food, avoiding predators, and producing offspring have long been recognized as the primary concerns of animals. The generalized dentition of *Ardipithecus ramidus* – with small incisors, relatively thick enamel, and lack of shearing surface – suggests a more varied, omnivorous diet than the mainly fruit-and-leaf fare of extant great apes. *Sahelanthropus*, *Orrorin*, and *Ardipithecus kadabba* varyingly share elements of this structure (Suwa et al. 2009). At the same time, locomotor limitations, ape-sized brains (300–370 cm³ based on a sample of two), and an apparent lack of modified stone tools associated with members of the *Ardipithecus* group suggest comparative limitations in abilities for the hunting of mobile game, as seen occasionally in living chimpanzees and bonobos (or with tool-assistance in *Homo*). The evidence suggests the beginnings of a marked dietary and ecological generalism that only increased with later hominids, and which the demographic success of this group was likely dependent upon (Sayers and Lovejoy 2014).

The locomotor traits of *Ardipithecus ramidus* suggest a relatively helpless animal little enabled to escape potential predators via speed and agility when compared to living great apes. Associated carnivores include hyenas, large cats, and bears; indeed, carnivore tooth marks are common on *Ardipithecus* remains, although the degree to which this represents predation versus scavenging has not been determined (WoldeGabriel et al. 1994). Also unknown is the degree to which members of the *Ardipithecus* group used their wits to avoid predators; later australopithecines, which also have modest brain sizes, do show endocast evidence of neural reorganization that might have been marshalled to meet such challenges. Evidence for comparison in the *Ardipithecus* group is limited, but preliminary work suggests that such changes might date to as early as *Sahelanthropus tchadensis* at 6–7 Ma (Bienvenu et al. 2013).

Then there is the matter of sex. The unimposing canines in members of the *Ardipithecus* group, and confirmed lack of canine dimorphism and lack of a functional honing

canine/P₃ complex in *Ardipithecus ramidus*, suggest a social system with less overt physical male-male competition than in extant great apes (Lovejoy 2009). In other words, gorilla-like polygyny is unlikely. Currently available evidence also suggests limited skeletal body size dimorphism, which would reinforce this conclusion (White et al. 2009).

Repercussions for the Savanna Hypothesis of Human Origins

In his *Philosophie Zoologique*, Jean-Baptiste Lamarck (1809/1984, p. 170) suggested that chimpanzee-like protohumans might have given up the habit of climbing trees “by force of circumstances.” At the same time, he reasoned, early human progenitors may have habitually stood upright to be able to see over long distances, resulting in an erect disposition and a foot that could no longer be used like a hand. The implications were that human origins might have occurred in a relatively open area. Such were the roots of the savanna hypothesis – the idea that humans initially evolved on relatively dry plains, while apes stayed in the forests – which would hold sway in paleoanthropology over the next two centuries (Bender et al. 2012). Reconstructed *Australopithecus* and early *Homo* habitats, while no means limited to savanna-like locales, included enough open country elements that the hypothesis was considered mainstream, if not accepted wisdom.

Findings associated with the *Ardipithecus* group present a definite challenge to this scenario. The fossil forms considered here lived in environments with varying amounts of canopy cover. The most detailed and damning reconstructions have been attempted for *Ardipithecus ramidus*. While the general environment where they lived consisted of a mosaic of ecotypes, the *Ardipithecus* remains themselves are strongly associated with woodland fauna. The woodland diagnosis is also compatible with isotopic evidence indicating an *Ardipithecus* diet heavy in C₃ plants and/or the animals which fed on them – most woody plants use a “C₃”

photosynthetic pathway, while four-carbon pathways are characteristic of those from dry or seasonal locations (Louchart et al. 2009; Suwa et al. 2009). If the postcranial features of *Ardipithecus* are indeed accepted as representing incipient adaptations for bipedality, then it is increasingly unlikely that this crucial shift occurred in an open habitat.

Repercussions for the Chimpanzee Model of Human Origins

Many workers have utilized living apes, especially the common chimpanzee, as anatomical or behavioral models of the last common ancestor of *Pan* and *Homo*, or of various early hominids. The influence this has had on a crucial part of the scientific process – how questions are framed – is probably incalculable. How do you get a human pelvis from a chimpanzee pelvis, while connecting the dots with fossils such as those from *Australopithecus*? How do you get a human social system from that of a chimpanzee?

Evidence from the *Ardipithecus* group – at present the fossils closest to the *Pan-Homo* last common ancestor – suggests that the wrong questions have been asked. None of these fossils bear an especially close resemblance to chimpanzees in major characteristics other than brain size. The postcranial elements suggest a contrasting style of locomotion, which by extension suggests differing strategies of finding food and evading predators. The dentitions and associated evidence also suggest differing foraging behavior from that of chimpanzees. And the meager, almost pathetic, canines suggest contrasting modes of association with fellow group members.

This does not lessen the importance of chimpanzees or any other animals in considerations of human origins. It merely indicates that, like all creatures, humans and their progenitors were and are unique. A holistic consideration of all evidence – from fossils, the archaeological record, many extant species, and evolutionary ecology – will be vital in ascertaining how they lived, and how the human form originated (Sayers and Lovejoy 2008; Sayers et al. 2012).

Conclusion

The *Ardipithecus* group includes those creatures most relevant to reconstructions of the *Pan-Homo* last common ancestor and earliest hominid evolution – and their fossilized remains have challenged several longstanding assumptions concerning hominid origins. Although their precise affinities to fossil and living primates are still being determined, future evidence from members of this group will undoubtedly shed further light on the human evolutionary journey.

Cross-References

- [Australopithecus Group](#)
- [Bipedal Locomotion](#)
- [Great Apes](#)
- [Orrorin tugenensis](#)
- [Paleoanthropology](#)
- [Primates](#)
- [Savanna Hypothesis, The](#)
- [Sexual Size Dimorphism](#)

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Ardipiths

► *Ardipithecus* Group

Arena Display

► Lekking

Argument from Nature

► Naturalistic Fallacy, The

Arguments

► Controversies

Arithmetic Mimicry

► Müllerian Mimicry

Arizona Life History Battery (ALHB)

► K-Factor (Figueredo)

Arousalability

► Stress Reactivity

Arranged Marriages

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Synonyms

[Parental choice](#); [Parental mate choice](#)

Definition

An arranged marriage occurs when the decision about whom to marry is made, entirely or in part, by people other than the spouses themselves. Generally, marriages are arranged by parents and/or other close kin (older siblings, aunts and uncles, grandparents), though marriage arrangements

may also be the purview of lineage heads, tribal elders, clan chiefs, or bureaucratic representatives of state authority.

Introduction

Arranged marriages come in a variety of forms, from those in which the spouses have no part in the decision to marry to those in which the spouses exercise full control; for the sake of clarity, this continuum can be broken into four types:

1. In the strongest form of arranged marriage, marriage decisions are controlled entirely by others, typically parents and/or other senior kin, and spouses have no say in the matter – their consent is neither requested nor needed for the legality or cultural legitimacy of the marriage.

2. More commonly, marital decisions are left to others, but the spouses themselves may have some influence over the process, through persuasion or veto power, and may be expected to state their consent as part of a marriage ritual or by signing a marriage registry.

3. The least strict form of arranged marriage occurs when marriage decisions involve a collaboration between parents (or other senior kin) and the spouses themselves; in such cases the bride or groom is simply one among several decision-makers; an alternate form is when spouses choose their own partners but their choice is subject to approval by parents or others.

4. Finally, in the absence of arranged marriage, marital decisions may be made by the spouses themselves, autonomously, without the legal or social need for reference to others – though even in societies where autonomous marriage decisions are normative, parents and friends may still have some informal influence over decisions (Buunk et al. 2008; Goode 1959). Marriages in which spouses choose each other are also referred to as “courtship marriages.” There is a correlation between courtship marriage and the privileging of love or attraction as a basis for marriage – a practice typically known as “love marriage” (Coontz 2006).

Two common misunderstandings should be dispelled here: First, *a marriage which is arranged for one partner may not always be arranged for the other partner*. For example, marriages may be arranged between the wife's parents and the husband; this is an arranged marriage from the perspective of the wife, but not from the perspective of the husband, though the use of the term "arranged marriage" will still generally be applied to the marriage as a whole. Second, *arranged marriage is not synonymous with forced marriage*, as a large fraction of arranged marriages are made with either the explicit or implicit consent of the spouses and do not involve coercion. That being said, societies that prefer arranged marriage may tolerate the coercion of spouses in some cases, especially when parents and elders view a marriage to be in the best interests of the family, lineage, or spouse. In such societies, the ability of junior family members to resist marriage decisions may be limited, yet the anthropological literature describes a number of ways in which prospective brides and grooms, even those who are young and relatively powerless, resist arranged marriages to which they are opposed. If repeated refusal will not work, they can engage in verbal arguments, refuse to participate in marriage rituals, refuse to speak or eat, run away, or even threaten to commit suicide (Apostolou 2015).

In arranging marriages, parents or elders may focus on the characteristics of the prospective spouse and/or the characteristics of their parents or families. In societies where arranged marriages are common for dynastic reasons such as family status or inheritance, family characteristics (wealth, social connections, rank, caste, title) are often more important than the personal characteristics of the spouse. In contrast, societies that allow spouses more input or autonomy in marriage decisions often give more weight to the characteristics of the spouse. In general, parents have been shown to have more interest in economic or socially important characteristics of spouses, such as family background, status, and wealth (e.g., Apostolou 2012; Buunk et al. 2008), while children have been shown to have more interest in personal and physical characteristics

of prospective spouses, such as their youth, physical attractiveness, or personality traits (e.g., Apostolou 2012; Buunk et al. 2008). From an evolutionary perspective, another way of putting this is that parents may favor spouses with high potential for investment and cooperative behavior with family members, while children may prefer traits signaling heritable fitness (Buunk et al. 2008).

The study of arranged marriage has been of interest to anthropologists and some sociologists for decades but has more recently become a focus of study in evolutionary social science. While different in emphasis, these approaches draw our attention to several key empirical and theoretical points that should be considered when contemplating the evolution and function of arranged marriage.

Arranged Marriage Is Normative in Most Preindustrial Societies

A close study of the ethnographic record makes it clear that arranged marriage is in one form or another normative in a large majority of traditional human societies (Apostolou 2007, 2010; Walker et al. 2011), meaning that *systems of arranged marriage have been far more common historically and cross-culturally than have autonomous or "love" marriages*. This is true even in most small-scale societies, including hunter-gatherers; in fact, there is good reason to believe that arranged marriage has a deep history that is central to the evolution of human social organization (see discussion below; Chapais 2008; Walker et al. 2011). The fact that autonomous marriage decisions are the exception rather than the rule suggests that there are two important questions in the study of arranged marriage. We not only need to explain (1) why human marriages are so commonly arranged, when this practice evolved, and how this fits into the evolution of human social organization and mate choice but also (2) why marriage decisions in a minority of societies are autonomous and how this relates to patterns of arranged marriage in human evolutionary history.

Arranged Marriage Is Linked to Alliance Formation and the Retention of Rank and Resources

In most societies, marriage links the kin groups of a couple economically and socially, with important consequences for the living members of both families as well as future generations. Yet in many societies, spouses, and especially women, often marry at young ages; thus, the decision about whom to marry is thought to be too important to be left to a young couple who may not have the knowledge, experience, or judgment to make the best decision about how to forge such a critical alliance. In some cases, autonomous marriage may even be seen as threatening the social order (Goode 1959). Under such circumstances, marriages are often arranged based on considerations of family compatibility with respect to the strategic resource, status, or reproductive interests of the parents or family, emphasizing such characteristics as social rank, wealth, religion, political faction, potential alliances, spousal age, perceived fecundity, or perceived likelihood of investment from one or both spouses (Apostolou 2012; Flinn and Low 1986; Trivers 1974). Compatibility of the couple may also be considered but may not be a high priority.

Arranged marriage is more common – and more strictly observed – in societies where marriage is tied to important social obligations or property transfers (Apostolou 2010, 2012; Lévi-Strauss 1949/1969; Flinn and Low 1986). In such societies, marriage is viewed partially or primarily as a contractual or practical arrangement rather than or in addition to a personal relationship; thus, personal and social expectations about marriage are often very different than in societies where marriage is organized around personal choice and/or romantic attachment. Specifically, in cultures practicing arranged marriage, marriage entails formal obligations to multiple groups of people, including one's spouse, in-laws, parents, children, lineage members, and possibly others. It is commonly claimed that personal fulfillment will come through family life, including children, supportive kin, and a respectable social position. Romantic love for one's spouse is thought of as either something that will develop after marriage

or as too unstable and risky an emotion to be the basis for the crucial social and economic decision of marriage (Coontz 2006).

Arranged Marriage Is a Mechanism of Norm Enforcement

Arranged marriage is also a primary mechanism by which marriage rules and customs are developed, perpetuated, and enforced (Apostolou 2013; Chapais 2013, 2014; Flinn and Low 1986); these include rules of exogamy (marriage outside of a socially defined group), endogamy (marriage within a socially defined group), preferential marriage norms (e.g., cross-cousin marriage), hypergyny (women marry into a higher social rank), and isogamy (women and men of equal rank marry). Rules of exogamy, for example, are generally thought to function to expand social connections to other families, lineages, or clans (Chapais 2013, 2014; Flinn and Low 1986; Lévi-Strauss 1949/1969); exogamy may also reduce competition within social groups and promote cohesion in larger social units. Endogamy, by contrast, maintains group boundaries, including those of social classes or castes; allows the retention of wealth, rights, and privileges within families or social groups; and maintains social compatibility among spouses (Flinn and Low 1986; Lévi-Strauss 1949/1969). Autonomous choice by spouses, particularly those marrying at young ages, may discount such customs in favor of personal attraction, while parents, kin, and elders may have a greater stake in the perpetuation of such norms which they perceive as serving the strategic interests of themselves and their extended family or kin group, many of whom may be affected economically or socially by marriage decisions (Coontz 2006).

Arranged Marriage Is an Evolved Practice with a Deep Evolutionary History

Humans resemble many other animals in that we form pair bonds. However, human mate choice is

not just about mating. Most human reproduction occurs within marriage and human marriages virtually always entail a complex series of cultural customs, rituals, norms, rules, restrictions, and sanctions that are culturally evolved and which serve to define the material/economic and social functions of marriage for a couple as members of kin groups and society at large. There are no clear equivalents of either marriage itself or the practice of marital arrangements among nonhuman animals (Chapais 2013, 2014; Flinn and Low 1986) making marriage both a human universal (or at least a near-universal) and also part of the argument for human uniqueness (Chapais 2008; Walker et al. 2011).

Classic evolutionary characterizations of mate choice among most species of animals – especially mammals – often emphasize the concepts of male competition and female choice, in which relatively low-investing males are seen as competing over the chance to mate with high-investing females (Trivers 1972). Though following the mammalian pattern of higher obligate investment by females (due to lengthy internal gestation and long periods of lactation), human mate choice frequently does not follow this pattern. In fact, as Apostolou (2007, 2010, 2012) and others (Buunk et al. 2008) have argued, in human societies, marriage is far more often controlled by parents or senior kin, or by husbands, and relatively infrequently by women themselves, making “female choice” – though a common assumption of evolutionary psychology models – a questionable assumption about or descriptor of human marriage behavior. In fact, “parental choice” has likely been just as important, if not more important, than female choice in human evolutionary history. Relatively unrestricted mate choice may be common in modern Western societies, but free choice of sexual or marriage partners has not been normative either historically or cross-culturally.

Arranged marriage is not just normative in preindustrial societies in general but also among modern foragers living in disparate parts of the world, suggesting that parental choice is likely to be ancient and may characterize the evolution of humans as a species (Apostolou 2007; Chapais 2008, 2013; Walker et al. 2011). In fact, a

phylogenetic analysis of marriage practices among foragers by Walker et al. (2011) suggests that arranged marriage is likely to be at least 50,000 years old. Moreover, many scholars (e.g., Chapais 2008, 2013, 2014; Coontz 2006; Lévi-Strauss 1949/1969) have made the argument that marriage evolved – or at least has as one of its primary functions – to create and/or cement alliances between families or lineages. This suggests that the practice of arranged marriage may have coevolved as a key aspect of the practice of marriage itself.

Two Evolutionary Models of Arranged Marriage

Evolutionary theorists generally view arranged marriage as a functional custom that arises as a result of past fitness benefits to parents/kin and the children for whom marriages are arranged – though the practice may be retained either because it continues to be functional or because of cultural evolutionary forces that make it difficult to change. There are two primary evolutionary perspectives on arranged marriage:

1. That parents and children have greatly overlapping fitness interests such that parental involvement in marriage decisions can be viewed as a form of parental investment beneficial for the child and the parent alike
2. That arranged marriage is a form of parental manipulation by which parents “win” a parent-offspring conflict over mate choice

As discussed above, since arranged marriages lie on a continuum from more to less coercive, these perspectives are not necessarily in opposition. Forms of arranged marriage in which children have some degree of choice or veto power, as well as situations in which children approve of and/or cooperate with parental decisions even if they were uninvolved in the process of decision-making, are more likely to represent mutually beneficial situations and/or milder forms of parental manipulation, whereas forms of arranged marriage in which parents have full power, or in which

offspring objections are ignored or overruled, are more likely to reflect parent-offspring conflict and stronger forms of parental manipulation.

Arranged Marriage as Parental Investment.

The social and genetic interests of parents and offspring overlap substantially given that they share 50% of their genes, that children represent parental fitness prospects, and that children are dependent upon parental investment for their own fitness prospects. For these reasons, both parents and children may benefit from shared decision-making about marriage, and, in fact, children may benefit more because of parents' greater social status, resource access, experience, and bargaining power. In fact, in many societies, a lack of parental participation in offspring marriage decisions may negatively affect the ability of children to obtain high-quality spouses or negotiate marriages.

Indeed, to the degree that parental interests overlap with those of their offspring, parental involvement in marriage decisions can be viewed as a form of parental investment in which parents (or other relatives) use their wealth, social rank, or alliances to improve the marital and thus reproductive prospects of children (Trivers 1972), particularly if children marry at young ages, when their own resource holdings, social rank, or negotiating powers are limited. Arranging a good marriage can directly improve reproductive prospects by enhancing the resource access and social status of the child, grandchildren, and future generations. In fact, marriage costs can be seen as a means of purchasing or securing the parental investment power of the spouse and his or her family for the benefit of grandchildren. Moreover, using one's influence or resources to arrange a good marriage for one child/relative also aids other children in the family by improving their social connections and access to wealth – indirectly improving their marriage prospects – and thus their potential long-term status, resource access, and fitness.

There is ample evidence that parental resources in the form of land, animals, household goods, houses, cash, education, and specialized skills – either transmitted through inheritance or marriage payments, or embodied in the characteristics of

the spouse – allow children to marry higher-status or wealthier partners, to marry at younger ages, or to have greater earning potential than would be the case without such investment (Boone 1986; Flinn and Low 1986; Kaplan 1996; Voland 1998). Moreover, the death of a parent before a child's marriage may have a negative effect on the status of the spouse obtained (Voland 1998). We could also predict that in societies with arranged marriage, parents will be more effective than children at obtaining high-status spouses on the marriage market and that people in arranged marriages will have higher quality spouses on average than those in love marriages, though these predictions have not been tested. Additionally, if polygyny results from mutualistic arranged marriage decisions, women in monogamous and polygynous unions should have similar levels of reproductive success, as is the case among the Kipsigis (Bergerhoff-Mulder 1990).

Arranged Marriage as Parental Manipulation of Offspring Mate Choice.

Arranged marriage may also be seen as a classic example of parental manipulation of offspring mate choice in the contest of parent-offspring conflict. Though all else being equal, parents are expected to invest evenly in all of their offspring, offspring are twice as related to themselves as to their parents, siblings, or offspring, creating an inherent motivation for parent-offspring conflict and sibling rivalry over the direction and degree of parental investment (Alexander 1974; Trivers 1974). Natural selection favors both sides of this conflict – children who are able to obtain more resources from parents and parents who are able to resist such attempts at manipulation – leading to an arms race whereby neither parents nor children have a consistent evolutionary advantage (Alexander 1974; Trivers 1974). Yet in humans, more so than in other animals, parents often control resources needed by offspring to effectively survive, reproduce, and compete for mates and resources – meaning that human parents may be more consistently favored in some types of parent-offspring conflict (Alexander 1974; Apostolou 2007; Buunk et al. 2008).

Where parents have more power than children, by virtue of their age and physical size (especially

when compared to young children), their higher status in the group, or their control of wealth and privileges (Alexander 1974), parents are expected to use their influence to arrange marriages for their children to assure the strategic interests of the parents in terms of both proximate goals, such as wealth or social status, and ultimate goals, such as long-term fitness. However, in societies where children have greater economic independence or physical autonomy, they may be more effective at subverting attempts at parental control of marriage decisions and instead be able to make decisions focused on their own social and reproductive interests (Apostolou 2011). The fact that marital arrangements operate on a continuum cross-culturally from full parental control to virtually no parental control and that significant flexibility also exists within cultures by social class and gender suggests that this is an area of active strategy and negotiation strongly affected by individual and family characteristics as well as local socioecology.

Since human parents or other senior kin generally control important resources (Boone 1986; Flinn and Low 1986; Voland 1998), to the degree that reproductive decisions are related to resource access, parents are likely to use these resources to exert control, or at least influence, over the marital decisions of their children of both sexes (Apostolou 2007). Likewise, for children in many human societies, access to resources and status are highly dependent on parental resources or status, meaning that the most effective reproductive strategy may be to allow one's parents to control one's mating and marriage decisions in order to ensure continued access to or inheritance of parental resources (Apostolou 2010; Voland 1998). In contrast, securing one's own resources may allow more control over mate choice, including marriage decisions, but the benefits of such actions may not outweigh the costs.

Key Factors Affecting Who Controls Marriage Decisions

There are several cross-cultural patterns with respect to whether, how often, or for whom

marriages are arranged. These patterns are causally interrelated but separated here to highlight trends useful for predicting the likelihood or form of arranged marriage, either across societies or between individuals in different socio-ecological positions within societies.

Age of Marriage

Arranged marriage is more common in cultures with younger ages at marriage. A common emic rationale for this is that given their lack of life experience, young people are unable to make good choices about marriage partners, and thus parents or other senior kin need to make these decisions for them. An alternative explanation (e.g., Apostolou 2007, 2010, 2012), is that when children are married at younger ages, parents will be more effective at implementing or enforcing their own choice of spouse, since children will be economically dependent and less able, either physically or socially, to resist parental decisions.

Gender

Cross-culturally women are more likely than men to have their marriages arranged for them and are also less likely to have influence over jointly made marriage decisions (Apostolou 2007, 2010). For example, the standard cross-cultural sample suggests that courtship (autonomous) marriages are the dominant marriage form of first marriages for women in only 8.3% of forager societies but the dominant form of first marriages for men in 40% of forager societies (Apostolou 2010). This pattern strongly covaries with age at marriage (as women often marry younger than men) and the economic autonomy of the spouses (cross-culturally men are more likely than women to be economically autonomous at the time of marriage).

Evolutionary social scientists have linked this pattern to the relative reproductive value of women on the marriage market. Given the larger obligate parental investments made by women (larger gametes, gestation, lactation), female parental investment is a limiting resource among humans, such that, in most ecologies, males are expected to compete over it (Trivers 1972). Parents of daughters will thus tend to have greater

leverage in the marriage market and are expected to use this leverage to exert greater control over the reproductive choices (including the marital decisions) of daughters as compared to sons (Apostolou 2007, 2010, 2012; Perilloux et al. 2008). With much to lose should a daughter receive less than her value on the marriage market, if only by way of lost opportunities, parents are expected to attempt to preserve her value by engaging in forms of “daughter guarding” (Perilloux et al. 2008). Yet parents are still expected to control or influence the marriage decisions of sons when possible, especially in high-status families or in circumstances of high paternal investment (Apostolou 2010, 2012).

Mothers are also less likely than fathers to be involved in marriage decision-making and may have less influence than fathers when they are involved (Apostolou 2007, 2010), though this pattern is more pronounced in agricultural and/or pastoralist societies in which marriage decisions are based on property and where property is often controlled by men.

Material Wealth

Marriages are more likely to be arranged in societies or subcultures where material wealth, heritable property, or physical capital are transferred at marriage or inherited only by the heirs of legal or socially recognized marriages (Apostolou 2010; Boone 1986; Flinn and Low 1986). The wealth being transferred is typically under parental control, giving parents influence over spousal decisions. Parents have strategic interests in seeing their wealth go to their children or their children’s families; thus, they are often interested in marrying their children to high-quality spouses with good connections and use their control of the purse strings to influence or enforce marriage decisions (Apostolou 2007, 2010, 2012; Buunk et al. 2008), even in modern industrial societies where parental influence on marriage is more limited (Apostolou 2011). In general, if there are larger marriage payments (bridewealth, dowry, indirect dowry) given at the time of marriage, or larger amounts of property to be transferred by parents to heirs, we should expect greater parental control of marriage decisions.

Titles, Rights, Statuses, and Offices

Marriages are more likely to be arranged in societies or subcultures where titles, rights, statuses, or offices are transferred at marriage or inherited by spouses or children through marriage. Examples are numerous cross-culturally, including the hereditary titles of the European aristocracy which were typically inherited patrilineally but only through church-sanctioned marriages and the inheritance of Jewish ethnicity through the mother among many Orthodox and Conservative Jews.

Family Alliances

Marriages are more likely to be arranged in societies or subcultures where alliances between families are of greater economic and/or political importance. Such alliances can be either made or strengthened through marriage, and the choice of spouse will affect not just the status and opportunities of the individual getting married but also the status and opportunities of the parents, siblings, and other more distant kin (Chapais 2013, 2014; Coontz 2006; Flinn and Low 1986; Lévi-Strauss 1949/1969). A good marriage can build family wealth and connections, while a bad marriage presents a significant loss in terms of opportunity costs. The more important such alliances are to family fortunes, the more control parents are likely to exert over the marriage decisions of their children.

Economic Independence

Marriages are more likely to be arranged in societies or subcultures where children are economically dependent on their parents. Economic dependence is common among children and adolescents in most cultures and among adult children in societies where subsistence relies on access to heritable resources such as land or animals. Increasing economic independence of children, due in large part to education-based job markets and late marriage, is one reason that the transition from agrarian to market economies is often associated with reduced parental control over marriage and increased marital choice by children (Apostolou 2011). This is also one reason why marriage decisions of daughters are more likely to be controlled than those of sons, since cross-

culturally, daughters are more likely to be economically dependent as adults and are married at younger ages when most children are still economically dependent (Apostolou 2007, 2010, 2011). The colonization of new territories may also have allowed for more spousal choice because of the existence of a frontier where young people without property could obtain land and resources without parental help (Voland 1998).

Laws and Institutions

A cultural evolutionary perspective draws our attention to the presence of institutions that may impact marital decision-making. Such institutions are the result of cultural evolutionary processes in which social norms, customs, or laws evolve as a means of adaptation to the physical environment, subsistence practices, and the social environment and may subsequently serve to constrain individual decisions in line with cultural niche construction (e.g., Odling-Smee et al. 2003). In a separate line of reasoning, Chapais (2014) has argued that arranged marriage is an example of an “evoked universal” in which the unique human kinship configuration interacts with aspects of the social, technological, and physical environments to produce cultural practices such as arranged marriage under predictable circumstances.

Institutional systems may affect whether marriages are arranged as well as who has the authority to arrange marriages. In societies where kinship provides a primary means of social organization, family or lineage heads might be responsible for arranging marriages, but chiefs or maximal lineage heads might play this role instead – or at least have to approve of marriages arranged by families or lineages (e.g., Harrell 1997). Alternatively, in preindustrial state societies, the power to arrange marriages might rest with the family head but might also be held by local government officials (Gose 2000; Harrell 1997) unrelated to the individuals whose marriages they are arranging. In fact, in some pre-industrial societies, the ability to arrange marriages for lineage members, coalition members, or subjects may even be seen as an attribute of good leadership (Chagnon 1967).

In contrast, traditional systems of marital arrangement may be challenged either by changes in subsistence practices which increase child autonomy and age at marriage, putting pressure on such systems from within, or increasingly by the application of international norms imported from industrialized countries, either as part of colonialism over the last several centuries or globalization in the present and recent past. Such new norms or laws may impact age at marriage, marriage payments, the transfer of marital or family property, or the form that consent to a marriage must take (Harrell 1997).

Missionaries, boarding schools, and colonial legal systems have especially eroded the authority of families to arrange marriages by:

- (a) Enforcing norms or laws allowing or prescribing that all individuals, but especially women, formally consent to marriage (e.g., Hanks and Hanks 1950; Mason 1967)
- (b) Directly undermining the rights of families to arrange marriages sometimes by substituting the authority of priests or mission schools (e.g., Hanks and Hanks 1950) but also by removing or reducing the traditional requirement for family approval
- (c) Making and enforcing norms or laws that prevent the marriage of children or adolescents (Apostolou 2013; Mason 1967), thus raising the age at marriage and putting individuals in a better position to influence their own marriage decisions.

Such changes were often made in the context of other attempts to alter indigenous marriage systems, including attempts to eradicate polygyny, polyandry, the levirate, or child marriage.

While legal changes may technically put decision power in the hands of children over parents, unless children also achieve economic or social independence of their parents, we should expect poor enforcement or uptake of such laws in places where children are more economically dependent, or where traditional dynastic considerations with respect to marriage (property, offices, alliances) still obtain.

Arranged Marriage Is Patterned by Subsistence and Social Organization

While human social behavior is highly diverse and thus any attempt at predicting practices of arranged marriage (or any other custom) cross-culturally is inherently tricky, there are broad patterns that are useful in understanding the custom of arranged marriage in evolutionary perspective as well as trends in arranged marriage in the modern world.

Arranged marriage is common among hunter-gatherers, particularly for first marriages and for women (Apostolou 2007; Harrell 1997). Apostolou (2007) reports that of 190 extant foraging groups for which sufficient ethnographic data exists, 69.9% had marriage that was primarily arranged by parents, 17.7% had marriages primarily arranged by the kin group, 8.1% had marriages arranged through courtship subject to parental approval, and only 4.3% of societies had courtship as the primary form of marital arrangement – though it should be noted that these numbers best classify the situation for women's marriages and first marriages, as men's marriages and second marriages are less likely to be arranged. Additionally, Walker et al. (2011) report 85% prevalence of arranged marriage among hunter-gatherer groups. Similar patterns also obtain in horticulturalist groups (Chagnon 1967), suggesting that these patterns may be linked to (relative) egalitarianism rather than to subsistence per se.

Arranged marriage among foragers is not related to environmental variables such as temperature or latitude (Walker et al. 2011) but does covary with several social variables. Differences in levels of gender hierarchy and/or female autonomy may help explain differences among groups (Begler 1978; Friedl 1975), with groups that are more gender egalitarian allowing for more autonomy of choice, particularly for women, as compared to groups that are more patriarchal. Societies where a greater role is played by bride service or bridewealth are also likely to have a greater degree of parental control (Walker et al. 2011). While first marriages are commonly arranged, divorce (or at least informal marital dissolution) is relatively common in small-scale

groups, and second marriages are often not arranged (Harrell 1997). Arranged marriage is also associated with a higher prevalence of polygyny (Walker et al. 2011), though this relationship is often primarily driven by the arrangement of marriages for women (Marlowe 2003).

Arranged marriage becomes more common and control by parents or elders over spousal choice stricter, in agricultural and pastoralist societies where heritable wealth in land or animals become the most important resources and are often strongly associated with marriage decisions. For example, Apostolou (2010) finds that only 7% and 0% of first marriages for women and 23.2% and 16.7% of first marriages for men are *not* arranged in agricultural and pastoralist societies, respectively. Apostolou (2010) also identifies two important trends in marriage decisions when comparing foragers to agriculturalists and pastoralists. First is increasing control of marriage decisions by men (primarily but not limited to fathers), likely due to increasing male control of the means of subsistence (land or animals). Second is the increasing control that parents have over the marriages of their sons; as parents increasingly control property use and inheritance, sons are increasingly motivated to comply with their parents' and especially their father's wishes in terms of marriage partners. In contrast, among hunter-gatherers, where there is little heritable property, a man's personal characteristics, including his foraging abilities, are a key factor in marital decisions, giving him comparatively more power over his own marriage.

Agricultural and pastoralist societies are also often stricter with respect to marriage in other ways, for example, by making divorce impossible or difficult, as was common in many large state societies in Europe and Asia in the medieval and early modern periods under Christian, Hindu, Buddhist, and Confucian leadership (as well as in their colonies in South America and elsewhere). In such societies, property transfers at marriage, such as bridewealth or dowries, generally paid by parents, also become more common and expensive, increasing both the ability of parents to control marriage decisions and their motivation to do so (Apostolou 2012; Boone 1986; Flinn and Low 1986).

Arranged marriage practices have commonly broken down as societies have undergone colonialism, industrialization, market transition, and/or other aspects of economic development (Apostolou 2011; Coontz 2006). As discussed above, this pattern has been linked to both (a) the growing economic independence of children from parents, as is true in modern industrial societies where children earn money through wage-labor jobs based on skills training and/or formal education, and (b) subsequent or concurrent changes in laws that restrict the power of parents to control the marriage decisions of children, either by reducing their power to disinherit children (as with the introduction of the Napoleonic Code), by enforcing rules of spousal consent, or by introducing laws establishing a legal age of marriage (a practice common in both the colonial period and more recently).

Cross-References

- [Bridal Cost](#)
- [Ecology of Pair-Bond Stability](#)
- [Parental Investment Theory](#)

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Art

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Definition

Art is conventionally defined as the corpus of human activities devoted to creating visual, aural, language-based, and/or performance-related artifacts and processes that express an individual's (or a group's) imaginative ideas, concepts, and/or skills and techniques, these artifacts having been designed to be consumed by an audience and enjoyed for their aesthetic beauty, emotional engagement, and/or intellectual stimulation.

A Darwinian definition of art would be a little different from this type of conventional definition of the scope of art. Art can better be defined in evolutionary terms as those artifacts that are produced by means of activities and thoughts that employ the corpus of evolved psychological mechanisms that are adaptations which have been designed to engage and fulfill a set of evolved emotional and intellectual capacities for aesthetic pleasure, technical ability, creative construction, critical engagement, expressing individual identities, and relational human experiences. These artifacts can even be specific results of biological evolution – such as the skin of the

human body or the horns of mammals – treated as an artist's canvas (Carmen et al. 2012).

Although both of these two definitions focus on very similar *Homo sapiens* cognitive capacities, how these cognitive capacities have been created and how they then function through the production of art are conceived of in different ways across the two definitions. In the non-Darwinian account, *Homo* cognitive capacity for art is seen as being primarily of learnt origins, while in the Darwinian account, cognitive capacity for art is seen as primarily of evolutionary origins.

Introduction

This entry will examine the origins and adaptive function(s) of art (including literature) conceived in its broadest terms. It will first discuss theories of the general role of art in human culture, and it will then consider four interconnected types of art as individual case-studies of how evolutionary themes are found at the center of all artistic genres and practices. The four interconnected genres/styles are: prehistoric art, erotic/pornographic art, horror narratives, and the Gothic imagination.

These particular genres/styles have been selected in part because the main issues related to them – sex/reproduction and the avoidance of death-by-predators – are some of the most important issues facing animal life as it has evolved on planet earth, and in part because Charles Darwin explicitly placed both erotica (“making rude pictures”) and horror (“evolved symptoms of terror”) within his evolutionary framework for understanding the origin of instincts (Darwin 1874 [1871], 577, 1999 [1872], 309).

This entry will also develop and present (in outline) a novel sexual-fantasy theory of the evolutionary origins of art. As has previously (and rightly) been explained: “in our species, love and art are, I suggest, inherently related” (Dissanayake 2010, 144). The importance of the connection between reproduction strategies and artistic expression has previously been partially acknowledged in the literature, but its significance within

the Darwinian framework has not been fully understood. Through a sexual-fantasy theory of the origin of art, the connection between art and animal reproduction will be placed at center-stage of *Homo-hominid* evolution.

The Adaptive Function(s) of Art

It is common in the literature on the link between art and evolution to debate the various possible adaptive functions of art in relation to its evolutionary origins, such as the by-product theory, the exaptation theory, Darwin's own sexual selection or display theory, the social cohesion theory, and the cognitive development theory.

In the by-product theory, art is not itself seen as an adaptation but as a by-product of the evolution of other cognitive adaptations such as language. Related to this is the exaptation theory in which art evolved initially for one reason, say in conformity with the sexual selection theory, but then evolved to fulfill other adaptive functions over time.

In Darwin's sexual selection or display theory, artistic practices have developed as adaptations that assisted individuals in creating display ornamentation that facilitated success in reproduction (Darwin 1874 [1871], 573–577). In the social cohesion theory, art has developed in order to help facilitate shared attention and thereby strengthen the coordination of social activities among the group. In the cognitive development theory, art functions as a means by which individuals can develop and rehearse social interactions that in turn aid cognitive development (Boyd 2005). The specific adaptive functions of both pornographic art and horror narratives that will later be advanced in this entry fit partly within the cognitive development theory.

Also, it is important to stress that art is not just the physical objects conventionally understood to be art products alone, it is also the practices and behaviors associated with making, viewing, using, and interacting with these art objects in their totality (Boyd 2005, 162). Thus, both art objects themselves and artistic practices and behaviors have been subject to significant long-term evolutionary pressures.

Prehistoric/Erotic Art

It is currently the conventional wisdom that art as a general *Homo-hominid* activity originated sometime between 60,000 and 30,000 years ago (Mithen 1996, 176–178). Although one or two items possibly older than this have been discovered (Levinson 2002, 72), there is a clear clustering of a range of art objects that have been found at this later date-range.

The discovery of various ancient human-made artifacts with graphic sexual content has raised the question of whether they can accurately be described as prehistoric erotica or pornographic art. For example, a 28,000-year-old dildo, 28,000-year-old erotic Aboriginal rock art, the 25,000 year-old Venus of Willendorf, ancient Greek and Roman pottery decorated with nude figures engaged in sex acts, and the Turin erotic papyrus dated from 1150 BC, all clearly either relate to or depict various forms of sexual activity, and some commentators have consequently described these artifacts as the earliest known forms of pornographic art (Anon 2013; Taylor 1996, 120–123). Without further evidence showing precisely how they were used, it is not possible to decide whether they were meant to be used as pornography or not, although the possibility that they were remains (Miller 2010, 160).

Collating these examples of prehistoric erotica with the previously given date-range for the origins of art, this means that pornographic art could have originated alongside the earliest forms of *Homo-hominid* art. Further circumstantial evidence for this is that in contemporary foraging cultures, “young men make charcoal drawings of breasts and vulvas on rock overhangs, carve them on tree trunks, and scratch them in the sand” (Pinker 1999, 472).

It is certainly true that sex, fertility, and reproduction were very common themes of much of ancient art (Levinson 2002, 72). As has been explained:

Prehistoric art, much of which has explicit sexual content, obviously depicts the things that people thought about, but it may not fairly reflect what they actually did. A Stone Age rock engraving made in eastern Siberia . . . depicts a man on skis, attempting to sexually penetrate an elk. (Taylor 1996, 12)

Again, due to the lack of evidence about how it was designed to be used, it is unknown whether this image was meant literally or symbolically. It could have been designed to celebrate the pleasures of having sex with animals (literally), or it could equally have been meant to show how all animal species are one whole within nature (symbolically).

It is more certain that Chinese pillow books (starting around 200 BC) had functions analogous to that of some contemporary pornography, these being pragmatic manuals on how to have sex in a variety of different ways (Hart 2001, 40). However, the term “pornography” did not come into use in English until 1857, being derived from Greek terms relating to the description of the activities of prostitutes. In between the birth of *Homo-hominid* art in prehistoric times and the mid-nineteenth century, it seems reasonable to assume that both written descriptions and images of sexual activity designed for use as pornography were created and have existed for some considerable period of time. This means in turn that pornography is not a modern invention and has evolved over a significant period of time.

A Sexual-Fantasy Theory of the Evolutionary Origins of Art

Even if the sexual imagery created by hominids 30,000 years ago was not initially designed as erotica or pornographic art, pornography certainly evolved from this type of imagery and hence it is an evolution from the naturalistic portraits of human figures that had begun in ancient art. This is not evolution in the Darwinian sense but the function that pornography could fulfill might conceivably be (or become) adaptive.

This issue of whether pornographic art could be adaptive in the Darwinian sense is further complicated by the fact that sexual behavior has evolved over a long period of time. For example, it has been suggested that the birth of language was linked to the evolution of the imagination. Out of the imagination then evolved poetry and the sharing of fantasies, which in turn affected sexual behavior by facilitating mutual empathy

and contemplation in relation to heightening the pleasures of sex (Taylor 1996, 50–51).

The creation of imaginary universes is, it has been claimed, unique to human beings (Carroll 2007, 640). Darwin was aware of this suggestion and posited that the faculty of the imagination had been “of inestimable service to man for his progressive advancement” and linked it to wonder, curiosity, and “an undefined sense of beauty” (Darwin 1874 [1871], 93). He described it as follows: “The *Imagination* is one of the highest prerogatives of man. By this faculty he unites former images and ideas . . . and thus creates brilliant and novel results” (*Ibid.* 74). In Darwin’s theory, the aesthetic senses of both animals and human beings had evolved partly through processes of sexual selection, as the ability to evaluate the display ornaments of the opposite sex (inter-sexual selection: usually but not always female choice) was crucial to reproductive success.

A novel sexual-fantasy theory of the evolutionary origins of art could be constructed along lines that are extrapolated from this set of ideas. Dating the origins of the evolution of language is controversial, but as the latest date suggested in the literature is around 50,000 years ago, it seems likely that some form of language had evolved by the time that the ancient erotic art objects considered here were created (Buss 2004, 383). It has correspondingly been suggested that:

. . . [the development of] language was responsible for the considerable cultural differentiation observed in Africa in the period 100,000 to 50,000 years ago. The development of art to incredible levels of sophistication is typical of behaviorally modern humans in the last 40,000 years. (Cavalli-Sforza 2002, E47)

The evolution of language, therefore, predated the evolution of sophisticated art and it is a plausible hypothesis to suggest that the former may have been linked to the evolution of the latter.

A sexual-fantasy theory of the origins of art could be developed in relation to the evolution of language and then art as a result of sexual selection processes as follows. As has been outlined, a number of changes in the sexual behavior of the *Homo* lineage developed as co-adaptations related

to an increased tendency to form long-term bonds between mates:

To aid in bond maintenance sexual activity is enhanced through sexual selection. Improved bonds provide security for children and hence a greater contribution to later generations from the effective bond formers. Women cease to show estrus and are sexually responsive more or less continuously. Coition becomes very frequent and highly rewarding. (Crook 1972, 249)

Together with these behavioral changes, physical changes in *Homo-hominids* occurred that enabled this more rewarding sex, such as a reduction in body hair and the evolution of a relatively large penis compared to other primates, these being similarly enhanced through sexual selection pressures.

In parallel with these changes in *Homo* behavior and physical form, after language had first evolved and in line with the evolution of the brain that facilitated this development, the cognitive ability of humans to imagine, fantasize, and communicate about sexual activity greatly increased at this time. With the evolution of artistic expression that followed on from this, involving the bringing together of pre-existing modules of mental cognition to create a more general form of imaginative intelligence, both sexual and non-sexual themes were then explored as art in various visual media such as wood/stone carvings and cave paintings, and in various forms of narrative such as songs and poems.

The evolution of the human capacity for imagination and fantasy was also linked to the ability of humans to use art objects in various different functional capacities, including (potentially) as pornographic art. As has been explained, human beings exhibit a “huge repertoire of mental imagery and sensual feeling” for use in their erotic experiences (Dutton 2009, 100). Darwin allocated a special courtship function to song and he implied that poetry and thereby art had initially developed from this type of courtship display (Darwin 1874 [1871], 567, 570–572). The sexual-fantasy theory of the origins of art is consistent with the archeological record, as much prehistoric art has sexual themes, but it is not conclusively proved by it. It also fits with a previously articulated suggestion that the human

orgasm is a vividly aesthetic experience (Comfort 1961, 105, 111–112).

Moreover, prehistoric art with sexual themes is not exclusively male-orientated, as ancient phallic batons have been found that look very similar to modern dildos (Taylor 1996, 128). Female sexuality was, therefore, expressed in erotic art from its very beginnings. As has been explained about the wider significance of female eroticism:

We must not believe that sexuality and the erotic for primitives were limited solely to the experiences of intercourse and orgasm. In practice sexuality, and especially female sexuality, is functionally expressed in pregnancy, birth and suckling no less than in intercourse . . . the female sees sexuality and the erotic as embracing a far wider functional spectrum. (Rawson 1973, 5–6)

It is also significant that the loss of body hair as early hominids evolved into modern human beings acted to facilitate the decorative adornment of the body (Taylor 1996, 98), the latter being a key part of the sexual selection theory of the origins of art.

It would be possible to combine the sexual-fantasy and the sexual selection theories of the origin of art into a single approach, which would hypothesize that both sexual fantasies and sexual enhancements partly found expression in the evolution of the decorative adornment that is central to the sexual selection theory of evolution.

The Adaptive Function(s) of Narrative Art

Another key evolutionary development for *Homo sapiens* art was the development of behavioral adaptations to assist in predator avoidance. In the Pleistocene environment of evolutionary adaptedness (EEA), violent threats to human life came from two main sources: attacks by animal predators (e.g., lions, tigers, bears) and by other human competitors (either in-group or out-group). Consequently, predator avoidance was a key skill that was required for survival (Tooby and Cosmides 2001, 15; Barnett 2018a).

It has consequently been hypothesized that a specific mental module or dedicated neural

network evolved to deal with predator avoidance issues that today can be detected in children as young as 3 years old (Buss 2004, 94). This anti-predator defense system has cognitive, auditory, olfactory, and visual components designed to detect specific aspects of predator behavior. The visual component is especially important, as detecting predator movements was a key defensive ability (Barrett 2005, 205), that was linked to the attention-summoning component of the emotions of horror and terror (Tooby and Cosmides 2001, 18). The emotions of terror and horror have, therefore, evolved in direct response to the threats to human life that were represented by animal predators and human competitors.

Horror narratives/art – or the predator-prey interaction *genre* – has an enduring popularity because its evolutionary equivalents rehearsed scenarios of extreme threat and danger from predators that were much more prevalent among our evolutionary ancestors than they are today. The fact that horror narratives operate most effectively using visualized modes of storytelling is not, therefore, a coincidence (Barnett 2014).

However, if individuals waited until they were actually under attack before they thought about how to escape such predator threats, then their chances of survival were less than if they had previously rehearsed such scenarios in a safe environment, and understood strategies that could be used to escape from such encounters alive. Becoming familiar with the strong emotions evoked by murderous assault in a relatively safe environment is another function of predator narratives, so that such emotions do not become overwhelming when they are experienced in real-life situations, as is the further development of relevant brain circuitry (Tooby and Cosmides 2001, 16).

The oral re-telling of “campfire” tales of predator attacks or deadly inter-human conflict was one effective means by which knowledge of previous incidents could be transmitted from individual to individual and also across the generations (Sugiyama 2006, 328–329). Early forms of visual art such as cave paintings and ivory, bone and stone carvings may have served a similar function

(Bahn 1992, 361), enabling the visual recording of information about animal movements and behavior both figuratively and symbolically (Mithen 1996, 196). Also, related story narratives such as forager oral traditions contained information about hunting, gathering, and their associated localized dangers.

The more detail about past predator attacks that was conveyed in such narratives – how exactly did the lion attack and what were the nature of the injuries that it inflicted? – then the better this would be for understanding how such attacks could be avoided in the future. As a basic tenet of predator-prey interaction is that the strategies of both sides continually evolve in mutual antagonistic interaction, new narratives providing updated information on the latest developments in strategy and tactics are always required.

However, although the basic reality of predator danger was an evolutionary constant that was experienced by all humans in the EEA, the specific predators that early humans faced varied considerably in relation to their geographical location. Therefore, the folk-fiction of each region provided stories of the animals that were common to that area, and sometimes embellished the animal behavior with supernatural traits:

In tropic[al] countries we have stories of supernatural snakes, who appear in various forms, as were-snakes ... We also see in the tropics elephants, lions, tigers, baboons, gorillas, and so forth ... while in colder climes we have the fox, the wolf, the bear, and their confreres. In island countries we find a large element of the supernatural associated with fishes and sea-animals ... (Scarborough 1967 [1917], 233–234)

Consequently there is a direct correspondence between the dangerous animals found in local literatures and those found in local environments (Sugiyama 2006, 328).

The Evolution of Gothic Art

It has been suggested that the origins of eighteenth-century Gothic literature involved the rediscovery of old folktales and oral traditions that had survived through nonliterary forms of

propagation (Scarborough 1967 [1917], 6–7). The interpretation presented here requires that these folktales, for example, about the dangers of predators and the animal side of human nature, were subconsciously transformed as needed by those in the eighteenth century involved in fashioning the Gothic movement.

Gothic fiction was thus in part a re-imagining of much earlier – what were described by its creators as “medieval” – folk-representations of predator and other natural dangers. This link to the EEA was explicitly recognized by early writers on Gothic fiction: “When well conducted, a grateful astonishment, a welcome sensation of fear, will alike creep through the bosom of the Sage and the Savage” (Drake 1800, 141). Predator dangers were also recognized: “There are many animals . . . considered as objects of terror. As serpents and poisonous animals of almost all kinds” (Burke 1792 [1757], 120).

The Gothic imagination can thus be identified with certain key themes: an interest in nature, both real and imaginary; a concern for the medieval/EEA past environment; a preoccupation with the consequences of marriage; the unleashing of dangerous animal passions; and an interest in the supernatural generation of terror. Most of these themes have direct Darwinian translations.

As well as providing the physical environment for much of the drama portrayed in the Gothic novel, the commonly employed imposing architectural edifice of the castle provided a key metaphor employed in Gothic literature. The castle became a symbol of a noble family lineage and its contemporary problems, either personal, familial, or in wider social terms, e.g., as in *The Castle of Otranto* (1764) and *The Castles of Athlin and Dunbayne* (1789). The architectural edifice of the castle was therefore a metaphor for ancient family heritage and the history of a family clan. It is also no accident that the Gothic novel is sometimes labeled the Gothic romance: if the setting is often a castle, then the narrative often relates to matters of mating/sex.

Another early writer on this topic linked the Gothic imagination to the natural environment/EEA of what she called “the Celtic nations”:

Climate, temper, modes of life, and institutions of government, seem all to have conspired to make the superstitions of the Celtic nations melancholy and terrible . . . the genius of the mountain, the spirit of the floods, the oak endured with sacred prophecy, made men walk abroad with a fearful apprehension . . . On the mountains, and in the woods, stalked the angry spectre . . . (Montagu 2000 [1769], 36)

In the Gothic tradition, the natural environment/EEA was a key source of potential danger, with nature sometimes being seen as animated by powerful supernatural forces, this being a central feature of ancient and medieval superstitions.

This emphasis on environmental dangers links the Gothic imagination directly to the evolutionary function of horror narratives as was considered in the previous section. In the Gothic novel, “there is a decided and definite attempt to use the terrible forces of nature to reflect the dark passions of man” (Scarborough 1967 [1917], 13), indicating that predators can be human as well as nonhuman.

Moreover, the psychological origins of Gothic romance have been laid firmly in a long-previous period in which supernatural beliefs were much more prevalent than they are today, when people were more given to the telling of “all the folk-tales of terror than at the present time,” even though “the idea of the inter-relations of the passions of man and nature is not original with the Gothicists” (*Ibid.*). The birth of eighteenth-century Gothic literature was thus dependent on much older forms of storytelling and the link between the evolution of human nature and the natural world of the EEA, a conception which produced Dorothy Scarborough’s definition of Gothic literature as the eighteenth-century novel of terror that deals with medieval materials.

The poet Samuel Taylor Coleridge wrote two lectures in 1818 on “The Gothic Mind,” in which he connected the aesthetic concerns of the Gothic imagination with the geographical origins of the Goths as a people, declaring that:

... Gothic art is sublime. On entering a cathedral, I am filled with devotion and awe . . . The Goths . . . Gazing on their rugged mountains, surrounded by impassable forests, accustomed to gloomy seasons, they lived in the bosom of nature . . . the dark wild imagery of nature, which surrounded him, and the freedom of his life, give his mind a tendency to the infinite . . . (Coleridge 2000 [1818], 96–97)

Here is described a type of interaction with the EEA that is suggested by Darwin's theory of evolution by means of natural selection applied to mental architecture, i.e., contemporary evolutionary psychology.

Conclusion

This entry has attempted to locate sex/reproduction and the avoidance of death-by-predators as two of the most important issues of human life that have driven the evolution of those psychological mechanisms that are focused on artistic expression, and the related artistic activities that are generated by the relevant cognitive architecture of *Homo sapiens*. A novel sexual-fantasy theory of the evolutionary origins of art was also presented in outline, although this sexual-fantasy theory is speculative to a degree and cannot be proved beyond any doubt in a short encyclopedia entry on the wide-ranging topic of art in general. Three other short case-studies of prehistoric art, horror narratives, and the Gothic imagination were also presented as a means of linking the two key art-focused themes of sex and death-by-predators together.

It is certainly the case that erotica/pornography and horror are the two most controversial *genres* out of the very wide range of *Homo sapiens* art and literature. This is probably because they are – arguably – two of the most important, socially valuable, culturally influential, and aesthetically stimulating *genres* (Barnett 2017, 2018b). In fact, a case could be made that, actually, all artistic content produced by *Homo sapiens* falls broadly within these two *genres* widely conceived, with the inclusion of some significant content focused either on sex/reproduction (erotica/pornography) or death-by-[animal/human]-predators (horror) in all art. However, this broad categorization of all art content might prove a little controversial for a few commentators.

Pornography is conventionally defined as a work specifically designed to evoke a sexual response in the viewer, but it seems implausible to suggest that so-called nonpornographic imagery depicting clothed women and men is not similarly sexually stimulating: evolution has designed the human physique (and certain forms

of human interaction) to be arousing in any and all of their various presentations. So-called non-pornographic imagery of two clothed individuals who are interacting in sexual activity can be just as deliberately arousing as so-called pornographic (or nude) imagery of the same subject-matter, so the “deliberately sexualized imagery” definition of porn is not particularly precise.

The fact that erotica/pornography and horror currently constitute the least worthy and respected *genres* among most art and literary critics and are also regarded by these same critics – with a few notable exceptions, e.g., Comfort 1961 (on erotica) and Clasen 2012 (on horror) – as the least artistically significant *genres*, illustrates how lacking in understanding these critics are of Darwin's work and its direct consequences for understanding the evolution of all human behavior, including all artistic behavior.

Cross-References

- Art Production, Appreciation, and Fitness
- Cultural Evolution
- Fiction
- Human Visual Neurobiology
- Music
- Music and Hormones
- Play
- Pornography and Women's Short-Term Mating
- Sexual Selection

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Art Production, Appreciation, and Fitness

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Synonyms

Aesthetic display; Art; Creative expression;
Cultural display; Symbolic behavior

Definition

“Line, color, pattern, and/or form used by humans to modify an object/body solely to attract attention to that object/body” (Coe 2003, p. 173).

Introduction

Although there are hints of earlier art activity (Malotki and Dissanayake 2018), the oldest, uncontentious evidence of art behavior

consists of shell beads and engraved ochre dated to roughly 75 ka (Henshilwood et al. 2002). This tells us that art behaviors emerged in a hunting-and-gathering context and thus are not an outgrowth of conditions associated with “civilization” – agriculture, permanent settlements, high population densities, social stratification, personal wealth, and economic specialization. Their presence in forager societies makes these species-typical behaviors (Brown 1991) particularly puzzling, because they impose considerable time and energy costs yet appear to yield no fitness benefits. Consequently, opinion is divided over whether these activities are adaptations or by-products: one camp explores their possible adaptive functions (e.g., Miller 1999; Coe 2003; Hagen and Bryant 2003; Malotki and Dissanayake 2018) and another explains their emergence in terms of the preexisting cognitive capacities they co-opt (e.g., Pinker 1997; Verpoorten and Nelissen 2010). Resolution of this debate requires precise ethological parsing of the phenomena in question. Although often referred to collectively as “the arts,” different art forms recruit different cognitive and motor capacities. For example, the capacities involved in painting (e.g., using the hands to apply pigment to a surface in the form of patterned marks and shapes) are very different from those involved in dance (e.g., making repetitive, rhythmic movements with various parts of the body). This suggests that “the arts” are not a unitary phenomenon and may not share the same evolutionary trajectory. Moreover, modern societies tend to assign these behaviors to different categories (e.g., visual arts, plastic arts, temporal arts), which appear to be based on the chief sensory mode through which they are affected: vision (painting/drawing), touch (sculpture), hearing (music), and kinesthesia (dance). Because each of these behaviors prioritizes a different sensory mode, it is unlikely that all are generated by the same set of procedural rules. Yet the fact that these behaviors are aimed at the senses, perceived as belonging to the same ethological category, and often deployed ensemble suggests underlying similarities in structure or usage.

Identifying these congruencies is critical to resolving the question of adaptation.

Ethology, Ecology, and Adaptation

Cross-culturally, art behaviors and/or their outputs (i.e., objects, performances) share several characteristics. The most obvious is that they arouse attention and emotion, and are the product of agency. Although rudimentary, this observation enables us to rule out phenomena that are aesthetically arousing but not produced by agents, such as sunsets and rainbows. It also points to the manipulative nature of these behaviors: they consist of actions performed to provoke aesthetic emotional arousal (e.g., pleasure, excitement, joy, awe, curiosity). This distinction is readily apparent in modern market economies, in which millions of individuals regularly consume products (e.g., music, fashion, décor) engineered to elicit aesthetic responses, and other individuals specialize in the design, manufacture, and/or delivery of these products (Pinker 1997). Thus, art behavior can be characterized as aesthetic behavior, and parsed into (a) the aesthetic responses elicited and (b) the actions that elicit these responses. The former includes art appreciation, and the latter includes art production/performance.

Aesthetic behavior is not unique to humans: many species engage in aesthetic displays, typically in the context of courtship or territory defense. As in humans, these displays can be multimedia events, involving movement, sound, and/or visuals (e.g., male cichlids vibrate their body when displaying their egg spots to females), and some species (e.g., bower birds, puffer fish) even produce aesthetic artifacts. These behaviors appear to be aimed at eliciting aesthetic responses via one or more sensory channels. In some species, aesthetic displays are generated primarily by males, but in others both sexes participate. For example, courting pairs of red-crowned cranes (*Grus japonensis*) engage in coordinated interactive displays that resemble pair dancing in humans, and courting/mated pairs in many bird and several gibbon species engage in duetting

(Fitch 2006). These characteristics suggest that human art behaviors are analogous to signals, animal traits designed to influence the behavior of other agents via their sense organs (Krebs and Dawkins 1984). For example, Verpoeten and Nelissen (2010) argue that two- and three-dimensional iconic representations are analogous to mimics, signals that exploit existing sensory biases by simulating cues to which the bias is sensitive. Just as egg spots in male cichlid fish simulate female eggs, they argue, figurative art simulates real-world entities such as animals and landscapes.

Many human art behaviors appear to operate in a similar manner, simulating environmental stimuli that recurrently impacted human fitness and to which humans have evolved sensory (a.k.a. perceptual) biases (Eibl-Eibesfeldt 1988). These biases serve to direct attention and motivate fitness-promoting responses to potentially beneficial or hazardous entities in the environment (e.g., water, predators, mates), the effect of which is to make some stimuli in our environment more attention-getting and emotionally arousing than others. Perceptual biases also help us make sense of the chaos of sights, sounds, textures, and scents in the world around us. For example, humans find it easier to detect a dark figure against a light background than vice versa. This bias reflects a regular feature of the environment, where figures are often silhouetted against the brightness of the sky. Another bias is contrast, used to detect the edges of objects and topographical features, which is critical to identifying objects by shape and navigating the landscape. The human visual system is also biased toward pattern; since many animals have spotted or striped bodies, this bias is useful for detecting both predators and prey. Another important bias is the *peak shift effect*, whereby an exaggerated form of a preferred stimulus is found more attention-getting and arousing than its normal form (Ramachandran and Hirstein 1999). This effect is likely at play in the bright, saturated colors used in fashion and marketing, the amplified movements and postures used in dance, and the intensified acoustics (e.g., timbre, volume, rhythm) used in music.

Our visual system also attends preferentially to symmetry, which is an important cue of agency (Zoeller et al. 2018) and mate quality (Sugiyama 2016). This may account, in part, for the popularity of the human form in visual art, and its foregrounding in dance. Other stimuli mimicked by dance are self-propelled movement (another important cue of agency) and speed and direction of movement (critical to predator-prey discrimination; Barrett 2005). Eyes, too, are an important cue of agency, and eye direction (like motion) is an important source of information about intentional state, especially in the context of predator evasion (Barrett 2005). Across species, a direct gaze is widely interpreted as a threat, which may explain the cross-cultural prevalence of bulging, staring eyes in representations aimed at warding off evil (Eibl-Eibesfeldt 1988).

Humans also exhibit landscape preferences, which are hypothesized to aid in habitat selection and navigation (Orians and Heerwagen 1992). By directing attention to cues of habitat quality (e.g., routes, resources, hazards) and triggering aesthetic responses, these biases are believed to help guide decisions about when to move, where to settle, and what activities to pursue in a given locale. For example, research indicates that humans prefer environments that have water, large trees, a focal point, changes in elevation, semi-open space, even ground cover, distant views to the horizon, and repeated patterns. Many of these features facilitate scanning, interpretation, and navigation of the landscape; others are cues to the presence of plants, game, and predators. These cues and biases can be exploited in painting, photography, film, architecture, and interior design to attract attention and trigger affective responses. This may explain why landscapes are such a popular subject in many Western and Asian art traditions. Although this genre is absent in forager populations, weather, seasonal, and navigational cues (e.g., stars, moon, rainbow, lightning) are frequently depicted in their art and myth cross-culturally. For example, abstract representations of topographical features and routes (painted on bodies, artifacts, and rock faces) feature prominently in Aboriginal ritual (Mountford and Tonkinson 1969), and tales that

describe landmarks, topographical features, and travel routes are common across forager oral tradition (Scalise Sugiyama 2017). This emphasis on cues rather than holistic representations of the landscape may reflect forager information-gathering techniques; for example, Ju/wa men view their environment “not as scenery . . . but as a series of small, very distinct messages—a freshly broken twig, flattened grass without dew where an animal was resting, the footprints of a certain kind of beetle” (Thomas 2006, p. 179).

Acoustic biases related to language processing (e.g., rhythm, intonation) may also figure in art behavior (Eibl-Eibesfeldt 1988). These biases are exploited in verbal art (poetry, oral storytelling; Scalise Sugiyama 2017) and are likely at play in music and dance (Eibl-Eibesfeldt 1988). All of these art forms are characterized by rhythm which, depending on the tempo, can accelerate or decelerate breathing, and tends to synchronize behavior and coordinate action in groups. Melody, too, affects breathing. Lullabies, for example, slow listeners’ heart rate and make breathing more flat and regular; inhalation coincides with the rise of the melody and expiration coincides with the descent. Not surprisingly, jazz has opposite emotional and physiological effects.

In short, although perceptual biases did not evolve for art production or appreciation, they play an important role in these behaviors because they influence what we find attention-getting and emotionally arousing. Given that there is no evidence of a neural network dedicated to aesthetic sensation, emotion, or meaning (Chatterjee 2014, p. 28), perceptual biases are the most likely source of the emotional responses evoked by aesthetic artifacts and performances. Consciously or unconsciously, artists can use these biases to grab our attention and engage our emotions. On this view, art behaviors stem from the ability “to manipulate the mechanisms which underlie our perceptual bias to trigger aesthetic experiences” (Eibl-Eibesfeldt 1988, p. 33). Even though (unlike female cichlids) humans can distinguish between the real thing and a representation of that thing, the representation nevertheless engages us because it mimics

features that our perceptual systems are designed to notice and respond to. In terms of their emotional effects, then, animal signaling and art behavior appear to be analogous.

This leaves the question of whether, like animal signals, art behaviors are evolved traits. In nonhuman animals, signaling behaviors typically evolve from already existing movements that originally had no signaling function. For example, many signaling behaviors in birds can be traced back to preening, feather-settling, and temperature-regulating movements or movements that prepare for flight (Krebs and Dawkins 1984). Through this process, known as *ritualization*, the structure or behavior pattern acquires a new, signaling function. Signals can also evolve from existing signals that originally evolved for a different communicative function. For example, the crouching movement used in courtship by females of several songbird species appears to derive from the food-begging crouch of juveniles. In the course of ritualization, a trait may become modified in ways that increase its effectiveness as a signal – for example, it may become highly repetitive, exaggerated in amplitude, or stereotyped in pattern. This process may be driven, in part, by the peak shift effect, with more exaggerated forms of the signal outcompeting less pronounced forms.

Several researchers have noted that art behaviors exhibit ritualization—that “what the artist tries to do (either consciously or unconsciously) is to not only capture the essence of something but also to amplify it in order to more powerfully activate the same neural mechanisms that would be activated by the original object” (Ramachandran and Hirstein 1999, p. 17). Some see this tendency as evidence of adaptation. Dissanayake, for example, argues that the temporal arts (e.g., music, song, poetry, and storytelling) evolved from infant-directed speech, which is characterized by higher pitch, exaggerated pitch excursions, broader pitch and amplitude variation, slower speed, longer pauses, and increased repetition (Malotki and Dissanayake 2018). Certain aspects of infant-directed demonstration – e.g., greater interactiveness and range of motion, repetitiveness, and exaggerated facial

expressions and body movements (Brand and Shallcross 2008) – also appear to be at play in art behavior (Eibl-Eibesfeldt 1988; Scalise Sugiyama 2017). Miller, in contrast, sees these properties as evidence that art and other cultural behaviors evolved as courtship displays, on the logic that “comparison between courtship displays is easier if the displays share many elements in common so deviations indicating inferior production ability can be easily noticed” (1999, p. 78).

These claims are complicated by the fact that teaching also exhibits these properties. Csibra and Gergely (2009) show that the transmission of generalizable knowledge is characterized by the use of ostensive-communicative behaviors, or *natural pedagogy*. These behaviors are hypothesized to be signals that communicate (a) intent to transmit generalizable knowledge and (b) the intended recipient of that knowledge. Significantly, ostensive communication is highly ritualized, exhibiting marked use of repetition, pattern-with-variation, exaggeration, and interactiveness. This behavior is present in other species as well. For example, humpback whale song features “consistent repetition of certain units at the beginning or end of phrases [that] might represent a form of ‘rhyme’ that enables easier recall, paralleling a function of rhyme in traditional human oral traditions” (Fitch 2006, p. 192). This research is consistent with the hypothesis that art behaviors are signaling behaviors and leaves open the possibility that they are adaptations, but does not shed light on what (if any) their adaptive functions are. The use of exaggeration and repetition appears to be characteristic of signaling in general; it is not limited to art behavior, infant-directed speech/demonstration, teaching, or even to humans.

Csibra and Gergely’s research suggests the intriguing possibility that art behaviors are subsets of teaching behavior. This is consistent with evidence that art behaviors transmit generalizable knowledge (Marshack 1972; Mithen and Mithen 1990; Scalise Sugiyama 2017). Nor does it preclude the possibility of their being co-opted for other purposes, such as advertising mate or

coalition quality (Miller 1999; Hagen and Bryant 2003), promoting intragroup or intergroup cooperation (Jochim 1983; communicating ethnic identity (Pardoe 1995), Coe 2003; Malotki and Dissanayake 2018), or demarcating/defending territory (Parkman 1986; Hagen and Hammerstein 2009). Whatever their evolutionary trajectory, the forager ethnographic record shows that art behaviors are used for diverse purposes and that none appears to be dedicated to a single function. For example, body decoration (e.g., hair style, tattoos, jewelry) is used to establish cooperative relationships (Marshall 1976), initiate warriors (Mendoza 2007), celebrate victory in battle (Owsley et al. 2007), ward off evil or bring good luck (Bogoras 1904–1909; Mendoza 2007), mark social status (Ray 1938), enhance attractiveness (Bogoras 1904–1909; Chagnon 1997), and advertise hunting or fighting prowess (Bogoras 1904–1909). Similarly, music and/or dance are used in a range of contexts, including healing (Lee 1984), shamanism (Chagnon 1997), alliance formation (Chagnon 1997; Hagen and Bryant 2003), warfare (Mendoza 2007), hunting (Turnbull 1983), conflict resolution (Rasmussen 1929; Marshall 1976), and status competition (Rasmussen 1929). Parietal and portable art (e.g., painting, petroglyphs, cupules, decorated artifacts) are used in the performance of rituals (Mountford and Tonkinson 1969; Parkman 1986), to mark resource locations and territorial boundaries (Parkman 1986), and to assert patrimony and associated rights (Barbeau 1929).

The use of art behaviors for so many different purposes challenges the claim that any or all of them are adaptations, and makes it difficult to determine which application came first. However, it also points to a characteristic that distinguishes human aesthetic display from that of other animals: nonhuman species do not appear to invent novel aesthetic performances or products. Most are limited to one stereotyped form of aesthetic output. For example, bower birds decorate their nests, but individuals within a given species decorate their nests in essentially the same way (e.g., with blue objects). Animals in the wild produce neither the range nor the volume of aesthetic artifacts that humans do. The variety of

human aesthetic output begs the question of how a single mechanism or module could generate such a wide range of behaviors, and suggests that they are most parsimoniously explained as inventions, not adaptations.

This explanation accords with one of the most distinctive characteristics of our species: the ability to innovate. Lacking the keen senses and anatomical advantages that other animals possess, humans depend for their survival on *improvisational intelligence*, a highly developed capacity for inventing new ways of doing things (Barrett et al. 2007). This ability enables humans to invent solutions to problems as they arise, as well as solutions for storing and sharing this knowledge. It also enables them to devise means of deploying information tactically, in order to manipulate the mental states and behavior of conspecifics. The latter ability casts the social nature of aesthetic display in a Machiavellian light: the visual, plastic, and temporal arts may be cultural inventions arising from a motivation to influence conspecifics in ways that advance the fitness interests of the producer/performer. In short, whereas the aesthetic repertoire of non-human species is limited to evolved display behaviors, humans can invent new types of aesthetic display and new applications for them. In the course of experimenting with line, color, sound, movement, etc., our ancestors would have discovered the attentional and emotional effects produced through exaggeration, repetition, and figurative representation; discovery of the social applications of these effects would have followed shortly.

Their Machiavellian applications can explain not only the diversity of forms and contexts in which art behaviors occur, but the demographic patterns they exhibit. With the exception of infants, humans of all age and sex categories engage in these behaviors, which is what we would expect from a species that depends on invention, cooperation, and manipulation of conspecifics to meet the problems posed by its environment. At virtually all points in the lifespan, humans can increase their fitness by devising new ways of influencing the behavior of others. Under

such conditions, selection will favor motivational mechanisms that encourage and reward curiosity, exploration, and experimentation across the lifespan. On this view, art behaviors can be seen as a form of play (Malotki and Dissanayake 2018). The emotional rewards of play encourage organisms to explore and experiment in ways that advance development of capacities needed later in the lifespan (Tooby and Cosmides 2001). An example is subsong, which occurs during the juvenile period in birds with vocal learning. Characterized by “random, muted warblings of greater duration than ordinary song” (Ficken 1977, p. 579), in some species this behavior is essential to accurate song learning, and may be analogous to the role that babbling plays in language development (Fitch 2006, p. 190). Similarly, drawing, painting, and carving may develop motor skills involved in tool making; singing may develop capacities involved in language production; and dance may develop capacities involved in locomotion and (in group dancing) coordinated action. Recreational engagement in these activities may also provide opportunities to observe their effects on others and discover new contexts for their deployment.

The use of art behaviors to influence conspecifics points to their symbolic aspect. Although art behaviors can be used solely to attract attention and arouse emotion (e.g., fashion, décor, landscape design), they are typically suffused with meaning by their producers, audiences, or both. Thus, although not all symbolic behavior (e.g., drum telegraphy, notation, Morse code) is art behavior, all figurative art is iconic, and much “abstract” art is indexical or symbolic. Instructive here are the comparative mark-making abilities of children and captive chimpanzees. Both begin by scribbling and experimenting with the types of marks they can make on a surface; however, in the fourth year of life, children begin to make marks that are representative, whereas chimpanzees never advance beyond making scribbles and crude circles (Morris 2013). Moreover, children’s mark-making has a distinct developmental trajectory: in a study of nearly one million children’s drawings

from thirty different countries, Kellogg (1969) identified twenty basic scribbles that all children make, and five stages of drawing development that all children go through. At each stage, children generate marks of increasing complexity until, in the last stage, they produce marks that are referential. The crudeness of chimpanzee mark-making and its apparent lack of content are most parsimoniously explained in terms of *Pan's* comparatively limited capacities for invention, tool manufacture/use, social manipulation, and symbolic behavior. Conversely, because these capacities are highly elaborated in *Homo*, it is likely that their developmental trajectory structures the ontogeny of mark-making in children, and that mark-making and other signs (acoustic, gestural, tactile) are cultural inventions, not adaptations.

Conclusion

Although certain art behaviors are species-typical in humans, there is disagreement over whether they are by-products or adaptations and, in the latter case, over their evolved function. The ethnographic record indicates that, across forager societies, art behaviors are used for a wide range of purposes, and thus does not clearly support one hypothesized function over another. The strong congruencies between animal signals and art behaviors suggest that the latter are most parsimoniously explained as the result of complex interactions between evolved perceptual biases and adaptations for innovation, communication, symbolic behavior, and manipulation of the physical and social environment.

Cross-References

- ▶ [Language](#)
- ▶ [Machiavellian Intelligence](#)
- ▶ [Music](#)
- ▶ [Ostensive Communication](#)
- ▶ [Play](#)
- ▶ [Signaling](#)
- ▶ [Storytelling](#)
- ▶ [Symbolic Behavior](#)

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Articulation

► Differentiation

Articulatory Loop

► Phonological Loop and Rehearsal

Artificial Insemination

► Medically Assisted Reproduction

Artificial Selection

- Breeding Systems
- Eugenics
- Silver Fox Domestication Experiment

Artificial Stimulus

- ▶ Supernormal Stimulus

Artificially Exaggerated Stimulus

- ▶ Supernormal Stimuli (Konrad Lorenz)

Artistic Expression

- ▶ Music and Hormones

As a Precursor to Partner Violence

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Synonyms

Mate guarding; Proprietariness; Proprietary mate retention tactics

Definition

Some mate retention tactics, especially costly tactics aimed at keeping an intimate partner faithful, may be precursors to violence in romantic relationships.

Introduction

Cost-inflicting mate retention tactics are a form of mate retention in which one partner uses mate

retention strategies that are costly to the other partner. Cost-inflicting mate retention tactics may take a variety of forms and can include derogating a partner, threatening a partner or a rival, and checking the whereabouts of a partner (online or in person). Costs that occur may include reduced ability to seek an extra pair partner (i.e., a partner outside of the pair bond), feeling scared or intimidated, reduced ability to work or forage, and lowered self-esteem. Cost-inflicting tactics are typically thought of as being caused by sexual jealousy and are aimed primarily at keeping a romantic partner faithful, especially when there may be an increased risk of infidelity (Cousins and Gangestad 2007; Shackelford et al. 2005). It has been well documented that sexual jealousy often precipitates violence, including homicide (e.g., Wilson and Daly 1995). There are a variety of cost-inflicting mate retention tactics as described in the literature including vigilance, emotional manipulation, proprietariness, controlling behaviors, and mate guarding.

Types of Costly Mate Retention Tactics That Predict Intimate Partner Violence

Generally, mate retention tactics are employed to preserve romantic relationships, but not all mate retention tactics predict intimate partner violence. In a series of studies assessing the relationship between intimate partner violence and mate retention, researchers found that men's emotional manipulation, one type of costly mate retention tactic that involved men stating they would "die" if their partner left them, was linked with violence, as was men's vigilance regarding their partner's activities and monopolization of their partner's time (Shackelford et al. 2005).

In other research that assessed both partners in dating couples, men's use of the costly mate retention tactic proprietariness predicted physical aggression, while attentiveness, a benefit-provisioning mate retention tactic, did not predict violence. Proprietary mate retention tactics included time monopolization and vigilance about a partner's activities, as well as bad mouthing their partners to other men and telling

their partners they would not find a better mate (Cousins and Gangestad 2007).

Sex Differences in Cost-Inflicting Mate Retention Tactics

Although both men and women may inflict costs on romantic partners, much of the evolutionary literature has focused on men's use of costly mate retention tactics (e.g., Wilson and Daly 1995). Two reasons for the focus on men's costly mate retention tactics are that, firstly, men risk being cuckolded while women do not and, secondly, during the course of evolution, the costs and benefits of using various mate retention tactics may have been different for men and women. Women faced higher costs from any tactic that could put them in physical danger because women's offspring are dependent on them (Campbell 2001). The fitness payoffs for physical aggression are much lower for women than for men, and for this reason, there is a large sex difference in the use of physical aggression; men are much more likely to use physical aggression than women. This is not to say that women are never aggressive, but they tend to use verbal or other indirect forms of aggression (Bettencourt and Hernahan 1997).

When assessing the link between cost-inflicting mate retention tactics and intimate partner violence, the sex difference in physical aggression remains. Both men and women who believed their partner was sexually interested in someone else increased their use of proprietary mate retention tactics (Cousins and Gangestad 2007). However, proprietary men, but not proprietary women, were more likely to be physically aggressive toward a partner. This indicates that both men and women may benefit from use of costly mate retention tactics, but men and women assess which tactics will result in the largest benefit. Women may benefit from being proprietary, but proprietariness does not lead to physical aggression in women. While women receive fitness payoffs for proprietariness but not physical aggression, men receive fitness payoffs for use of both proprietariness and physical aggression.

Other research has not shown a sex difference in the link between costly mate retention tactics and physical aggression. For instance, Graham-Kevan and Archer (2009) did not find a difference in men's and women's use of controlling behaviors. They also found that controlling behaviors were correlated with physical aggression in both men and women, contrary to other evolutionary research.

Men's Use of Cost-Inflicting Mate Retention Tactics and Women's Fertility

Evolutionary theorists have predicted that men are more likely to use cost-inflicting mate retention tactics on women that are (a) young and (b) in the fertile phase of the menstrual cycle. Since women are not always fertile, men should seek cues of fertility in mates. One gross measure of fertility is age. Women that are postmenopausal are no longer fertile. Even younger women are only fertile for a small portion of the menstrual cycle, during the late follicular phase when there is a mature egg. In one study, researchers found that women's fecundity was related to men's use of control, but not to violence (Graham-Kevan and Archer 2009). In this case, women were considered fecund if they had no children and were under 40 or if they had a child over age 1 but under age 4. In a study assessing women's fertility status and their partner's use of mate retention tactics, researchers found that men were more proprietary when women were in high fertility, especially when women showed an interest in other men (Gangestad et al. 2002).

Fertile women may also use some forms of costly mate retention tactics more than non-fertile women. For instance, studies indicate that younger or fecund women, compared to older women, may isolate partners more (Graham-Kevan and Archer 2009), use more emotional manipulation (Buss and Shackelford 1997; Graham-Kevan and Archer 2009), conceal mates more, and cause more injuries toward their partner (Graham-Kevan and Archer 2009). Other studies show a different effect. For instance, in a classic

study on mate guarding, Flinn (1988) did not find evidence for higher levels of mate guarding among fecund women. Differences across studies may be due to how costly mate retention tactics are measured or which specific tactics are assessed.

Conclusion

Some forms of costly mate retention tactics have been linked with physical aggression. For instance, proprietariness has been linked with physical aggression in men, but not women (Cousins and Gangestad 2007), while controlling behaviors have been linked with physical aggression for both men and women (Graham-Kevan and Archer 2009). Infidelity risk appears to increase the use of costly mate retention tactics, but does not increase the use of benefit-provisioning mate retention tactics (Cousins and Gangestad 2007).

Cross-References

► [Prevention of Infidelity](#)

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A

ASD

► [Special Case: Autism](#)

Asexual Reproduction

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Assessment of Fighting Ability

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Synonyms

[Formidability assessment](#)

Definition

The process by which cognitive programs predict the winner of a physical conflict in order to make adaptive decisions about whether to engage in or withdraw from conflict.

Introduction

Although humans and other social species faced many different recurrent problems over evolutionary history, accurately gauging the fighting ability of same species competitors was undoubtedly a pressing concern. Organisms that could accurately identify competitors' fighting ability would have been better at assessing the likelihood of succeeding in a physical conflict, which in turn would have facilitated decisions to escalate or withdraw. In the long run, making strategic decisions based on accurate assessment of fighting ability would have led to a longer lifespan with more opportunities for mating, increasing an organism's reproductive success. Thus, it seems likely that natural selection would have favored the evolution of a cognitive program that could accurately assess fighting ability.

What Would a Cognitive Program that Assesses Fighting Ability Look Like?

To work well, a program that assesses fighting ability would have to be sensitive to cues that accurately track fighting ability. Such cues, including size, weight, and weaponry, are well documented amongst nonhuman animals (Arnott and Elwood [2009](#)). In addition, there is a long history of evidence that nonhuman animals can accurately assess the fighting ability of other same species competitors. For example, betta fish (*Betta splendens*) use lateral displays of body size to determine whether to engage in conflict (Simpson [1968](#)). Red deer (*Cervus elaphus*) employ roaring contests before escalating against other deer (Clutton-Brock and Albon [1979](#)). These examples and others like them demonstrate three important points. First, there are cues that provide reliable information to the organism about the likelihood of success in conflict. Second, organisms adjust their behavior based on this information. Third, the program must be sensitive to cues from multiple sensory modalities.

Recently, evolutionary psychologists have proposed that humans are also likely to have cognitive programs that track fighting ability. Humans, like other nonhuman mammals, have a long history of intrasexual (same-sex) male physical aggression (Daly and Wilson [1988](#)). Thus, it would greatly benefit men to be able to accurately assess when aggression is likely to result in a beneficial or detrimental outcome. Although women are far less likely to participate in these aggressive encounters, being able to accurately predict the outcomes of male-male conflicts would have still been important when choosing a mate. Evidence supports this idea that women's mate preferences favor men with greater fighting ability (Fink et al. [2007](#)). Given these pressures, it seems likely that both men and women would have evolved cognitive programs that can accurately assess this critical variable.

Although many traits contribute to fighting ability, by and large the most reliable cue to fighting ability in humans is upper body strength. This is because for the vast majority of human evolutionary history, the most effective means of

fighting was by using the upper body to strike, choke, or otherwise injure a competitor. Even after combat tools such as rocks, clubs, and spears became common, upper body strength was still necessary to wield these tools. In sum, upper body strength is an *honest signal* (i.e., one that cannot be faked) of fighting ability as it reliably indicates capability to use physical force. Thus, any easily identifiable cue that accurately tracks upper body strength (e.g., muscle mass) would be a likely cue for the cognitive program to track.

Insofar as upper body strength is a reliable cue to fighting ability, selection would have favored cognitive programs that could accurately assess strength while minimizing risk to the assessor. These programs would be most effective if they could quickly pick up subtle strength cues from competitors and remain reliable when these cues are obscured (e.g., when clothing is worn). Similarly, they should rely minimally on direct interaction with the competitor, so as to minimize the risk of physical harm. The visual system is a likely candidate to meet these design requirements. Minimizing risk, humans can assess others from a distance without any physical interaction, and the visual system is acute enough to ascertain small differences in body size.

In addition to the visual system, another system that is a likely candidate to detect cues of fighting ability is the auditory system. Although vision is very useful for directly assessing the size of a competitor's upper body, it is not uncommon for vision to be impaired by darkness or obstructed by intervening obstacles. Given this recurrent problem, supplementary programs that could assess formidability in different ways are likely to have been selected, and these programs may convey different information about fighting ability than visual assessment. Like the visual system, the auditory system can make assessments of strength from a distance, minimizing the risk of physical harm to the assessor. However, it is unclear what auditory cues humans use to detect fighting ability. One potential cue is vocal pitch. Although men rate lower pitched voices as dominant (Puts et al. 2006), pitch does not track physical strength (Sell et al. 2010). Despite this disconnect, it is possible that pitch might provide incremental

information about fighting ability independent of physical strength or that there are other unknown acoustic cues aside from pitch per se that track fighting ability.

Evidence for a Cognitive Program that Assesses Fighting Ability

The aforementioned design requirements for a cognitive program that assesses fighting ability can be grouped into three hypotheses. First, humans must be able to assess cues to upper body strength. Systems that would be likely to track these cues include the visual and auditory systems. Second, upper body strength should strongly track judgments of fighting ability. This is necessary if upper body strength is actually relevant to assessing fighting ability. Finally, upper body strength should predict the likelihood of engaging and succeeding in physical conflict.

In support of this first hypothesis, Sell and colleagues (2009a, 2010) demonstrated that judgments of men's upper body strength from photographs correlated strongly ($r = 0.71$) with strength as measured by weight-lifting equipment. Similarly, judgments of men's upper body strength from voice recordings also correlated moderately ($r = 0.45$) with weight-lifting strength. Both of these relationships were stable at the level of the participant when analyzed with multi-level modeling, demonstrating that accuracy is an individual level phenomenon and not just an artifact of averaging across multiple raters. Finally, humans were still able to accurately assess strength from facial photos alone, which obscure the most salient cue to upper body strength, the musculature of the upper body.

The second hypothesis posits that observed upper body strength should also strongly track judgments of fighting ability. Support for this hypothesis has been found as well. Judgments of perceived strength and the likelihood of winning a physical fight are almost perfectly correlated, suggesting production by the same cognitive program. This same pattern emerges regardless of whether those ratings are based on photos or recordings of the voice (Sell et al. 2009a, 2010).

Moreover, these judgments are strongly predicted to the same degree by strength as measured with weight-lifting equipment. Not only do individuals agree that fighting ability and upper body strength are related but both judgments accurately track observed physical strength.

The final and most important hypothesis posits that upper body strength should predict willingness to engage and succeed in physical conflict. For men, upper body strength moderately predicts actual history of fighting (e.g., fights in the past 4 years) as well as reported success in conflict (Sell et al. 2009b). However, this work has relied extensively on retrospective self-report, rather than directly testing whether strength predicts success in actual dyadic interactions. One reason this indirect approach may be common is because of ethics; regardless of how enlightening it would be to have raters assess the formidability of male targets and then test their accuracy by having those men fight, it would be highly unethical to do so.

However, in an ingenious design, Little et al. (2015) were able to test this exact question. They showed untrained individuals several headshots of mixed martial arts (MMA) fighters who had recently fought against each other. In a forced choice task, these untrained individuals were able to predict the winner of such fights at rates greater than chance (55%). Furthermore, these judgments of who would win the fight were highly correlated with judgments of strength ($r = 0.82$).

What is most impressive about this result is that MMA fighters are a highly physically homogenous group: they are all extremely physically fit and further matched in classes by their weight. In addition, raters were untrained and could only rely on facial features. The fact that raters were able to perform above chance at all is impressive. In more naturalistic settings where raters have more sources of information and the fighters are less homogenous, it is quite likely that human assessment is much more accurate.

In sum, humans do seem to be able to accurately assess upper body strength. Upper body strength not only tracks ratings of fighting ability but also actually predicts a greater likelihood of

success in physical conflict. These results have been verified with highly controlled lab studies where strength is measured using weight-lifting machines as well as in more realistic designs where individuals must predict the results of actual bouts between professional fighters.

Sex Differences in Fighting Ability and Its Assessment

One of the largest sex differences in humans is in muscle mass and, as a result, muscular strength. In particular, human men have approximately 90% more upper body strength than women, with 99% of women being less strong than the average man (Lassek and Gaulin 2009). Additionally, variability in men's strength is also considerably higher than for women. This huge degree of sexual dimorphism is likely the result of intrasexual (same-sex) competition between men for mates. As fighting ability is largely due to upper body strength, stronger men would have been more likely to succeed in these aggressive competitions. This would in turn have given them more access to desirable mates and increased their reproductive success.

This sexual dimorphism means that human men are better equipped to use aggressive strategies than women and in fact have historically been the perpetrators of physical violence (Archer 2004). This raises the possibility that the cognitive program that measures fighting ability might be especially tuned to assess upper body strength in men. There is some evidence in support of this hypothesis; Sell and colleagues demonstrated (2009) that strength ratings of men (from facial photographs) correlate more strongly with actual upper body strength ($r = 0.39$) than strength ratings for women ($r = 0.21$). However, it is possible that this attenuated relationship for women may simply be due to the restricted range of female strength relative to male strength. The cognitive program that assesses fighting ability has less variability to rely on when making assessments of female strength, which may artifactually constrain estimates of accuracy.

Another possibility is that men and women might have different abilities in assessing strength. One plausible reason might be that men, who are exposed to more aggressive conflicts, might be better able to ascertain the strength and fighting ability of other competitors. However, it is also possible that there are no sex differences in assessment of these variables. Predicting the likely outcome of a physical confrontation is relevant for both men and women, even if women do not typically participate in the conflict. Additionally, as fighting ability is an honest cue to male mate quality, it is likely that women would have need for the same cognitive program to make judgments about who to mate with. Existing data suggests that any differences in strength assessment are small and inconsistent.

Although sex differences in muscular strength are one of the largest in humans (Cohen's $d = 3$), they are dwarfed by differences in vocal pitch. Male pitch is only half as high as female pitch (Cohen's $d = 4.5$), and these differences develop during puberty (Puts et al. 2006). This immense sex difference in pitch is unique to humans and suggests that sexual selection may be responsible for the emergence of lower pitched voices in men. Several lines of research support this hypothesis. Men rate lower pitched voices as more dominant (Puts et al. 2006). Women prefer men with deeper voices, and these differences are exaggerated at times close to ovulation (Puts 2005). As mentioned previously, however, there is currently no direct evidence that pitch accurately tracks physical strength (Sell et al. 2010).

Sexual dimorphism in vocal pitch occurs during puberty and is primarily due to physical changes in men's vocal cords that result from elevated testosterone levels. Testosterone also increases muscle growth (Bhasin et al. 1996), providing a potential explanation for why pitch might accurately track fighting ability. These changes are exclusive to men and raise the possibility that the cognitive program that measures fighting ability through vocal cues might be especially tuned to assess men. Consistent with this idea, Sell and colleagues found (2010) that strength ratings of men (judged from voice recordings) correlate more strongly with actual upper body

strength ($r = 0.51$) than strength ratings for women ($r = 0.26$). While this may point to a cognitive adaptation that is better designed to operate on men's voices, it is still possible that this smaller relationship may be due to a restriction of range on female strength.

The existing evidence strongly supports the idea that men and women are equally skilled at assessing fighting ability from both visual and auditory cues, even though men are much more likely to engage in and be victims of aggression. Similarly, there is some evidence that humans are better equipped to assess male fighting ability than female fighting ability. However, a key issue with this conclusion is that there is considerably more variability in male strength (and thus fighting ability) than there is for female strength. This restricted range makes prediction more difficult, as the cognitive program must make judgments about smaller fluctuations in strength.

Evidence that Assessment of Fighting Ability Is Species Typical

If a cognitive program did evolve through natural selection to assess competitors' fighting ability, this program should operate effectively regardless of whether the individuals assessed are from similar or foreign cultures. In contrast, if the assessment of fighting ability is transmitted through culture specific cues, it should be worse when judging foreign individuals. In support of species-typical assessment, American raters were able to accurately judge strength from facial photographs and recordings of voice for American men, Tsimane men from Bolivia, and Andean men from Argentina (Sell et al. 2009a, 2010). These strength estimates tracked perceptions of fighting ability as well as actual history of fighting, suggesting that a species-typical cognitive program is likely.

Conclusion

There is considerable evidence that aggression between humans has long been a part of our

species' history. Nonetheless, there are considerable costs of escalating conflict when one is unlikely to win. It seems likely that humans would have evolved cognitive programs that could accurately assess fighting ability by tracking reliable cues like upper body strength. Experimental evidence supports this prediction; both men and women can assess upper body strength from visual and auditory cues, and upper body strength in turn predicts willingness to engage in and succeed in physical confrontations. In addition, these adaptations appear to be species typical. There is some evidence that such programs are better equipped to assess male fighting ability, but this evidence might just be a statistical artifact of the restricted range of female strength.

Cross-References

- [Aggression](#)
- [Evolution of Fighting Assessment Abilities](#)
- [Fighting Assessment](#)
- [Intrasexual Competition](#)
- [Male Adaptations to Assess Fighting Ability](#)
- [Male-Male Competition](#)
- [Mate Preferences](#)
- [Physical Aggression](#)
- [Psychological Mechanisms](#)
- [Resource Competition](#)
- [Sex Differences in Ability to Assess Fighting Ability](#)
- [Signals of Body Size](#)
- [Size and Dominance](#)
- [Tactics to Solve Adaptive Problems of Sperm Competition](#)
- [Upper Body Strength](#)
- [Upper Body Strength and Fighting Ability](#)
- [Upper Body Strength from Photo](#)
- [Vocal Indicators of Dominance](#)

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Assessment of Unfaithfulness

- [Perceptions of Infidelity](#)

Assimilation

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Synonyms

Absorption; Adaption; Adjustment

Definition

The act of absorbing or adjusting experiences, information, etc. into an existing system.

Introduction

The term assimilation describes the process of absorbing or adjusting experiences or information into an existing system. It is derived from the Latin word *assimilatio*, meaning “likeness” or “similarity.” Assimilation hence refers to making something more similar. In psychology, the term is used in various theoretical circumstances with differing connotations. We will focus on three highly influential theoretical models in which the concept of assimilation plays a central role: (a) Jean Piaget’s genetic theory of learning, (b) the inclusion-exclusion model of social judgment formation by Schwarz and Bless, and (c) John Berry’s theory of acculturation strategies.

Jean Piaget’s Genetic Theory of Learning

Developmental psychologist Jean Piaget (1936) described his work as genetic epistemology, i.e., the scientific study of the origins of human rationality and thinking. Piaget studied children’s ability to count, to talk, or to reason, but did not seek to assess their performance. His primary questions were, in a sense, deeper, seeking to understand how children acquire the fundamental concept of

numbers, how they learn to differentiate between a word and the concept it identifies, or how they process causality. Before Piaget’s work, children were primarily seen as less competent thinkers than adults. Piaget became intrigued by children’s thinking errors and the reasons they gave for them. To him, these reasons revealed that the errors are due to systematic and necessary steps in the development of concepts that children have to take in order to ultimately generate appropriate mental models of the world.

According to Piaget, children are born with a genetically inherited and evolved mental structure on which all subsequent learning and knowledge are based. This mental structure is of course very basic and needs refining. Piaget saw mental schemata as sets of linked mental representations of the world that humans use both to understand and to respond to situations. He defined schemata as “cohesive, repeatable action sequence possessing component actions that are tightly interconnected and governed by a core meaning” (1957, p. 7). Put more simply, Piaget’s schemata are the basic modules which allow humans to organize knowledge since their infancy. Obviously, the first schemata that children possess are extremely simple. They are the reason why children are equipped with innate, i.e., genetically programmed, reflexes. For instance, newborn babies have a sucking reflex that is triggered once something touches their lips, be it nipples, a person’s finger, or a comforter. In Piaget’s terms babies have a sucking schema. Intellectual growth is viewed as adaptation or adjustment of mental schemata to the world. According to Piaget this adaptation can take place through two distinct processes: assimilation and accommodation. Assimilation means that an existing schema is used to deal with a newly encountered object or situation, even if the schema does not fully fit. If the existing schema does not work at all and needs to be changed to deal with a new object or situation, the process is called accommodation. Assume, e.g., that the only four-legged animal that a child has ever seen is a dog. The process of assimilation would imply that the child calls all other

four-legged animals of similar size (e.g., cats) a dog, simply because cats are similar enough to dogs. This generalization, albeit incorrect, is a necessary and adaptive step in dealing with the new encounter. If the child acquires more knowledge about the differences between cats and dogs, it builds new and more fine-graded mental schemata that are yet derived from the initial simple ones. This latter process of changing an existing schema and adapting it to newly acquired knowledge about the world is called accommodation. In sum, Piaget described cognitive development as the interplay of assimilating and accommodating mental schemata.

Social Judgment Formation

How do we generally judge or evaluate other people or objects in a given context? How does contextual information shape our judgments? Norbert Schwarz and Herbert Bless (Schwarz and Bless 1992) have argued that if individuals are asked to form a judgment about some target stimulus, they first need to retrieve some cognitive representation of it from their memory. Additionally, they need to determine some standard of comparison to evaluate the stimulus. Both the representation of the target and standard of comparison are, in part, context-dependent. One critical source of contextual information is preceding judgmental tasks a person has been confronted with. Information that has been used for answering those preceding questions is most likely to come to mind again when later being asked related questions. This can happen in two different ways: assimilation and contrast. Assimilation effects occur if later judgments reflect the information that has been rendered accessible in the respondent's mind by previous questions, as well as the implications of that knowledge. This is to say that a later judgment is more similar to the preceding one than it would have been had no prior question been asked. Contrast effects describe the opposite direction of influence.

Whether assimilation or contrast effects occur is a function of how the information that comes to mind due to the preceding questions is

mentally categorized. In order to form a judgment about a certain target, people construe a temporary representation of it. If this mental representation includes the information rendered accessible by preceding questions, assimilation effects are likely to be found. However, the same piece of information may also result in a contrast effect. This is expected to be the case when the information is excluded from the cognitive representation of the target. To illustrate, in one classic empirical test of this model, Schwarz and Bless (1992) assessed how evaluations of the German conservative party, the Christian Democratic Union (CDU), would be biased by reminding respondents of one of its most highly esteemed members, Richard von Weizsäcker. In one experimental condition, respondents were reminded of von Weizsäcker in such a way that they were likely to include him into their temporary representation of the CDU. To this end, the participants were asked to recall the party of which "Richard von Weizsäcker has been a member for more than 20 years." Relative to a control condition without this preceding question, the participants evaluated the CDU more positively, thus exhibiting an assimilation effect. In another condition, however, people were reminded of von Weizsäcker in such a way that they were unlikely to include him in their mental representation of the CDU. This was achieved by asking them "which office Richard von Weizsäcker holds, that sets him aside from party politics?". At the time the study was conducted, von Weizsäcker served as Federal President of Germany, an office that required him to take a neutral stand on party issues. When later being asked to evaluate the CDU, these participants provided less positive judgments than those of a control group without preceding question. As compared to the highly esteemed Richard von Weizsäcker, the overall representation of the CDU appeared to be less positive. In sum, whether information that is rendered accessible in the respondents' mind yields assimilation or contrast effects in later judgments depends on whether it is included in the mental representation of the judgment target or not.

Intercultural Relations and Acculturation Strategies

The term assimilation is also used in the context of intercultural relations. In this context, assimilation refers to the process whereby persons acquire the culture of another group in which they come to live, by adopting its attitudes and values and its patterns of thinking and behaving – in short, its way of life. Assimilation is one of four acculturation strategies identified by John Berry (1997). Acculturation is the sum of those phenomena taking place when individuals of different cultural backgrounds come into continuous first-hand contact with each other, yielding subsequent changes in the original cultural patterns of either or both groups. It is mainly used to refer to the patterns that describe how migrants adapt to a new host society. According to Berry, acculturating individuals have to actively manage a central conflict inherent in such contexts: cultural maintenance versus contact and participation. Cultural maintenance refers to the consideration of whether it is valuable to maintain one's original identity and characteristics ("yes" or "no"). Contact and participation refer to the consideration of whether it is of value to maintain relationships with the larger/host society ("yes" or "no"). Depending on these answers, four different acculturation strategies can be identified (those being, separation, marginalization, integration, and assimilation). The assimilation strategy is characterized by the unwillingness to maintain one's own original cultural identity while instead seeking daily interactions with members of the host culture only. The opposite strategy, placing very high value on holding on to one's original culture while avoiding contact with the new one, is called separation. Integration, as the third strategy, is followed, if people seek to find a balance between participating as an integral part of the new culture while at the same time maintaining some degree of cultural integrity. The fourth strategy is called marginalization which means that there is no or little interest to get into contact with the new culture while also not trying to maintain one's culture of heritage.

While assimilation has previously been seen as the integral part of any individual's journey into acceptance by the host culture, more recent

studies have shed doubt on the assumption that assimilation is invariably positive. This is best reflected in its effect on mental health and well-being. For example, assimilation is reported to be related to more risky sexual behavior, higher risks of delinquency and substance abuse in adolescents, as well as lower educational outcomes. However, it has been found to boost migrants' self-esteem and increase positive attitudes toward the host culture. Based on these findings, Berry argues that host societies will likewise be most successful in dealing with immigration, if they endorse multiculturalism, i.e., valuing and fostering diversity, rather than seeking assimilation of the immigrants.

Conclusion

The term assimilation means making something similar and describes the process of absorbing or adjusting experiences or information into an existing system. We have described three different circumstances in which the term plays a central role in psychological theorizing. Jean Piaget's genetic theory of learning is one of the first attempts to systematically study cognitive development. According to Piaget, children are born with genetically inherited mental schemata which are used and modified during the course of learning and development. Piaget described cognitive development as the interplay of assimilating and accommodating these mental schemata. Assimilation means that an existing schema is applied to a newly encountered situation or object. Changing an existing schema if it is not sufficient to deal with the new information is referred to as accommodation. The second theoretical context where the term assimilation is used is related to models of social judgment formation which are concerned with how contextual information shapes human judgments. In this context, assimilation effects are identified by judgments and contextual information being positively correlated. If, however, contextual information biases judgment into the opposite direction, this is called contrast. The inclusion-exclusion model by Schwarz and Bless specifies conditions under which either

assimilation or contrast can be expected. Finally, assimilation is one of four different acculturation strategies identified by John Berry. It is characterized by individuals giving up their own cultural identity while becoming absorbed into the host society. Assimilation has less beneficial psychological consequences than the strategy of integration, meaning that the individual maintains his or her cultural heritage while at the same time becoming an active participant in the host culture.

Cross-References

► [Differentiation](#)

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Assisted Reproduction

► [Medically Assisted Reproduction](#)

Assisted Suicide

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Synonyms

[Death](#); [Euthanasia](#); [Physician-assisted death](#); [Self-inflicted suicide](#); [Suicide](#)

Definition

Suicide with the help of a third party, usually by terminally ill patients with the help of a physician.

Introduction

The terms physician-assisted suicide, physician-assisted death, and euthanasia are often used interchangeably, though there are notable differences. The difference between assisted suicide and assisted death is mainly semantic. Both are defined as a physician aiding the patient in initiating his or her own death with prescriptions, medications, or other means. Alternatively, voluntary active euthanasia, by definition, has a physician actively employing the means to initiate death (Quill and Batlin 2017). For the purpose of this focus, the term assisted suicide (AS) will suffice for all types of suicide aided by physicians and exclude euthanasia.

Although the Hippocratic Oath forbade the practice of assisted suicide, there are reports that physicians of antiquity were known to give suffering patients poison to accelerate their death. However, the advent of Christianity took the Hippocratic Oath a step further by linking suicide with eternal damnation, thereby ending physician participation with suicide in Western culture for nearly 2000 years. The American debate on AS was stoked by an article (eventually found to be a fabrication), published in 1988 in the *Journal of the American Medical Association* entitled, “It’s over Debbie.” The article described a resident physician giving a lethal dose of morphine to a terminally ill and suffering 20-year-old woman, with her mother giving tacit approval at her bedside (Anonymous 1988). The discussion of AS in the United States exploded with the notoriety of Dr. Jack Kevorkian, a Michigan pathologist, who eventually facilitated the death of at least 130 people. He was eventually sentenced to prison although not for the AS that he had practiced with his first 129 patients but rather for participating in euthanasia with his last patient. In addition, he had the audacity of having the taped event nationally televised on CBS’ “Sixty Minutes” (Lessenberry 1994).

Current legal and moral conflicts remain. Though a clear majority of the American public favors AS (as high as 70%), the majority of physicians oppose it (see Van Norman 2014). Assisted suicide became legal in Oregon in 1994, followed by Washington, Vermont, Montana, California, the District of Columbia, and most recently Colorado. Other nations that allow for suicide (and in some countries, euthanasia) include the Netherlands, Switzerland, Belgium, Luxemburg, Columbia (Van Norman 2014), and as of 2015, Canada.

The moral divide has strong voices on both sides. The most commonly cited argument affirming AS is the issue of autonomy: Individuals have the right to determine the fate of their own lives, including the right to die on one's own terms. A second point of affirmation includes the idea of beneficence, that the relief of suffering is for the greater good. Third, the termination of life-sustaining treatment is thought by some to have no moral difference than AS, thereby neutralizing it to a moral equivalent. And on a practical level, 60% of Medicare payments in the United States are expended in the last 6 months of life (Lessenberry 1994), which brings into focus the discussion of where health-related financial resources are best spent. The question arises as to whether or not AS would become a benefit to society as a whole by containing costs or represent what others fear may become akin to "death panels" and lead toward a slippery slope.

The arguments in opposition of AS are frequently the affirming opinions turned on their head: that the power of autonomy ends before suicide, because suicide precludes further autonomy. As for beneficence, the premature ending of life denies any further possibility of the good that comes with life itself. Commonly, the slippery slope argument is offered up that AS is the first of several steps leading toward a Nazi-like political utility used for self-serving needs. Further, complications with AS have occurred creating a potential for increased suffering as well: difficulties with infusions from IVs, potential for additional pain, and the possibility of failure in the process of dying, stoking dread in patients and families (Quill and Batlin 2017). The arguments

fearful of the slippery slope are tenuous; clusters of data from both the Netherlands, and the state of Oregon demonstrate the use of AS to be numerically stable over nearly two decades (Steck et al. 2013).

Often, and mistakenly, the perception of the primary use of AS is to relieve intractable pain. In the United States, less than 25% of AS involves a primary concern related to pain, the most frequent usage (over 60%) in the United States of AS stems from the diagnosis of cancer (Steck et al. 2013). By a large majority, the most frequent subjective request for AS was due to loss of autonomy, followed by loss of enjoyable activities, then loss of dignity (Yang 2016). The most likely people to change their minds in pursuing AS are depressed patients. The issues of consent, and the potential need for further psychiatric treatment in the depressed individual, creates persistent controversy. The depressed patient brings into question the significance of existential suffering and, further, whether a physician is best suited to judge the quality and significance of that quality of pain. The non-depressed, fully informed patient that has agreed to follow through with AS is often referred to as "the rational suicide." The demented patient, whose family may request AS, presents further controversy in that the patient is unlikely to be able to demonstrate capacity and has no true autonomy in the matter.

Conclusion

The greater need for palliative care, psychiatric intervention, family involvement, and community support is evident as AS becomes a greater part of the fabric of our culture. These situations emphasize and reinforce the need for appropriate screening and second opinions. Controls and legal safeguards preventing abuse of AS consist of admixtures of waiting periods, witnesses, diagnostic criteria, capacity, written requests, and the option to opt out by the patient as well as the physician.

The debate regarding AS remains active and emotional, with religious, academic, political, and ethical considerations.

Cross-References

- ▶ Death
- ▶ Factors Associated with Suicide
- ▶ Jack Kevorkian
- ▶ Kin Selective Suicide
- ▶ Suicide

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Associationism

- ▶ Associative Learning

Associations

- ▶ Cost of Same-Sex Friendships
- ▶ Same-Sex Friend

Associative Learning

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Synonyms

Associationism; Conditioned associations; Instrumental associations; Learning through associations

Definition

Associative learning is a type of learning that involves the acquisition of new associations between environmental conditions and/or interoceptive states that govern and regulate the learning outcome.

Introduction

Associative learning constitutes a fundamental notion in numerous theoretical and operational models of learning (McSweeney and Murphy 2014). The basic theoretical models related to associative learning indicate either in an explicit and/or implicit way the acquisition of new associations that govern the learning outcome (Shanks 1995). Specifically, associative learning constitutes the capacity of living creatures to detect reliable and consistent associative relationships that are formed between environmental conditions and/or interoceptive experiences (Delamater and Lattal 2014). This type of learning enhances the capacity of living creatures for adaptation and survival as it renders organisms able to expect upcoming events and maintain resources (Baum 2017).

Historical Background of Associative Learning

The idea that organisms possess the capacity to achieve learning through the acquisition of new associations has its historical origins back to the Ancient Greeks and associationism (McSweeney and Murphy 2014). Aristotle, a Greek philosopher described associative memory principles, an approach that became widely known as associationism. Specifically, Aristotle suggested that the retrieval of thoughts or images evokes the retrieval of other thoughts or images that have formal similarities with the initial thought or image. In other words, Aristotle proposed that learning is achieved through the association of environmental conditions that constantly occur together (Baum 2017).

Even though early philosophers in the associationist movement and early researchers in the fields of both human associative memory and behaviorism had studied associative mechanisms that today would be considered to be similar to the ones that Ivan Petrovich Pavlov described, I. P. Pavlov was the first who officially and methodologically designated and described an associative learning process at a theoretical as well as at an operational level in the scientific community through the publication of conditioned reflexes in 1927 (Shanks 1995). Pavlovian and/or classical conditioning is a type of associative learning that involves the formation of new behavioral responses through the acquisition of new associations. Specifically, during the course of classical conditioning, an organism adjusts in response to the detection of sequential relationships between stimulus of environmental and/or proprioceptive nature (Spence 1978).

This type of associative learning is named “conditioning” since its inventor, I. P. Pavlov, used the term conditioned reflex to label and designate the learning outcome (Schachtman 2011). I. P. Pavlov assumed that new reflexive responses can be developed through the acquisition of classically conditioned associations between neutral stimuli, that is, stimuli which originally do not induce any particular response, and unconditioned stimuli, that is, biologically relevant stimuli which reflexively evoke an unconditioned response (Spence 1978). Through the acquisition of a classically conditioned association between a neutral stimulus and an unconditioned stimulus, the first turns into a conditioned stimulus and acquires the capacity to induce a conditioned response that is qualitatively similar to the unconditioned response. I. P. Pavlov examined various reflexes, yet his most widely known experiments revolved around responses to food (Schachtman 2011).

The Study of Gastrointestinal System and Its Role in Classical Conditioning

I. P. Pavlov discovered the associative mechanism of classical conditioning accidentally while examining the physiological processes of the

gastrointestinal system. Specifically, I. P. Pavlov was examining the alternations of dogs’ saliva and digestive fluid secretion through their mouth and stomach while feeding. At some point, during the experimental procedures that I. P. Pavlov set in order to observe the alternations of dogs’ saliva and digestive fluid secretion in response to feeding, he observed that the subjects’ (i.e., dogs) saliva and digestive fluid were also secreted every time he and his associates arrived in the laboratory. Consequently, I. P. Pavlov decided to experimentally examine the mechanisms and functional structures that let the dogs secrete saliva and digestive fluid in his presence as well, rather than exclusively to the presence of food in response to which the dogs reflexively and automatically secrete saliva and digestive fluid (Spence 1978).

I. P. Pavlov and his associates systematically and methodologically administered for several times a neutral stimulus (i.e. sound of a bell) to the dogs just before they were presented to their usual food, that is, a meat powder. When this trial was conducted numerous times I. P. Pavlov and his associates observed that the dogs were also secreting saliva and digestive fluid when the stimulus of the sound of the bell was administered alone, that is, in the absence of food (Shanks 1995). Ultimately, I. P. Pavlov came to the conclusion that the constant pairings of the sound of the bell and the food resulted in the formation of an association between the sound of the bell and the food. Specifically, the sound of the bell which at the beginning was neutral stimulus, a stimulus that does not elicit a response, acquired the capacity to elicit a response, which is qualitatively similar to the one that the food naturally and automatically elicits. The dogs’ response became classically conditioned and respectively the sound of the bell turned into a conditioned stimulus. Consequently, the new response that was learned as a reaction to the sound of the bell is termed a conditioned response (Schachtman 2011).

The Evolution of Classical Conditioning

The theory of Classical conditioning has considerably evolved after the work of I. P. Pavlov

in conditioned reflexes. The initial model of classical conditioning was operationally and theoretically elaborated by the work of several learning theorists in the USA. Specifically, theorists in the field of learning in the USA formed different techniques for assessing the functional qualities of associations between conditioned stimuli and unconditioned stimuli (Allen and Madden 1985). In addition, they also found new conditioning processes and reinterpreted the fundamental processes of the conditioning that became known through the procedures that I. P. Pavlov proposed (Wills 2012).

A considerable factor that led to substantial modifications of the initial theory of classical conditioning is the integration of cognitive functions in it. Specifically, even though, the work of I. P. Pavlov on conditioned reflexes was widely spread in the USA, it received a considerable amount of criticism in 1950. Most of the criticisms on his ideas were expressed in 1950 by the well-known Polish neurophysiologists named Jerzy Konorski and Stefan Miller. Jerzy Konorski and Stefan Miller initiated the primary cognitive conceptualization of respondent conditioning. Their work constitutes the precursor of the well-known and highly influential Rescorla–Wagner model of classical conditioning (McSweeney and Murphy 2014). In addition, at the same period, the psychiatrist Joseph Wolpe as well as the psychologists John Watson developed treatment plans that were based on the principles of classical conditioning so that to change dysfunctional behaviors into functional ones. This attempt to apply learning principles in the development of clinical interventions became known as behavioral modification and significantly increased the use of such interventions by psychiatrists and psychologists (Staddon 2014).

The theoretical conceptualization of classical conditioning has significantly changed with the introduction of the Rescorla–Wagner model in classical conditioning in 1972 (McSweeney and Murphy 2014). The Rescorla–Wagner model proposes that while living beings interact with their environment, develop causal expectations that enable them to estimate the relationships between environmental conditions. According to

this model, learning involves acquiring knowledge related to the way that the environment is causally organized. Specifically, an organism becomes able to achieve learning by developing solid associations between environmental components (Rescorla 2008). Yet even if the environmental components become contiguous and in turn organisms form associations between them, the environmental components need to also allow the acquisition of knowledge related to causal relationships. In other words, the fundamental idea is the concept of contingency and how an organism perceives it (McSweeney and Murphy 2014). This model by integrating cognitive elements within the formation of associations indicated the acceptance of both cognitive functions and associative processes in the brain, something that quickly earned the favor of experimental psychologists (Klein and Mowrer 1989).

Even though living beings sometimes form conditioned associations based only on a conditioned stimulus-unconditioned stimulus contiguity, there are numerous cases in which learning appears to enable living beings to anticipate the presentation of the unconditioned stimulus due to the presentation of the conditioned stimulus (Pearce and Hall 1980). In such cases, learning takes place through a contingency relationship that is probabilistically manifested (McSweeney and Murphy 2014). For instance, when the likelihood of the unconditioned stimulus being presented is equal to the likelihood of the conditioned stimulus being and not being presented the conditioned association cannot be achieved. In contrast, when the likelihood of the unconditioned stimulus being accompanied by the conditioned stimulus is higher than the likelihood of the unconditioned stimulus being presented in the absence of the conditioned stimulus, a conditioned association could be achieved. For that reason, respondent conditioning is considered to reflect the ability of living beings to identify and learn possible associations between signals and important environmental conditions (Staddon 2014).

Nowadays, respondent conditioning is viewed as a multifaceted associative mechanism that involves many types of responses, rather than involving only glandular and visceral reactions,

as it was initially considered. Respondent conditioning among other factors also relies on how relevant is the conditioned and the unconditioned stimulus, the appearance of other stimuli while conditioning takes place, and the degree of surprise that the unconditioned stimulus evokes (McSweeney and Murphy 2014). In addition, the evolution of the connectionist framework that models human cognition revived the attention in respondent conditioning as a productive technique for the study of associative learning. Therefore, nowadays, classical conditioning is most accurately defined and designated by its procedural method, which encompasses the preservation of firm control over the presentation of stimuli (Shanks 1995). In addition, it is highly important to take into consideration that the principles that accurately differentiate classical conditioning between other forms of associative learning, such as operant conditioning and associative memory, are limited. Specifically, classical conditioning is most accurately differentiated by the extent to which the form of the conditioned response is determined by the choice of the unconditioned stimulus (Allen and Madden 1985). Furthermore, a classically conditioned response is usually unaffected by instrumental contingencies. For example, pigeons cannot be easily prevented from pecking (conditioned response) at a separate key light (conditioned stimulus) which was paired with food (unconditioned stimulus) even if pecking stops the distribution of food (Wills 2012).

Further Conditioning: Second-Order Conditioning, Generalization, and Discrimination

Second-Order Conditioning

Stimuli that have acquired conditioned associations can set the ground for further conditioned associations. For example, when a kid experiences fear in the presence of darkness resulting to the darkness being a conditioned stimulus that induce a response of fear, an additional stimulus that exists in the setting of darkness such as specific noises can acquire too qualitatively similar

operations with the conditioned stimulus and induce a fear response despite the fact that these noises did not accompany the stimulus that initially induced the fear response in the dark setting (Ramnero and Torneke 2011). This phenomenon is usually termed second-order conditioning. Once more, the stimulus of darkness is likewise one that is not so neutral, as humans are biologically predisposed to more easily associate it with fear than other stimuli (McSweeney and Murphy 2014).

Generalization

An additional and very significant functional process of classical conditioning is the propensity to react in a qualitatively comparable manner to similar stimuli, a process that is termed stimulus generalization (Staddon 2014). The term stimulus generalization when it comes to classical conditioning defines the process through which a specific response would spread in such a manner that other stimuli that have qualitatively similar traits with the initial classically conditioned stimulus would acquire the ability to also induce the classically conditioned response (McSweeney and Murphy 2014). For instance, a kid that has been scratched and wounded by a dog would not only respond with fear whenever sees that specific dog. Specifically, this kid is very well likely to respond with fear to the presence of dogs which are similar enough. However, if the kid was scratched by a large dog and the height of the dog is a dominant feature of the conditioned stimulus, it is likely that a very small dog would not induce a conditioned response of fear. Yet if the dog's barking is a dominant feature of the conditioned stimulus, then a very small dog's barking could operate as a conditioned stimulus and induce a conditioned response of fear. In other words, in order for an organism to respond in a qualitatively similar way to different stimuli, the stimuli must be similar enough (Ramnero and Torneke 2011).

Stimulus Discrimination

The opposite conditioning operation to generalization is a process termed stimulus discrimination. Stimulus discrimination is the capacity of an organism to detect and respond to differences

between stimuli, that is, the capacity to detect similarities among stimuli. For example, I. P. Pavlov's dogs at the beginning exhibited stimulus generalization since they were secreting saliva and digestive fluid in response to a variety of sounds that were different than the sound that was initially classically conditioned (Ramnero and Torneke 2011). However, if the dogs had consistently received only a specific sound before they were fed, their capacity to differentiate, that is, to discriminate, among similar stimulus would be enhanced and in turn, they would secrete saliva and digestive fluid only in response to the specific sound that precedes feeding (Shanks 1995).

The processes of generalization, discrimination, as well as the equilibrium among them, are of vital importance for living beings in order to learn to adapt and survive (Baum 2017). Specifically, in some situations is of vital importance to exhibit stimulus discrimination and just respond to specific stimuli. For instance, a living being that must assess an area which is full of ice where a discrepancy in the white-color shows the degree to which is safe or dangerous to pass through the ice must have the capacity for stimulus discrimination. However, in other situations, stimulus generalization has higher adaptive and survival significance, such as the case of an organism which is chased by a variety of predators. In such a scenario, this living organism must respond to everything that presents in front of it.

Classical Conditioning and Emotional Functioning

Classical conditioning could be used to gain an insight into the way that a person's emotive experience of the world is developed during childhood (McSweeney and Bierley 1984). For instance, despite the fact that only certain stimulus could induce fear responses early on in an individual's life, as the person grows up would acquire further associations which will obtain qualitatively similar operations with the ones that an unconditioned stimulus possesses, that would from then on induce fear responses (McSweeney and Murphy 2014). Therefore,

through classical conditioning, phenomena acquire new associations with external stimuli such as behaviors of other people, certain environmental conditions as well as internal stimuli, such as other emotions and interoceptive experiences. For example, a young boy who experiences sadness and is recurrently challenged by a father who is behaving in a manner which induces fear in the boy, via the process of classical conditioning, the father's behaviors could lead the young boy to develop an association between the affects of sadness and fear, and thus every time he feels sadness (conditioned stimulus) a response of fear is induced. In other words, this boy has learned through classical conditioning to experience fear every time he is sad (Thines 1987).

Classical conditioning shapes individuals' responses from early on in their lives and continues to influence the way in which a person relates to the world during the course of all of his/her life (Ramnero and Torneke 2011). The recognition that affective responses could also be induced by classically conditioned associations has its roots early in the development of behaviorism (Thines 1987). Specifically, John Watson, who is considered the father of "behaviorism," embraced I. P. Pavlov's work on conditioned reflexes and decided to implement its principles to investigate the way that the affective response of fear emerges in people. In addition, classically conditioned responses are fundamental to gain an insight in the way that individuals who experience trauma respond to a specific stimulus such as loud noises, fire, dark, or a preparator's perfume (Shanks 1995).

Classical conditioning enables environmental components and/or conditions to acquire a physiological capacity that did not have before. In other words, an environmental component and/or a condition that possessed other functions or none now acquires a new function, an acquisition that has adaptive significance for any species. Specifically, classical conditioning provides to a living being the chance to alter its behavior and thus increasing its capacity to adapt and survive (Ramnero and Torneke 2011). For example, a kid might jump on a road full of cars, lacking the association between such situations and threat.

However, the kid possesses a physiological system that responds to specific unconditioned stimuli such as abrupt cries, screams, and violent acts with an unconditioned response of fear. In a plausible scenario where his/her mother or his/her father responds with a loud scream or exhibits a violent act when the kid tries to jump on the road, the road and/or other relevant stimuli would acquire qualitatively similar functions with the unconditioned stimulus of a loud scream, enabling the road and other relevant stimuli from then on (conditioned stimulus) to induce a conditioned response of fear. The acquisition of this new association would enable the kid to alter his/her behavior when it comes to a crowded road. A further example that depicts the way that classical conditioning could enhance the capacity for adaption and survival is a woman who is attacked in a remote parking place. One month later she goes to the same parking place and she begins to feel dizzy, chest pains, numbness in the hands, and a sense of terror and as a result, she immediately leaves the place. In this scenario, the woman became classically conditioned to a previously neutral stimulus (remote parking) which has now induced a physiological response of fear due to its association with the unconditioned stimulus of assault leading the woman to leave immediately from the remote parking and avoid a possible future attack (McSweeney and Murphy 2014).

The Contributions of Edward Thorndike in the Study of Associative Learning

The experimental studies of Edward Thorndike with cats in puzzle boxes widened the theoretical notion of associative learning by integrating the concept of consequences to the associative processes of learning (McSweeney and Murphy 2014). Thorndike through his work depicted that the theoretical notion of associative learning is applied not only in reflexive responses and sensory substitution but also to the acquisition of new behavioral responses. Specifically, Thorndike restrained cats in a puzzle box, and then he prompted the cat to escape so that to be able to obtain

food (i.e., fish) that was left outside of the puzzle box (Ramnero and Torneke 2011). Consequently, the cat tested various ways in order to get outside of the puzzle box and obtain the food. Ultimately, and through experimentation, the cats learned that when they pressed the lever they were obtaining the food and thus they experienced positive consequences. As a result, the frequency with which the cats were pressing the lever significantly increased (Shanks 1995).

The cats' behavioral responses of trying to press the lever were not reflexive in nature as the unconditioned responses in Pavlov's experimental studies (Staddon 2014). Specifically, the cats' behavioral responses were governed by the consequences that followed them. In other words, when the cats pressed the lever the door was opening, a sequence that enabled the cats to acquire the association between the lever pressing and the opened door. This type of learning that enables living beings to operate in their environmental context became widely known as operant conditioning. In contrast to Pavlov's process of learning through which organism passively acquire new associations, operant conditioning constitutes a general as well as an active theoretical model of learning (Shanks 1995).

Thorndike's experimental studies related to the associative mechanisms that govern animal behavioral responses let him develop the law of effect which constitutes the primary official law of associative learning that is psychological in nature (Wills 2012). Thorndike's law of effect assumes that a behavioral response that is followed by positive consequences is more likely to become associated with the environmental conditions where it was initially exhibited and thus increase in frequency. In contrast, the behavioral response that is followed by negative consequences is less likely to appear when a living being faces equivalent environmental conditions in a future time and thus the behavioral response reduces in frequency until it is eliminated (Shanks 1995). In addition to the law of effect, Thorndike proposed the law of exercise which assumes that the intensity of an association between a behavioral response and environmental conditions is highly influenced by the rate of occurrence of

previous pairings between that environmental conditions and the specific behavioral response (Ramnero and Torneke 2011).

The Contributions of Skinner in the Study of Associative Learning

The work of Thorndike related to the mechanisms that underlie associative learning was spread and expanded by B.F. Skinner (McSweeney and Murphy 2014). Specifically, Skinner, in addition to the notion of consequences, integrated the concept of reinforcement as a functional means through which associations are acquired, regulated, and maintained (McSweeney and Murphy 2014). Specifically, Skinner claimed that the extent to which a behavioral response becomes associated with environmental conditions relies on the proportion and the rate of intensity of reinforcement that occurs as consequences of the behavioral response that is exhibited by an organism. In other words, in operant conditioning, a living creature responds intentionally on associations that are formed between environmental conditions so that to acquire and/or maintain reinforcement that follows the response (Wills 2012). Therefore, in operant conditioning reinforcement constitutes the crucial factor that influences the acquisition and preservation of the learning outcome (McSweeney and Murphy 2014).

Skinner (1938) examined operant conditioning through experimental studies with animals that were placed in a box called the “Skinner box” which was analogous to Thorndike’s puzzle box (Shanks 1995). Through his experimental studies related to the functional processes of operant conditioning, Skinner observed three kinds of responses that have the potential to occur after the performance of behavioral responses (Klein and Mowrer 1989). Those include the neutral responses, that is, responses that do not affect the frequency of an action. The reinforcers that constitute responses that can be positive (i.e., adding a response) or negative (i.e., removing a response) that increase the frequency of the behavioral response that precedes the reinforcer. Finally, Skinner observed responses that

possess punishing qualities (i.e., punishers), which could also operate either positively or negatively, yet contrary to reinforcers, punishers decrease the frequency of a behavioral response (Schachtman 2011).

Types of Reinforcement

As already mentioned, positive reinforcement increases the probability that a behavioral response will be exhibited in the future by offering a consequence that the organism perceives as rewarding, that is, offers a favorable outcome. For instance, if a mother cooks to her son his favorite food every time he is cleaning his room, he will be more likely to repeat this behavioral response in the future, thus strengthening the behavioral response of cleaning his room (Schachtman 2011). In negative reinforcement, a behavioral response is strengthened by ending, eliminating, or avoiding an aversive consequence such as a distressful stimulus and/or condition (Shanks 1995). For instance, a person that has a headache and takes an aspirin which stops the headache she/he would be more likely to take an aspirin when she/he reexperience a headache in the future to eliminate the headache, thus strengthening the behavioral response of taking an aspirin when a headache is experienced by that person (Ramnero and Torneke 2011).

Reinforcement of peoples’ behavioral responses could be achieved by a variety of stimuli, that is, from a favorite food or a nice compliment. Yet reinforcers are categorized between primary reinforcers and secondary reinforcers (Ramnero and Torneke 2011). The reinforcers that are biologically important are called primary reinforcers. They are also referred to as unconditional reinforcers. A primary reinforcer arises naturally and does not necessitate any effort or type of learning. For instance, nutrition, sleep, oxygen, and sexual activity are only a few examples of primary reinforcers that occur naturally, that is, they operate without the need for previous learning. The majority of primary reinforcers are evolutionarily significant (Shanks 1995). That is, they have been taking place since the beginning of time and enhanced organisms’ capacity to adapt and survive. Furthermore, primary reinforcers are more

efficient in comparison to secondary, that is, conditioned reinforcers, regarding the learning outcomes (Baum 2017). For instance, a young boy that is hungry is more likely to clean his room if his mother tells him that when he finishes he could have his favorite food, rather than cleaning his room for 5 euros. Primary reinforcers could be used to positively as well as negatively reinforce a behavior. Secondary reinforcers and/or conditioned reinforcers obtain their reinforcing capacities through the acquisition of an association with a primary reinforcer and/or other secondary reinforcers (Schachtman 2011). For instance, money could positively and/or negatively reinforce a behavior due to their association with the acquisition of numerous primary reinforcers such as nutrition, water, clothes, and accommodation just to name a few. In addition, attention and approval are reinforcers of interpersonal nature that are referred to as social reinforcers, and they also have the capacity to positively as well as negatively reinforce a behavior (Ramnero and Torneke 2011).

Furthermore, it is highly important to distinguish reinforcers that exert their effect through feedback, a central element of cognitive learning (Wills 2012). Specifically, in cognitive learning feedback is considered to be a reinforcer that exerts its effect through associative learning (Shanks 1995). Specifically, feedback, that is, information related to the environmental influences, that a behavioral response exerts significantly influences the learning outcome (Schachtman 2011). Shanks (1995) adds that the adaptive qualities that the feedback possesses provide a theoretical framework to explain the reasons why a lot of human learning is achieved despite the nonappearance of apparent reinforcers such as nutrition, clothing, and shelter.

Responses with Punishing Qualities

Punishment constitutes an important notion in the theory of operant conditioning. The main functional quality of punishers is to decrease the frequency of an undesired behavioral response. Specifically, in positive punishment, an aversive stimulus is added when an organism displays an undesired behavioral response (Ramnero and

Torneke 2011). Consequently, the organism learns that whenever that specific behavioral response is exhibited, he/she receives negative consequences and thus the possibility of repeating that behavioral response decreases. For instance, an individual who receives a fine because she/he was driving above the speed limit (McSweeney and Murphy 2014). The punishment in response to her/his behavior would discourage her/him from driving above the speed limit in the future. In negative punishment, a needed object is removed in response to the performance of a certain undesirable behavior by an organism. Consequently, the organism learns that whenever that behavior is exhibited the needed object is removed; thus, the organism would be less likely to exhibit that behavior in the future so that to avoid the removal of the needed object (Shanks 1995). For example, every time a young boy speaks impolitely to his mother, the last take away his mobile phone for a week away, a consequence that is discouraging him from repeating that behavior again in a future time.

As mentioned above, Thorndike claimed that learning is composed of the development of associations between stimuli and reactions and that these associations are developed every time a reaction is rewarded (McSweeney and Murphy 2014). The work of Thorndike on learning theory set the ground for the development of a number of theoretical models of associative learning that postulate that learning is governed by the formation of stimuli-responses associations (Ramnero and Torneke 2011). Despite that stimuli-responses associations are still considered to be involved in learning, theoretical models of associative learning since 1970 directed more their attention on stimuli-stimuli rather than stimuli-responses associations (Shanks 1995). This shift was done for a number of reasons. Firstly, this shift is considered by many researchers to be entirely practical. Specifically, Thorndike supported his theoretical inferences on experimental research of operant conditioning during which an animal (i.e., usually a cat) exhibited a behavioral reaction (i.e., press a lever) which was followed by the acquisition of a reward (i.e., food). The issue with this experimental design is that the cat, not the researcher,

determined when the response will be rewarded; thus, it is hard to determine the exact occurrence of each episode of learning (Wills 2012). Therefore, theorists and experimenters directed their focus on classical conditioning where a neutral stimulus signifies the occurrence of a biologically relevant stimulus and thus induces a classically conditioned response. Despite that each trial is completely controlled by the person that conducts the experiment, the indications of learning in this experimental procedure task are detected when the neutral stimulus acquires qualitatively similar qualities with the ones that the unconditioned stimulus has and in turn induces a classically conditioned response that is also qualitatively similar with the unconditioned response (Schachtman 2011).

Associationism as a Theory of Mental Structure

The notion of associative learning has been adopted by a variety of related theoretical perspectives which understand learning as the acquisition of associations between stimulus-response contingencies (i.e., instrumental conditioning) or the acquisition of associations between stimulus-stimulus contingencies (i.e., Pavlovian conditioning) or the acquisition of associations between stimulus-valence contingencies (i.e., evaluative conditioning) (McSweeney and Murphy 2014). Associative learning theorists have consistently proposed that the acquisition of associations between environmental contingencies is encoded in the form of an associative structure (Hall 2002). The operational concept of associative structure depicts the nature of the relationship that associates two separate mental states. An example of an associative structure is an association between honey and mustard. Specifically, in this scenario honey and mustard develop an associative structure which functions operationally (Delamater and Lattal 2014). That is, when the mental state of honey becomes activated, triggers also the activation of the mental state of mustard and the other way around.

The operational and theoretical conceptualization of associative structures indicates that

associations maintain symmetric cause-effect relations. That is, if an individual has formed an association between honey and mustard, the honey should trigger the activation of mustard and the mustard should trigger the activation of honey. However, Thorndike and Skinner claimed that the order through which organisms learn affects the causal order of recall. In other words, if an individual hears only honey and mustard, then honey would be more likely to acquire the capacity to trigger the activation of mustard rather than the other way around. Therefore, a central operational principle in the examination of associative structures indicates that organism must learn the associative elements in a randomized sequence (Hall 2002).

In addition, it has been cited that the philosophical movement of British Empiricism wanted to designate a systematic and well-defined theoretical perspective based on associationism that would enable them to decrease the extent to which they had to rely on intrinsic functions (Staddon 2014). Similarly, the behavioral movement wanted also to develop a systematic and well-defined theory based on associationism. Theorists that advocate about the development of a theoretical perspective of thinking entirely have consistently proposed that the formation and maintenance of an association between two elements is regulated, by the rate of recurrence of former associations between the associated elements (Shanks 1995). This perspective hypothesized that associative structures encrypt, at least covertly, the rate of recurrence of former associations between elements that become associated. Additionally, the intensity of this associated connection is regulated through the past experience of these two elements by an organism. That is, the past experience of learned associations by an organism regulates the present operational outline of the analogous associative structures (Hall 2002).

Contemporary Study of Associative Learning

Throughout the twentieth century, a substantial amount of time was devoted for the extensive study to the fundamental mechanisms that

underlie both classical conditioning and operant conditioning (Wills 2012). Yet the study of classical and operant conditioning was conducted for different purposes. On the one hand, there were theorists and researchers who advocate that the experimental study of behavior merits a distinct and experimentally solid type of analysis (Staddon 2014). Theorists and researchers that were advocates of this view proposed that the study of the operational associations between environmental conditions and behavioral dynamics was adequate for understanding, predicting, and controlling behavior (Shanks 1995). On the other hand, there were theorists and researchers that advocated that the experimental analysis of learning in behavioral terms was just a means through which one can study the fundamental processes of the mind. For instance, Pavlov claimed that the operational procedures related to the study of classical conditioning phenomena could have utility exclusively to the degree that the role of the relevant brain processes is considered (McSweeney and Murphy 2014).

Furthermore, due to the operational procedures of classical conditioning in which two stimuli are presented at the same time, it is considered that learning related to this associative connection relies on the dynamic characteristics of stimuli-stimuli associations. Additionally, research related to this hypothesis indicated that the conditioned stimulus acquires the capacity to trigger a representation of the unconditioned stimulus that has been associated with it (Shanks 1995). As mentioned above theorists and experimenters directed their focus on classical conditioning for various reasons. Firstly, classically conditioned associations acquire the capacity to fundamentally influence organism's behavioral responses. Specifically, classically conditioned associations constitute a mechanism which enables an organism to adapt to impending biologically important conditions (Schachtman 2011). Moreover, the operational principles of classical conditioning enabled mental health professionals to develop and implement effective treatment interventions for affective abnormalities and substance abuse. Last but not least, Pavlovian conditioning equipped

learning theorists and researchers with an efficacious experimental design that enables for a significantly accurate analysis of the way that organisms form associations between environmental and interoceptive stimuli (McSweeney and Murphy 2014).

The Rescorla–Wagner Model of Classical Conditioning

A highly influential model of classical conditioning was developed and presented by Robert A. Rescorla and Allan R. Wagner (McSweeney and Murphy 2014). Despite that over than 40 years have passed from its publication, there are no indications of a decrease in its influence in the field of learning in general and in the subfield of associative learning specifically (Schachtman 2011). The Rescorla–Wagner model proposed that while living beings interact with their environment, develop causal expectations that enable them to estimate relationships between environmental conditions (Wills 2012). According to this model, learning involves acquiring knowledge related to the way that the environment is causally organized (Rescorla 2008). An organism becomes able to achieve learning by developing solid associations between environmental components (Shanks 1995). Yet even if the environmental components become contiguous and in turn the organism forms associations between them, the environmental components need to also allow the acquisition of knowledge related to causal relationships (Wills 2012). Actually, the fundamental idea is the concept of contingency and how an organism perceives it. This model by integrating cognitive capacities within the formation of associations indicated the acceptance of both cognitive functions and associative processes in the brain, something that quickly earned the favor of experimental psychologists (Shanks 1995). However, despite its great influence, the theoretical model presented by Robert A. Rescorla and Allan R. Wagner did not go without challenge. Specifically, it has been cited that various research data within the learning literature could not easily be explained through this

model, and some of these data led to the development of other theoretical models related to associative learning (McSweeney and Murphy 2014).

The Role of Prediction Error in the Study of Associative Learning

Contemporary research related to the environmental conditions that are necessary to assist and enhance learning has consistently suggested that learning progresses as an operation of the difference between the predicted and the acquired result (McSweeney and Murphy 2014). That is, the level of learning that is achieved by an organism in a given moment is reflected in the degree of this prediction error. For instance, high level of prediction error results in high degree of learning, whereas the small level of prediction error results in a smaller degree of learning (Delamater and Lattal 2014). Moreover, the concept of the prediction error is significantly important as it enhanced understanding of conditioned responses of fear and modified the lens through which the operations of specific neurobiological mechanism are understood (Wills 2012).

In addition, the process of the prediction error is not only involved in the acquisition of new associations but is also involved in the inhibition of that learning. That is, in trials where the predicted result is higher than the one that it is acquired, that is, the prediction error is negative, the associative intensity is considered to be loosened (McSweeney and Murphy 2014). The associative phenomenon of the negative prediction error is usually examined through the process of extinction (Rescorla 1993). That is, the process where a contained stimulus consistently occurs without the anticipated unconditioned stimulus, something that ultimately leads the conditioned response to weaken and finally extinguished (Schachtman 2011).

Most of the current theoretical perspectives related to learning propose that extinction is governed by the error correction process, a conceptualization that became widely known through the classical conditioning model of Rescorla–Wagner (McSweeney and Murphy

2014). This model claims that learning takes place when an important incident that constitutes an unconditioned stimulus is surprising (Rescorla 1968). In addition, this model proposes that when the process of extinction begins, the absence of the unconditioned stimulus when the conditioned stimulus is received is surprising too (Wills 2012). In order for the prediction error to be fixed, the association with the unconditioned stimulus is loosened till the conditioned stimulus precisely foresees the no unconditioned stimulus result (Rescorla 1993). Given an adequate quantity of extinction, this model presumes that the force of an association could be fully extinguished (Schachtman 2011).

Theoretical perspectives related to error correction are also congruous with neurobiological research related to the mechanism of associative learning. Specifically, it has been consistently cited that the brain encrypts error signals throughout the course of extinction (McSweeney and Murphy 2014). For instance, in appetitive conditioning, the firing of midbrain dopaminergic neurons is considered to hold a variety of significant roles, such as detecting reward prediction errors (Rescorla 1993). Furthermore, it has been consistently proposed that the extinction mechanisms are based on the process of prediction error correction. Specifically, learning initiates a reinforcer with surprising qualities when signals and/or actions foresee one (Wills 2012). In addition, the process of extinction is defined as an additional type of learning and not a process that erases learning. Therefore, it is assumed that prediction error develops a new form of learning which is challenging or interfering with the initial learning (Shanks 1995).

Conclusion

Pavlov's and Thorndike's operational procedures related to the study of the formation of conditioned behavioral responses are now considered conventional illustrations of simple types of associative learning that enabled researchers to experimentally examine the significance of generating intelligent action (McSweeney and

Murphy 2014). In addition, due to its examination with regard to recently developed associative bonds between elements derived from the environment and actions, the commitment of forming a fully mechanistic conceptualization of behavior is almost within grasp. Moreover, understanding in depth the mechanistic abilities as well as their operational importance across species enabled theorists in the field of experimental psychology to conduct efficacious comparative examinations of behavioral responses (Wills 2012). Theoretical models of associative learning are interested in the underlying mechanisms that regulate the associative connection that is developed when two stimuli accompany each other. During the twentieth century, the theoretical notion of associative learning has to a great extent been influenced through theoretical perspectives in the fields of behavioral psychology, cognitive psychology, social psychology, developmental psychology, and evolutionary psychology (McSweeney and Murphy 2014). In the late twentieth century, some of the underlying mechanisms of both classical and operant conditioning have been significantly elaborated in a theoretical as well as in an operational level. Specifically, the work of Robert A. Rescorla in classical conditioning, the work of Allan R. Wagner on associative learning, and the work of Nicholas Mackintosh in conditioning and associative learning had a great influence on the contemporary theoretical as well as operational advances that have been achieved in the fields of classical and operant conditioning and our understanding of behavioral dynamics.

In addition, the contemporary study of associative learning has been mainly focused on three central domains: firstly, to the environmental conditions that are necessary to assist and enhance associative learning (Wills 2012), secondly, to the contextual as well as the structural characteristics of associative learning, and thirdly, to the theoretical as well as the operational processes required in interpreting associative learning into overt behavioral functioning. Conceptualizing the central difficulties related to associative learning in such a manner proceeds a long way in the direction of designating standards for a

sophisticated analysis of associative learning mechanisms. In addition, provides a solid basis for the organization of research findings that can add to the preexisting knowledge related to associative learning (Schachtman 2011).

Cross-References

- [Adaptive Learning](#)
- [Classical Conditioning](#)

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Associative Tool Behavior

► Sequential Tool Use

Assortative Mating

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Synonyms

Assortment; Endogamy/exogamy; Homogamy/heterogamy

Definition

Assortative mating is the nonrandom coupling of individuals based on resemblance on one or more characteristics (Buss 1984).

Introduction

“Tell me what company thou keepest and I’ll tell thee who thou art” (Miguel de Cervantes, Don Quixote, Chap. XXIII).

Assortative mating (AM) is one of the major departures from random mating. It occurs in two forms, positive AM or homogamy, when phenotypes of mated partners are more similar than would be expected under random mating, and negative AM or heterogamy (disassortative mating), when the mated partners are more dissimilar than they would be under random mating. Assortment is usually measured as a correlation between the values of the same phenotypic or genotypic characteristics across mating partners. The primary effect of AM is a change in the expected genotypic frequencies from those expected under the Hardy-Weinberg law. Positive AM has much the same effect as inbreeding. It increases the relative frequency of homozygotes, while negative AM has the opposite effect, i.e., it increases the relative frequency of heterozygotes. Until now, AM has been explored on a vast range of variables including sociodemographic, physical characteristics, health behaviors, psychopathology, intelligence and other cognitive abilities, values, attitudes, as well as a wide range of personality traits. For almost all of them, positive assortment has been found to a greater or lesser degree, while negative AM has rarely been found. One example is spousal dissimilarity at human leukocyte antigen alleles within the major histocompatibility complex region, although the evidence has been equivocal (Havlicek and Roberts 2009). Regarding psychological variables, Buss (1984) obtained negative AM for dominance and submissiveness dimensions on spouse reports and interviewers’ ratings. Similarity between partners is usually considered as a trait-specific assortment, but sometimes also as a cross-trait assortment. Trait-specific assortment is similarity in a particular characteristic such as height, intelligence, or extraversion, while cross-trait assortment is a coupling that is based on congruency on different, but similarly valued traits, such as a tendency for extraverted women to mate with conscientious men (Buss and Barnes 1986).

Theoretical Considerations and Possible Functions of AM

Several theoretical explanations of AM are proposed. The theory of complementary needs is based on the modified version of Murray’s needs scheme (Winch et al. 1954). The authors proposed

that during mate selection, individuals choose a person who shows the highest potential to satisfy one's needs. The rule for needs satisfaction is complementarity rather than similarity. It comes in two forms: (1) a need of a person A is qualitatively different than that of a person B (e.g., one person has high need for dominance, and the other for deference), and (2) the intensity of a need is opposite in a person A compared to the same need in a person B (e.g., one person has high, and the other low need for achievement). Although the authors reported some supporting evidence, later studies were unable to replicate them. A social psychological explanation of AM is based on the concept of consensual validation. It is assumed that people choose similar partners simply because finding commonalities with other people is inherently rewarding (Byrne 1971). Therefore, if there is a correlation between similarity and validation of one's worldview, learning through conditioning will eventually lead to the preference for similarity. In a theoretical explanation of AM, Buss (1984) suggested that people create extensive and enduring environments through the selection of a mate. By choosing a similar mate, a partner is also selecting a social environment that corresponds to his/her existing characteristics. Therefore, AM may be considered as an important mechanism for creating genotype-environment correlations that may consequently affect adult personality development. For example, if two extraverts mate, they are likely to reinforce each other's initial personality predispositions by selecting specific environments (e.g., attending big parties) and avoiding others (e.g., going to the cinema). Another process through which AM may affect adult personality development includes the concept of a pacer, i.e., a person who is moderately discrepant in a certain trait from the target individual, and is therefore an optimal model for the development of the target person (Buss 1984).

The genetic similarity theory proposed by Rushton et al. (1984) is a more general version of Hamilton's inclusive fitness theory. They suggested that organisms behave in a way to increase the fitness not only of their blood relatives, but also of all genetically similar organisms regardless of their kinship status. The authors

applied this assumption to many aspects of human behavior, including AM. Specifically, they hypothesized that phenotypical matching of mates is only a proximal mechanism whose function is to increase the probability of mating with a genetically similar organism. The theory predicts many advantages of mating with optimally genetically similar individuals such as increased altruism, relationship stability, increased genetic similarity with progeny, all of which result in a higher parental investment as well as fecundity. Some of the supporting evidence for this theory are positive associations of assortative mating and marital quality, stronger assortment on more genetically based characteristics, and genetic similarity of couples in genes coding for blood types (Rushton 1989). However, the theory as well as the evidence was strongly criticized by many authors (see Open Peer Commentary of Rushton 1989). The objections were mostly related to the irrelevance of genetic similarity for the prediction of altruism for nonkin because it does not predict similarity in other genetic loci, methodological and statistical issues in correlating heritability and assortative mating index, as well as potentially biased results of blood antigen analyses in the sample of disputed paternity cases. An alternative evolutionary explanation of AM involves an imprinting-like process. According to this explanation, an opposite-sex parent's image is imprinted early in the child's development. During this sensitive period, only closely related persons, usually parents, are likely to be present. After reaching maturity, a person will try to find a partner similar to the opposite-sex parent resulting in the similarity between the person and his/her partner. It seems that individuals have been selected to reach an optimum balance between inbreeding and outbreeding, because both types of mating have reproductive cost and benefits (Bereczkei et al. 2002).

Figueredo and Wolf (2009) explain AM in the context of Life History Theory (LHT). As it is well known, LHT describes the strategic allocation of resources between major components of fitness such as survival and reproduction. LHT assumes that species living in harsh (high-risk of mortality), unpredictable, and uncontrollable environments evolve fast LH traits, while species

living in predictable, stable, and relatively safe and controllable environmental conditions evolve slow LH traits. Conditions favoring faster LH strategies have a selective advantage from the higher rates of genetic recombination and hence exogamy that leads to lower parental effort and a greater number of offspring, thus increasing the probability that at least some proportion of them will survive under unpredictable conditions. On the other hand, in order to preserve well-adapted genomes, conditions favoring slower LH strategies lead to endogamy, higher parental effort, and lower rates of genetic recombination. Therefore, AM coefficients for heritable characteristics will be higher for slower than for faster LH strategies (Figueroedo and Wolf 2009).

Mechanisms Underlying AM

Relevant question regarding AM is whether it is due to initial assortment, i.e., partners are already similar in some phenotypic characteristics at the beginning of their relationship, or convergence, i.e., partners become more similar in these characteristics over time as a function of increased familiarity, interactions, and synchronized routines (Luo 2017). Furthermore, similarity correlations may reflect active assortment or a preference for mating with a partner who is similar on a particular characteristic, or social homogamy, which refers to the mating with a partner who lives in a shared social environment and has similar social background (e.g., similarity in age, education, socioeconomic status). In contrast to active assortment, social homogamy refers to passive, indirect influences on partners' similarity, because people similar in social background may also share other characteristics such as attitudes, values and interests (Luo 2017). For most examined characteristics, evidence provides stronger support for initial assortment rather than convergence, and active assortment rather than social homogamy (Watson et al. 2004). Along with the processes mentioned above, mating market operation may also contribute to the similarity between partners. Based on the principle of social exchange theory, mating market operation affects the selection of a mate in a way that partners with highly desirable characteristics have more

opportunity to mate with similarly desirable partners, leaving the less desirable to mate with each other (Luo 2017). Similarity between partners in a long-term relationship may be also due to the process of attrition. Namely, partners with lower levels of similarity may end their relationship earlier, which may lead to the increased similarity in partners who remained in a relationship (Luo 2017).

Assortative Mating for Various Characteristics

Compared to other characteristics, socio-demographic variables show the strongest assortment across human populations, with the highest AM for age (from 0.70 to 0.95) (Watson et al. 2004), and education (from 0.50 to 0.65) (Hur 2003; Rosenfeld 2008). An increase in educational homogamy has been found in USA, but the results vary across the education distribution and are sensitive to the measures of couples' similarity (Schwartz 2013). A strong assortment for race and religion has been found, but at least in USA it has declined over the twentieth century (Rosenfeld 2008).

AM is widespread for a number of physical characteristics including height, weight, and BMI, the degree of these assortments being low to modest (from 0 to 0.30) (Hur 2003). A meta-analysis has shown that AM for height is relatively constant over time and that it is slightly, although not significantly stronger in Western than in Non-Western populations (Stulp et al. 2017). Regarding weight, research has shown that partners do not become more similar in this characteristic with increased length of their relationship. Furthermore, research of facial similarity showed that partners are perceived to be more facially similar to one another than it was expected by chance, but the association between relationship length and facial similarity remains unclear. A meta-analysis has obtained mean correlation of 0.49 between partners for physical attractiveness (Feingold 1988).

Generally, AM for social and personal values and attitudes tends to be moderately positive, ranging from 0.20 to 0.50 (Luo and Klohnen 2005). However, political and religious attitudes consistently show higher AM correlations (from

0.42 to 0.74) (Watson et al. 2004). It appears that partners' similarity in political attitudes depends partly on shared genetic factors (genotypic AM) and also on similarities in social and cultural background (social homogamy) as well as partner-specific shared environmental effects such as common habits and friends (Kandler et al. 2012). However, evidence concerning convergence has been somewhat inconsistent, with some studies showing convergence in values and attitudes, while others show that partners' similarity in social and political attitudes was present at the beginning of the relationship and increased very little over time (Luo and Klohnen 2005).

The majority of studies report a positive assortment between married partners for cognitive ability measures ranging between 0.20 and 0.45 (Watson et al. 2004). Some studies have found that AM is particularly strong for verbal abilities (around 0.50) compared to nonverbal, such as spatial ability, perceptual speed, and visual memory (around 0.30), that may be due to the easier assessment of someone's verbal than nonverbal ability. AM for *g* factor has also been found to be substantial, with average correlations between the partners of about 0.40 (Plomin et al. 2013). Higher positive assortment has been found for those abilities that are more saturated by *g* factor, i.e., those showing higher heritability (Nagoshi and Johnson 1986). It seems that the mechanisms underlying AM for intelligence are initial assortment rather than convergence, and active assortment rather than social homogamy (van Leeuwen et al. 2008).

Low to moderate degree of positive AM has been found for numerous personality traits, with correlations rarely exceeding 0.30. However, one of the exceptions seems to be sensation seeking, for which the strongest AM has been repeatedly found (McCrae et al. 2008). The majority of evidence has been obtained on Five Factor model, which is assumed to provide a comprehensive account of personality (McCrae et al. 2008; Watson et al. 2004). The studies usually show the most consistent evidence of positive AM for openness, followed by agreeableness, conscientiousness, and neuroticism, while extraversion shows inconsistent results varying from low negative to moderate

positive assortment (McCrae et al. 2008; Watson et al. 2004). For example, in a sample of newlywed couples, Watson et al. (2004) have found significant negative assortment for extraversion on both self-(-0.17) and spouse-ratings (-0.14). However, some studies have found little or no AM for five factor personality traits (e.g., Luo and Klohnen 2005). On the level of five factor personality traits facets, differences in assortment have been especially pronounced for openness domain, showing moderate positive assortment for aesthetics and values, and no assortment at all for fantasy and feelings (McCrae et al. 2008).

AM for socially undesirable personality traits has been rarely explored. Moderate positive assortment has been obtained for all Dark Triad traits, a cluster of three antisocial personality traits, psychopathy, Machiavellianism, and narcissism (Kardum et al. 2016). Machiavellianism has shown the highest degree of assortment probably because this trait is a more attitude-like concept, and attitudes, as already mentioned, show a higher degree of positive assortment. Positive assortment has also been found for numerous other personality traits, with low to moderate correlations between partners (McCrae et al. 2008; Watson et al. 2004).

For most personality traits, evidence supports initial assortment more strongly than convergence because similar effects have been found in both younger and older couples (McCrae et al. 2008), as well as when relationship length has been controlled for (Watson et al. 2004). Additionally, few existing longitudinal studies have found some convergence, but limited only to several traits (see Rammstedt and Schupp 2008). Research has also shown that AM in personality traits is due to active assortment rather than socio-demographic background variables such as age and education (McCrae et al. 2008; Watson et al. 2004).

Other factors influencing AM for personality traits have been rarely and nonsystematically examined. Although there are theoretical reasons for assuming that AM may be universal because mating patterns have been strongly influenced by evolutionary pressures, there is some evidence of cross-cultural differences in assortment for

personality traits. Examining AM for five-factor personality traits on married couples in four Western cultures, McCrae et al. (2008) have found some subtle cultural differences. However, the results obtained on newlywed couples from mainland China showed stronger similarity on personality traits (from 0.33 to 0.66) than those usually obtained on Western cultures, while the degree of AM in demographic variables and attitudes was mostly similar to Western cultures (Chen et al. 2009). This suggests that cultural differences may promote assortment in personality. The level of a trait can also affect the degree of AM. Namely, assortment may be differentially expressed across trait levels. For example, a higher degree of positive assortment has been found for slow rather than fast LH strategy (Figueiredo and Wolf 2009). Furthermore, Lee et al. (2009) showed that a degree to which certain traits serve as indicators of individuals' values could be an additional factor that modifies the degree of AM. They found higher positive assortment for honesty-humility and openness to experience than for other HEXACO personality traits. Furthermore, these two traits serve as dispositional bases for individuals' value system, thus exerting important effects on one's identity. Additionally, some features of personality traits such as visibility, malleability, and social desirability (Luo 2017), as well as different data sources may also affect the degree of AM. For example, McCrae et al. (2008) have found the largest differences in the degree of AM between self-self and partner-partner reports for extraversion and the smallest for agreeableness. The abovementioned factors influencing the degree of AM in personality traits are often atheoretical, and their effects relatively weak.

Positive AM has also been obtained for numerous adverse behaviors including alcoholism, smoking, aggression and violence (Agrawal et al. 2006), as well as disorders including anxiety, depression, schizophrenia, bipolar disorders, and autism (Nordsletten et al. 2016). Studies have found low to moderate positive correlations (from 0.07 to 0.45) between partners for drinking behavior (Grant et al. 2007), as well as for ever-smoking (0.18) and current smoking status (0.43) (e.g., Boomsma et al. 1994). It seems that partners'

similarity for cigarette smoking, nicotine addiction, regular alcohol consumption, and alcohol dependence is mainly due to initial assortment (Agrawal et al. 2006), although some studies support both initial assortment and convergence hypotheses of partner similarity for substance use (Fleming et al. 2010).

Positive AM between romantic partners has been found for various antisocial behaviors. For example, moderate to strong assortment for violent offending has been found (about 0.40), and it may be attributed to both phenotypic assortment and social homogamy (Frissell et al. 2012). It seems that convergence could also be a mechanism underlying AM for antisocial behaviors. The convergence for these behaviors has usually been explained by behavioral contagion, implying that behavior of a partner "infects" the behavior of other partner, thus increasing the similarity between them over time (Moffitt et al. 2001).

Examining the patterns of AM within and across 11 major psychiatric disorders on population-based cohort, Nordsletten et al. (2016) have found widespread positive assortment both within and across this spectrum of disorders. The highest AM has been found for autism (0.47), and the lowest for bipolar disorder (0.15). Within-disorder correlations were marginally higher (from 0.11 to 0.48) than cross-disorder correlations (from 0.01 to 0.42). However, the correlations were either not obtained or were weaker among the selected cases of non-psychiatric conditions (e.g., Crohn's disease, multiple sclerosis), but of similar incidence and age at the onset of the relationship (from -0.03 to 0.10). Several mechanisms underlying AM for psychiatric disorders have been recognized including initial assortment, secondary assortment (i.e., mate selection based on characteristics that correlate with psychiatric morbidity such as personality traits, age and education), social homogamy, marital interactions, and exposure to common negative stressful environment. However, the evidence concerning these mechanisms is weak and inconsistent, especially in the context of specific psychiatric disorders.

There is also meta-analytic evidence of modest positive AM for both traditional and emerging risk factors of ischemic cardiovascular disease (e.g., blood pressure, smoking, factors linked to

bodyweight, metabolic syndrome). Furthermore, a concordance for dichotomous outcomes such as hypertension, smoking, diabetes, and obesity has also been obtained. Initial assortment seems to be responsible for similarity between partners in most traditional cardiovascular risk factors, while shared marital environment influenced mainly lipid metabolism (Di Castelnuovo et al. 2009).

Consequences of AM

AM has several important evolutionary, genetic, psychological, and social consequences. Two major evolutionary benefits from positive assortment have been suggested. Positive assortment for similar genes adds to the parents' inclusive fitness by increasing gene representation in their offspring and genetic potential for altruistic behaviors between parents and between parents and their offspring (Thiessen et al. 1997). Regarding genetic consequences, AM increases the contribution of additive genetic variance so that the offspring differ more from the average than they would if partners mate randomly. Even if similarity between partners is modest, it may increase genetic variability in the population because its effects accumulate over relatively few generations (Plomin et al. 2013). For example, the increase in heritability due to AM may explain why some psychiatric disorders (e.g., schizophrenia, ADHD) have such high heritability notwithstanding reduced fecundity (Plomin et al. 2016). Furthermore, positive assortment may influence the estimates of heritability because it increases correlations for first-degree relatives, and if it was not taken into consideration, it could decrease heritability estimates and its effect would be attributed to shared environment (Plomin et al. 2013).

There are several complex interactions between genetic and social consequences of AM. As already mentioned, AM creates genotype-environment correlations that can have numerous important implications. For example, homogeneity of the rearing environments created by similar partners may have important consequences for their children's development. Positive AM increases, while negative decreases the variability of a certain characteristic in future generations, which may have important psychological and social consequences. For

example, characteristics that are more variable also become more salient and thus represent the bases for differentiation among individuals as well as for their social evaluation (Buss 1983). Greater variability in certain characteristics may increase the number of individuals at the tails of the distribution with either positive (e.g., exceptionally creative individuals) or negative consequences (e.g., autism as the genetic result of assortative mating of two high systemizers; Baron-Cohen 2006).

Positive AM for numerous characteristics such as intelligence, attitudes, interests, and personality traits predicts various relationship outcomes such as higher satisfaction and quality of relationship and lower relationship dissolution (Luo and Klohnen 2005). There are several partly overlapping psychological explanations for similarity-satisfaction effect. The first suggests that similarity fosters partners' self-verification, improves understanding, and increases closeness (Luo 2017). Other explanations encompass mere exposure effect or a preference towards familial stimuli and implicit egotism or a preference towards whatever reminds us of ourselves (Pelham et al. 2002). Because AM for socioeconomic variables (education, occupation, income, class background, race/ethnicity, and religion) is an important factor that determines the characteristics of families and their reproduction, it may have relevant social consequences such as inequality within and between generations, as well as long-run population change (see more in Schwartz 2013).

Conclusions

On a vast range of variables, positive rather than negative AM has been found. The highest degree of similarity has been obtained for socio-demographic variables and attitudes, followed by moderate similarity for cognitive abilities, psychiatric disorders, antisocial and adverse behaviors, and the lowest for physical characteristics and personality traits. Initial and active assortments have most frequently been suggested as mechanisms underlying AM, with the evidence for convergence and social homogamy being scarce.

Advances in theory and empirical research are highly needed because AM has important evolutionary, genetic, psychological, and social consequences.

Cross-References

- [Dating](#)
- [Marriage](#)
- [Mate Choice Effects](#)
- [Mate Preferences](#)
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Assortment

- Assortative Mating
- Cooperation Varies with Genetic Relatedness

Athletic Competition

- Team Sport

Atrophy

- Use It or Lose It

Attachment

- Parent Influences

Attachment in Adulthood

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Synonyms

[Adult attachment](#)

Definition

Attachment in adulthood addresses the role of the attachment system in adult relationship functioning and dynamics. In the normative course of development, individuals transfer attachment functions from the child-caregiver relationship to peer relationships, principally to romantic relationships. Within these, individual differences regarding romantic attachment have been found to exert significant influence over important aspects of relationship functioning, including the stance toward intimacy, communicative strategies, and emotion regulation.

Introduction

Originating in British psychoanalyst and child psychiatrist John Bowlby's formulations about the nature of human bonds (see "John Bowlby: Pioneer of Attachment Theory"; "Evolutionary Foundations of the Attachment System and Its Functions"), attachment theory has stimulated an enormous corpus of research, particularly on attachment during infancy and childhood. Bowlby himself was however convinced that attachment is an integral part of human life not just in childhood, but "from the cradle to the grave" (Bowlby 1969, p. 208). This statement remained a hypothesis until the end of Bowlby's active career but has spurred a growing body of

theory and research during the past three decades. The results and current status of this research are the main focus of the current entry.

Since a major part of the research concerning attachment in adulthood has explored the role of attachment in pair bonds, the following depiction mainly revolves around this specific type of relationship. Theory and research pertaining to the status of pair bonds as the normative attachment relationships of adult life are described and discussed, and methodological issues as well as research regarding individual differences in romantic attachment are reviewed. Finally, the entry also addresses an important controversy regarding the status of the attachment system in romantic relationships.

Pair Bonds as Attachment Relationships

The Defining Features of Attachment Bonds

Attachment in childhood denotes the affectional bond that children form to their primary caregiver(s), and that is typically established within the first 8 months of life (Bowlby 1969). The bond is complementary (i.e., the child forms the bond to the caregiver – not the other way around) and has four defining features: (1) *proximity maintenance*, referring to the maintenance of proximity to the caregiver and the monitoring of the caregiver's availability; (2) *separation distress*, referring to the child's distress and protest in response to separations; (3) *safe haven functioning*, referring to the child's turning to the caregiver for comfort and support when distressed; and (4) *secure base functioning*, referring to the child's use of the caregiver as a reference point for exploration of the environment. In addition, and as implicated by these features, the attachment construct presupposes that the attached individual perceives the attachment figure as stronger and wiser than the self, particularly in challenging situations.

In conceptualizing adult relationships as attachments, theorists have argued that these features of the child-caregiver relationship eventually become transferred to the close relationships of adult life. However, important changes are also expected to occur in the development from

infancy to adulthood (Hazan and Shaver 1994). First, adults come to develop a significantly higher capacity for emotion regulation and mental representation of others, leading to important differences between child and adult attachment dynamics, not least regarding the capacity to tolerate separations. Second, whereas the child's relationship with the caregiver predominantly involves the attachment system and the caregiver's relationship with the child predominantly involves the caregiving system, in adult relationships, these systems typically become integrated together with the sexual mating system, with sexual attraction usually being the precipitating force that brings adult partners into intimate contact. Third, and related to the integration of these behavioral systems, the complementary or asymmetrical nature of child attachment relationships becomes substituted for more reciprocal or symmetrical relationships, with adult partners mutually seeking and providing security (Hazan and Shaver 1994; Mikulincer and Shaver 2016).

From Parents to Peers: The Gradual Transfer of Attachment Functions

Cindy Hazan and colleagues (Fraley and Davis 1997; Hazan and Zeifman 1994) have suggested that children gradually transfer attachment functions from the caregiver(s) to other relationships, which may eventually come to display the defining features of attachment bonds. Based on their studies exploring children's and adolescents' preferences for specific people in attachment-relevant situations, they argue that children, from approximately 6 years of age, generally prefer to spend time with peers than with their parents, indicating that the proximity-seeking function of the attachment system has been transferred to peer relationships. They further note that by adolescence, peers generally seem to be preferred over parents even as sources of emotional support, at least in mildly distressing situations, with the confiding and comfort-seeking aspects of teen relationships paralleling the safe haven behaviors previously directed primarily toward caregivers. However, at this stage of development, most adolescents still seem to regard their caregivers as bases for security and sources of separation distress. Full-

blown attachments to peers (i.e., bonds involving the four defining features of attachment relationships, including the secure base function) seem not to be established until late adolescence or early adulthood. Among the individuals who, by that time, have transferred their principal attachment from a caregiver to a peer, 80% refers to a romantic partner, indicating that pair bonds be the prototypical or normative instantiation of attachment in adulthood (Fraley and Davis 1997; Hazan and Zeifman 1994).

The establishment of adult attachment seems to follow a chronological sequence that corresponds with the child's establishment of attachment to a caregiver, with proximity-seeking and safe haven behaviors arising early in the relationship, while separation distress and the secure base function take longer to develop (see "Offspring-Parent Attachment"). Importantly, the occurrence of separation distress and secure base functioning in adult relationships seems to depend on relationship status (Hazan and Zeifman 1994). Whereas most romantic partners in relationships of at least 2 years regard their partner's presence as the primary source of security and their absence as the most distressing, the majority of romantic partners in shorter relationships still locate these components of attachment in the relationship with parents, indicating that romantic relationships require approximately 2 years to develop into attachment relationships (Hazan and Zeifman 1994). It is worth noting, though, that a more recent study has indicated that merely 6 months may suffice (Heffernan et al. 2012).

Similarities Between Pair Bonds and the Child's Bond to Its Caregiver

Beyond the findings described above, pair-bond and infant-caregiver relationships also display a number of unique similarities, which are thought to indicate the presence of attachment dynamics in pair-bond functioning and hence adding to the plausibility of conceptualizing pair bonds as attachment relationships (Zeifman and Hazan 2016).

Phenomenological similarities. In the seminal work first conceptualizing pair bonds as attachments, a number of phenomenological

similarities were noted between infant-caregiver and romantic relationships (Hazan and Shaver 1987; Shaver et al. 1988). One such similarity concerns the nonverbal behavior in infant-caregiver and pair-bond relationships, with behaviors such as holding, touching, cuddling, kissing, caressing, smiling, and clinging, as well as sustained eye contact and body investigation, being characteristic of both types of relationship. Although, admittedly, some of these behaviors can appear in isolated form even in other relationships (e.g., friendly kisses, caressing as a part of “casual sex”), the occurrence of these intimate behaviors together is largely unique for relationships between romantic partners and between children and caregivers (Hazan and Shaver 1987; Shaver et al. 1988).

Unique similarities are also evident in the verbal domain. For instance, verbal communication between infants and caregivers typically involves “cooing,” “singing,” and “babbling” on the infant’s part and high-pitch, slow-tempo verbalizations with a “singing” pattern of intonation on the caregiver’s part (i.e., “infant-directed speech”). Most adult relationships are void of this type of communication, but similar phenomena are visible in pair bonds, where partners tend to communicate with a “singing” pattern of intonation and speak with a higher and wider pitch, rendering their voices a more caring tone.

Yet another similarity concerns reunion behaviors, where infants typically display active signaling behaviors (smiling/crying, vocalizing) and proximity seeking (e.g., requests for being lifted) following short separations. Similar behaviors also occur between romantic partners – albeit after more prolonged separations – with positive vocalizations, feelings of euphoria, and requests for physical proximity being typical behaviors upon reunion.

A fourth similarity concerns the idealization occurring in both infant-caregiver and pair-bond relationships. The infant’s appreciation of the caregiver as stronger and wiser – a crucial aspect of the attachment bond – regularly implies a tendency to attribute to the caregiver an unrealistic degree of strength and knowledge. A similar pattern of idealization normally occurs in the initial

stages of romance, where the partner’s negative qualities are usually downplayed and the other is given a certain air of perfection.

Reactions to separation and loss. Bowlby (1969) demonstrated what appears to be a universal pattern of reactions in children, in response to prolonged separations from caregivers. This pattern, which he termed the “protest-despair-detachment” sequence, involves initial reactions of protest, in the form of hyperactivity, agitation, extreme anxiety, and resistance to comfort from others, generally followed by a period of depressive reactions, including inactivity, apathy, and disrupted sleeping and eating. Ultimately, if the caregiver remains absent, the child typically detaches emotionally and gradually regains normal functioning.

Adults’ reactions to inexplicable and involuntary separations from, or the death of, a romantic partner generally follow the very same sequence, further indicating that the attachment system is operative in pair bonds (Zeifman and Hazan 2016). For instance, adults initially tend to react with intense anxiety and denial in response to unexpected loss of a partner, and disorganized behaviors are common (e.g., looking for the deceased one or talking about him/her as if he/she were still alive). This phase is later replaced by a prolonged period of mourning, usually characterized by painful yearning and depressive reactions, such as withdrawal and food or sleep disturbances. With time, most adults regain their organization regarding the loss of the partner; the loss becomes accepted, and a certain degree of emotional detachment takes place, facilitating the resumption of normal functioning and enabling the remaining partner to “open up” to new pair-bond relationships.

Apart from infant/child-caregiver relationships, the protest-despair-detachment sequence is observed almost exclusively in pair bonds. Although the loss of dear relatives and friends can cause profound emotional pain, these losses typically don’t evoke the intense anxiety or panic associated with the loss of a partner, and they are generally less challenging for the individual’s mental organization. The stronger reactions specifically associated with the loss of a partner are

easily understandable from an attachment perspective – they make adaptive sense, if the lost partner served as a primary source of emotional security. Their normative occurrence in adults facing loss of their long-term partners also further strengthens the notion of pair bonds as attachments in adulthood (Zeifman and Hazan 2016).

Physical and psychological health effects. Child-caregiver and pair-bond relationships also seem to have a similar and uniquely powerful impact on physical and psychological well-being. Paralleling the importance of attachment for the child's physical and psychological development (see "Effects of Attachment Quality and Organization"), there is also ample evidence for the health benefits of close adult relationships, especially pair bonds, as well as for the health decrements of not establishing or loosing such bonds. Loss of romantic partners has been associated with increased susceptibility to a number of physical and psychological ills, including impaired immune system functioning and various forms of psychopathology (Ehrlich 2019; Keyes et al. 2014). Indeed, except for the death of a child, divorce or death of a partner are generally perceived as the most distressing events in adult life. Moreover, this distress appears to be qualitatively different from the distress following from the loss of friendships and seems not to be sufficiently compensated by the social provisions of other adult relationships, indicating that certain emotion-regulating functions of the pair bond are not fully available in other adult relationships (Zeifman and Hazan 2016). Neither is this distress evoked in the early stages of relationships that only later develop into attachment relationships. For children, the loss of a primary caregiver is associated with long-term developmental consequences only if it occurs after an attachment bond has been established. Correspondingly, the protest-despair-detachment sequence of reactions following a partner's decease is generally only observable in romantic relationships of at least 2 years' duration (i.e., relationships of the duration typically associated with the formation of full-blown adult attachments; see above). In sum, the severe distress following the loss of a deeply loved other – the very hallmark of

attachment bonds – is mainly present within child-caregiver relationships and long-term pair bonds (Zeifman and Hazan 2016).

Neurobiological Evidence of the Pair Bond as an Attachment Relationship in Adulthood

The advent of neuroimaging techniques and advances in hormonal assays have allowed researchers to examine possible neural and endocrine underpinnings of adult attachment. This research has further strengthened a number of the findings and theoretical proposals described above. For example, Bartels and Zeki (2000) have found that, compared to photographs of friends, photographs of long-term romantic partners evoke a different pattern of neural activity in individuals, implicating regions involved in attachment, a finding that seems to support the idea of pair bonds as the normative instantiation of attachment in adulthood. Subsequent research has also demonstrated different patterns of neural activation at different stages of romantic relationships. Whereas partners in early stages of romance display increased release of dopamine and norepinephrine in response to photographs of their partners (Xu et al. 2011), partners in the more advanced stages of romantic relationships show increased release of serotonin and endogenous opioids (Acevedo et al. 2012). While the former is associated with reward, the latter is associated with stress regulation and implied in infant-mother bonding, further supporting the claim that attachment-related processes are involved primarily in later stages of romantic relationships. Moreover, they also point to the centrality of emotion and stress regulation in both infant-caregiver and pair-bond attachments. In infancy, the hypothalamic-pituitary-adrenal (HPA) axis (a neuroendocrine system essential for regulation of stress) is responsive to caregiver interventions, reflecting the infant's use of the caregiver as a safe haven for comfort and stress regulation (Gunnar and Donzella 2002). Corresponding findings from studies on adult romantic relationships have shown physical contact with the partner to reduce cortisol levels (the end product of the HPA axis stress response) in long-term partners (Ditzen et al. 2007). Furthermore, just as in infant-

caregiver relationships, the cortisol stress response tends to be coordinated within long-term romantic relationships, but not within friendships (Feldman 2017), with the specific nature of coordination varying with relationship quality (Saxbe and Repetti 2006). Adult romantic relationships and infant-caregiver relationships also display a unique endocrine synchrony, not the least with regard to oxytocin (a neuropeptide associated with feelings of calm and well-being; Feldman 2017).

Individual Variations in Romantic Attachment

Based on the large body of evidence described above, it has become generally accepted that long-term pair bonds typically develop into definitional attachment relationships. However, having focused on the normative development in romantic relationships, the previous discussion has left unanswered the question of how to view individual variations in romantic attachment. Bowlby argued that early experiences with the primary caregiver(s) gradually become internalized, forming internal working models of self and others (IWMs; cognitive-affective representations; see “Effects of Attachment Quality and Organization”). The IWMs were thought to display a relatively high degree of stability throughout development and to become generalized to other close relationships later in the individual’s life (i.e., general continuity). Due to new experiences in the attachment relationship (e.g., depression in the caregiver or a caregiver becoming increasingly available after recovering from substance abuse), they were however also thought to be open for revision to some extent (i.e., lawful discontinuity).

Early accounts of adult attachment (Hazan and Shaver 1987; Shaver et al. 1988) drew on this idea, in hypothesizing that the continuity and generalization of IWMs would typically result in distinct adult romantic attachment styles, largely analogous with the major attachment categories in infancy (i.e., secure, avoidant, and anxious-ambivalent; the disorganized category in

childhood was introduced later; for a further description, see “Individual Variations in Attachment”), and exerting influence over different aspects of adult relationship dynamics. The existing research pertaining to this hypothesis is the main focus of the current section. However, before proceeding, some remarks on methodology are made.

The Measurement of Individual Variations in Adult Attachment

In reviewing research on individual variations in adult attachment, it should be noted that existing research has emerged from two different research traditions: one stemming from the field of social-personality psychology and one from developmental-clinical psychology. While the former has largely explored attachment-related dynamics in adult relationships, mainly through the use of different self-report instruments, the latter has focused on adults’ representations of *childhood* attachment relationships in relation to different developmental aspects of life (e.g., the intergenerational transmission of attachment). The developmental-clinical tradition has also employed more in-depth methods of measurement, principally the Adult Attachment Interview (AAI; for a description, see Hesse 2016), a well-validated interview instrument, measuring the adult individual’s current state of mind with regard to parent-related attachment. However, although a large number of important findings have been obtained within the developmental-clinical tradition, not least regarding correspondence between parents’ own attachment representations and their children’s attachment classifications (Hesse 2016), these findings fall outside the scope of the present entry.

Second, while assessments of child-caregiver attachment regard the quality of the relationship, assessments of romantic attachment concern the individual’s stance regarding attachment-related aspects of pair bonds. Theoretically, the latter is motivated by the assumed continuity and generalization of IWMs that imply a relative stability in individuals’ ways of relating, even between different and somewhat varying relationships. There has however been a considerable debate within

the social-personality tradition, regarding how to capture this stance most accurately. Early self-report measures of romantic attachment (e.g., Hazan and Shaver 1987) were based on the assumed analogy with childhood attachment and therefore assigned individuals to one of the major attachment categories. However, these measures were soon criticized for rendering unstable results, for disregarding evidence of overlap between the categories, and for neglecting important within-category variations. Consequently, the categorical approach came to be largely abandoned, in favor of a view on adult attachment variations as dimensional, and possible to capture by scaling individuals with respect to attachment-relevant dimensions – predominantly dimensions of avoidance and anxiety.

The most widely used instrument based on this view is the Experiences in Close Relationships Scale (ECR; Brennan et al. 1998), a 36-item scale based on extensive factor analysis of previous measures, which yields scores on two orthogonal, continuous dimensions, “avoidance” of closeness, intimacy, and dependence and “anxiety” about abandonment and of being insufficiently loved. The first dimension represents a disposition for attachment system deactivation, while the second represents a disposition for attachment system hyperactivation, and the two factors can also be used (via factor rotation) to obtain measurements of negative versus positive models of self and others (Mikulincer and Shaver 2016).

Psychometric evaluations clearly support the dimensional conception of romantic attachment (Mikulincer and Shaver 2016). Mainly for didactical reasons, the categorical or typological terminology has however partly been kept within the social-personality tradition. Individuals scoring low on both dimensions on the ECR, or displaying a positive model of self *and* others at the representational level, are then said to have a secure “attachment style.” An avoidant attachment style is represented by two different types: dismissing avoidant and fearful avoidant attachment. Whereas the first type is characterized by high avoidance but low anxiety, or a (defensively) positive model of self but a negative model of others,

the latter is characterized by high avoidance *and* high anxiety, or a negative model of *both* self and others. Finally, the preoccupied (cf. resistant/ambivalent) attachment category is characterized by high anxiety but low avoidance, or a negative model of self but a positive (though inconsistently so) model of others (Mikulincer and Shaver 2016).

While the use of such terminology could give the impression of discrete types, it should be borne in mind in the discussion below that the categorical terms sometimes used usually refer to regions in a two-dimensional space, in which people are continuously distributed.

The Developmental Continuity of Individual Differences in Attachment

Bowlby’s idea about general continuity and lawful discontinuity of attachment representations has gained support from empirical studies. Some (but by no means all) longitudinal studies investigating the link between infant behavior in the strange situation procedure (SSP; the predominant instrument for assessment of infant attachment; see “Individual Variations in Attachment”) and later classifications on the AAI have shown a correspondence between the two, especially with regard to the broader secure-insecure dimension (i.e., secure versus insecure SSP-behavior in infancy has been predictive of secure versus insecure response patterns on AAI in adulthood). Changes in attachment representations, particularly from secure to insecure, have also been linked to major distressing events within attachment relationships (i.e., divorce, parental psychopathology), supporting the notion of lawful discontinuity (Waters et al. 2000). A relatively high degree of correspondence has also been found in research examining the stability of romantic attachment over time, as assessed with repeated self-reports as well as with interview measures (Feeney 2016). However, as regards to one of the main assumptions of romantic attachment theory – that the continuity and generalization of IWMs from childhood partly explain variations in romantic attachment – existing evidence is limited. Although longitudinal data suggest associations between various aspects of

caregiving in childhood and subsequent romantic attachment, these associations seem not to be strong and consistent enough to offer a reliable set of predictors for romantic attachment (Fraley and Roisman 2019). Other efforts to evade this problem have also have been limited in their success; for example, studies investigating the link between representations of childhood attachment, as measured by the AAI, and self-reported romantic attachment have at best established weak correlations (e.g., Haydon et al. 2011).

Admittedly, attachment theory assumes no full correspondence between childhood and romantic attachments. According to most theorists (e.g., Overall et al. 2003), individuals develop a hierarchy of IWMs, with generalized models of self and others at the top, models for classes of relationships (e.g., parents, romantic partners) at an intermediate level, and models for specific relationships (e.g., mother, present partner) at the bottom. While the generalized models are thought to inform perceptions of self and others on the lower levels in a top-down manner, new relationship experiences with a specific partner could also, in a bottom-up manner, affect the models for the class of romantic partners, without altering the models for parents. However, since the models emerging from the parental relationships are thought to form the basis for subsequent models on other levels, some degree of correspondence is still expected.

Although the weak evidence of such developmental correspondence poses an issue for romantic attachment researchers, caution should be raised against interpreting from weak or inconsistent evidence for correspondence that no correspondence exists. One explanation for the lack of consistent evidence is that the self-report measures predominantly used when assessing romantic attachment mostly capture limited, conscious parts of an individual's IWMs, while in reality IWMs are to a large extent unconscious (e.g., due to defensive exclusion; see "Psychodynamic Foundations to Attachment Theory"). This might cause trouble for researchers employing self-reports – especially when studying insecure forms of attachment – because insecurity is characterized by incoherent IWMs, as manifest, for

example, in conscious self-perceptions that might well be incompatible with the individual's actual (unconsciously motivated) organization of behavior in attachment-relevant situations. Supporting this line of thought, a tendency has been found in individuals classified as dismissing/avoidant on the AAI to report themselves as secure on self-report measures (DeHaas et al. 1994). Other studies (e.g., Roisman et al. 2005) have found a stronger link between childhood and romantic attachment, when controlling for idealizing tendencies (associated with the dismissing/avoidant category on the AAI). Hence, weak or inconsistent developmental correspondence may partly be due to measurement issues, rather than to profound theoretical problems. It should also be accentuated that the issue at hand only pertains to the explanatory value of childhood attachment in explaining variations in self-reported romantic attachment, and not to the presence of attachment dynamics in romantic relationships, which is well established (as seen above). Neither ought it be thought to cast too dark a shadow over the extensive and rich research that has been conducted based on self-report measures. Even if the degree of congruency with *childhood* attachment remains unclear, decades of research have indicated that the most widely used instruments are reasonably valid with regard to *romantic* attachment at the group level (see Mikulincer and Shaver 2016), yielding an abundance of important and theoretically coherent results. Some of these results are briefly depicted below.

Adult Attachment and Relationship Quality

Individual variations in romantic attachment have been robustly linked to multiple aspects of relationship quality. In early studies (e.g., Hazan and Shaver 1987), self-designated secure individuals tended to be accepting, supportive, and trusting toward their partner and could depend on the partner without losing autonomy. Avoidant individuals were found to display fear of closeness, a pragmatic view on romance, and difficulties in trusting the partner, while anxious-ambivalent individuals, in contrast, tended to fall in love often and easily and to demand a high degree of closeness and reciprocity from their partner.

Although these initial studies, as noted by their authors, suffered from methodological limitations, results from subsequent and more methodologically advanced research has broadly been in line with these findings. Secure romantic attachment tends to be predictive of higher relationship satisfaction and higher levels of trust and commitment, while insecurity generally predicts sub-optimal relationship functioning, with high avoidance being specifically associated with low levels of intimacy and support and high anxiety with demanding behavior and conflict. Increasingly, researchers have also investigated variables mediating the effect between romantic attachment style and relationship quality. The results indicate that many of the positive effects of secure attachment are, at least partially, mediated by the more constructive communicative strategies and higher levels of emotional openness associated with this attachment style (for an overview, see Feeney 2016).

Adult Attachment and Emotion Regulation

A vast number of studies have linked the insecure forms of adult attachment to various deficiencies in emotion recognition and regulation (see Mikulincer and Shaver 2016). Generally, highly avoidant individuals facing distressing situations attempt to inhibit any emotional state that interferes with the deactivation of attachment-related needs, through defensive strategies such as cognitive distancing or suppression of emotions. The vulnerability of this strategy has been highlighted by studies investigating individuals' reactions to prolonged stress, where these defensive strategies have been found prone to collapse under the pressure of chronic demanding conditions, resulting in high levels of distress in avoidant individuals (e.g., Reizer et al. 2010). In line with these findings, avoidant individuals' ability to suppress distressing thoughts and emotions has been found to diminish with increased cognitive load (Mikulincer and Shaver 2016). Interestingly, while being inclined to suppress distressing emotions and thoughts, a *heightened* perceptual vigilance for emotional stimuli at an early stage of information processing has also been observed in avoidant individuals (Chun et al. 2015). Contrary

to common belief, these results suggest that avoidant individuals are in fact highly attentive to emotional stimuli – albeit in order to keep them from being processed further.

Anxious individuals, in contrast, often display a heightened focus on, or even exaggeration of, negative emotions and potentially threatening stimuli, leaving them vulnerable to rumination and self-amplifying cycles of distress. Numerous studies also indicate a hyperactivation of attachment-related painful emotions and thoughts in anxious adults and a weak ability to control separation-related thoughts, resulting in an exacerbation of the distress related to separations (Mikulincer and Shaver 2016).

Romantic Attachment or Reproductive Strategies?

Attachment theory regards the developmentally immature infants' tendency to form attachment bonds as rooted in evolutionary benefits of securing protection and care from stronger and wiser others, with individual variations in childhood attachment ultimately reflecting different strategies for maintaining this protection (i.e., survival strategies; see "Evolutionary Foundations of the Attachment System and Its Functions"). However, while the infant's survival until reproductive age can arguably be viewed as the primary biological function of the child's bond to its caregiver, reproduction could reasonably be held as the primary function of romantic relationships. Indeed, evolutionary psychologists within the attachment field (e.g., Kirkpatrick 1998) have argued that the sexual mating system, rather than the attachment system, should be regarded as the primary behavioral system in romantic relationships and that romantic "attachment" styles ought to be viewed as variations in mating strategies (i.e., reproduction), not as organizers of protection (i.e., survival). Other theorists (e.g., Zeifman and Hazan 2016) have responded by pointing out that evolution could well "make new use" of systems originally developed with a different function and that the evolutionary function of romantic attachment could be to promote enduring pair bonds so

mates could provide better mutual support (see “Pair Bonding” for a further discussion of evolutionary aspects of pair bonds). Variation with regard to mating behavior is also far too widespread within the different attachment styles for them to be reduced to mating strategies. Leaving this dispute unsettled, it nevertheless highlights an important gap in existing research on adult attachment. As noted by Mikulincer and Shaver (2016), although the importance of the attachment system for adult relationship dynamics is well established, little empirical work has investigated the mutual influence of attachment, caregiving, and sexual mating systems on pair-bond dynamics, and the available evidence does little to verify the presumed superior influence of the attachment system.

Conclusion

In line with Bowlby’s assertion about the lifelong importance of attachment, research has demonstrated the crucial role of attachment in adulthood. Close adult relationships, most notably long-term romantic relationships, typically develop into attachment bonds, displaying all the characteristic components of attachment relationships. Moreover, individual variations in adult attachment have been shown to be of great significance with regard to a multitude of important aspects of relationship functioning. Nonetheless, important research questions, not least regarding the link between childhood and romantic attachment and the interrelations between the attachment, caregiving, and sexual mating systems in adult relationships, still largely remain to answer.

Cross-References

- ▶ Effects of Attachment Quality and Organization
- ▶ Evolutionary Foundations of the Attachment System and Its Functions
- ▶ Individual Variations in Attachment
- ▶ John Bowlby: Pioneer of Attachment Theory
- ▶ Offspring–Parent Attachment

- ▶ Pair Bonding
- ▶ Romantic Attachment and the Prototype Hypothesis

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Attachment Opportunity

► Effect on Attachment

Attachment Parenting

► Co-sleeping

Attachment Security

► Effect on Attachment

Attachment Theory

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Definition

Bowlby's theory of attachment includes several important foundational constructs. First and foremost, attachment relationships are clearly presented as a biological predisposition evolved to ensure survival. Individuals are proposed to

develop attachment relationships with caregivers and seek and maintain proximity to these caregivers when stressed, ill, or afraid. Differences in sensitivity of care were proposed to be associated with individual differences in attachment. Although Bowlby was particularly interested in the parent-child relationship, he was clear that attachment representations would be important for relationship functioning from “cradle to grave.” Infants tend to develop a primary attachment with their predominant caregiver; however, infants can develop multiple attachment relationships, and, throughout childhood and adulthood, we organize these attachment relationships into a hierarchy. And finally, Bowlby proposed that once formed, attachment representations would be stable – in particular in adulthood – although attachment representations could change in response to changes in caregiving during childhood or traumatic or salient events during adulthood.

Early Years

The roots of attachment theory were first established in the 1930s and 1940s when a number of clinicians observed the negative effects of maternal separations early in life. John Bowlby was one of many who observed this effect; for example, in 1944 he outlined how poor parenting influenced the behavior of a group of juvenile thieves. It was not until 1950, when he was offered a short-term contract to work at the World Health Organization (WHO), that he had the opportunity to organize his and others’ work in the area. The resulting report from his WHO contract, published in 1951, summarized what was known to date about the negative effect of poor caregiving and maternal separation on infants’ health and well-being. Bowlby later reported that several reviewers pointed out that an overarching theory to explain these observations was missing. In Bowlby’s quest to develop such a theory, he was greatly influenced by both psychoanalytic theory and ethology. Perhaps, it would be more accurate to state that his development of attachment theory, rooted in his psychoanalytic training, was further strengthened as he acquired knowledge about evolutionary theory and ethological principals, in particular work of

Robert Hinde, Konrad Lorenz, Harry Harlow, and Charles Darwin. It was not until the late 1950s that Bowlby presented his theory of attachment to the British Psychoanalytic Society in London, and the initial reactions were quite negative. In Bowlby’s words “many psychoanalysts... remained unconvinced and sometimes very critical.” Despite this criticism, Bowlby’s research group at Tavistock continued to amass support for the theory of attachment which culminated in his trilogy – attachment and loss (volume 1, Attachment; volume 2, Separation: Anxiety and Anger; volume 3, Loss: Sadness and Depression).

Bowlby consulted and collaborated with several notable scientists while developing his theory of attachment including Harry Harlow, Konrad Lorenz, and Robert Hinde, but it was, however, his collaborations with Mary Ainsworth that helped to put attachment research on the psychological map. In 1950, Mary Ainsworth traveled to London and, by chance, applied for a research position advertised in the London Times and joined Bowlby’s research team at Tavistock. With Bowlby, she began studying the effects of maternal separation on child development; however, she was well prepared to contribute to his work. Previous to this move, Ainsworth had completed her PhD at the University of Toronto, and there had begun exploring the concept of security with William Blatz in her dissertation work – it was Ainsworth who defined the concept of the “secure base” building upon her research initiated in Canada. Ainsworth worked at Tavistock until 1954 when she traveled to Uganda, but she, of course, continued both her work in attachment and her lifelong collaboration with Bowlby. Following her time in Uganda, she moved to Baltimore, and finally in 1958 she was given a permanent position at Johns Hopkins all the while continuing her collaborations with Bowlby and her operationalization of attachment.

Use of Attachment Behaviors

Attachment relationships, and the use of attachment behaviors, are clearly presented as a biological predisposition evolved to ensure survival.

Bowlby (1969/1991) spent considerable time describing the nature and function of behaviors that lead to attachment. Infants use several behaviors to seek proximity to their attachment figures (e.g., crying, vocalizing, following) and also use behaviors to maintain proximity (e.g., smiling, clinging). Once infants are mobile and confident in the care of their attachment figure, they tend to use the attachment figure as a “secure base from which to explore,” returning to the caregiver’s safe haven (i.e., proximity to the attachment figure) for comfort and reassurance when needed. He proposed that infants are biologically predisposed to seek and gain proximity to caregivers and in these relationships develop a sense of whether they are worthy of love and support and a sense of whether their caregivers can be trusted and relied upon to provide care and support. Over the course of infancy and childhood, these views of the self and the other develop into sophisticated internal working models of what to expect from close others, and these internal working models guide behavior over the lifespan.

His observations and work with John Robertson on the destructive impact of early parent-infant separations lead him to conclude that children learn to tolerate longer parental separations; however, both children and adults find separations from attachment figures to be distressing and will go through a predictable sequence of behaviors – distress, despair, and detachment (see below). In fact, even predominately secure individuals report distress when separated for prolonged periods of time with little or no contact (Bowlby 1973/1991). This focus on separations is not surprising given his tendency toward ethology and the importance of parental protection on survival.

When separated from caregivers, infants were observed to react with a predictable sequence of behaviors which Bowlby suggested would have ensured their survival. First, when initially separated, infants will protest to attract the attention of caregivers and, if possible, attempt to search for caregivers. Sensitive and responsive caregivers respond to these initial vocalizations by returning and comforting infants; infants with less sensitive or unresponsive caregivers (in our evolutionary past and the present) develop representations that

care will not be given or inconsistently received. Over time, the individuals’ experience supports the development of internal working models of attachment – individuals’ belief that the self is worthy of care (or not) and that the care needed when they express distress will be forthcoming (or not).

From Bowlby’s observations of children who experienced prolonged separations from their primary caregivers, he proposed that the next phase of separation – if protests and searching are not successful – would be a period of despair. In this phase, infants stop their protests as well as their search; this reaction is proposed to have developed to protect infants from predators when their initial vocalizations to seek proximity to caregivers were not successful.

Finally, Bowlby observed that infants who experienced prolonged separations – and following a period of distress and despair were not reunited with their caregivers – moved to a phase he described as detachment. He believed that these infants were proposed to experience detachment from their separated caregiver, thereby allowing the opportunity to develop attachment relationships with new caregivers who may be better suited to provide the necessary care and support needed to ensure survival.

Separations and Reunions

Ideally, children should feel secure in the presence of caregivers, and when threatened they should seek proximity to caregivers for protection. Children, who are separated from insensitive or rejecting parents, may have developed insecure representations of their relationship with these parents, and therefore they may struggle when coping with the stress of the separation and the associated effects on the family. Furthermore, regardless of degree of security, both children and adults find separations from attachment figures to be distressing – even predominately secure children and adults go through the phases of distress, despair, and detachment when separated for prolonged periods of time with little or no contact (Bowlby 1973/1991).

Ainsworth continued to provide support for Bowlby's theory and expanded upon the idea that although the goal of attachment (i.e., seeking a secure base) is similar for all children, their mechanisms for seeking proximity differ depending on caregiving experiences, in particular the sensitivity and responsiveness of the caregiver (Ainsworth et al. 1978). It was Ainsworth and colleagues who first suggested that the reunion, as well as the separation, is informative in understanding attachment. In a series of articles in the late 1960s and early 1970s, Ainsworth and colleagues introduced the *Strange Situation* (SS). For example, Ainsworth and Bell (1970) presented one of the first studies to describe their methodology. Interestingly, although perhaps deliberate on their part but clearly overshadowed by subsequent work, their initial focus was on the attachment behaviors during the separations and reunions and not attachment categories: Their article clearly summarized the SS procedure and behind-the-scenes observation techniques. In particular, they highlighted the importance of infants' signaling of the parent, actively approaching the parent, and the aversive behaviors of the infants that illustrated distress. They outlined that the experimenters were trained to record observations of infants' locomotion and crying as well as manipulation and visual exploration of available toys. Furthermore, the importance of coding infants' behaviors such as proximity and contact seeking, contact maintenance, interaction avoiding, and interaction resisting as well as search behaviors during the separation episodes was highlighted. Their findings hint at individual differences and, perhaps more importantly, provide empirical support for Bowlby's earlier assertions that infants separated from their caregivers will go through a predictable sequence of distress.

Sensitivity of Care

Attachment theory provides an interesting framework work to explore the effects of parenting and caregiving for several reasons. First, Bowlby (1973/1991, 1980/1991) proposed that our attachment representations developed from sensitivity

of care received from our primary caregiver. Bowlby proposed that attachment security resulted from responsive, appropriate caregiving and that as a result of this care, individuals developed a sense of the self as worthy of care and a belief that others would be responsive and sensitive when caring (Bowlby 1980/1991) – it was Bowlby's assertion that personality development was influenced consciously by these experiences that caused criticism from his psychoanalytic colleagues. He proposed, and considerable research has supported, that children should feel secure and contented when safely in the presence of caregivers (secure base), and when threatened they should seek proximity to caregivers as a safe haven.

Measurement of Individual Differences in Infant Attachment

Ainsworth's most prolific contribution to attachment theory and research is without a doubt the operationalization of infant attachment categories (Ainsworth et al. 1978): secure (B), avoidant (A), and resistant (C) – as well as Main's fourth category disorganized (D). Ainsworth's work not only provided the theoretical and empirical foundation for decades of research in infant attachment; her earlier operationalization of infant attachment also provided the foundation for research in adult attachment. Based on their responses to the SS, infants are classified into one of the following four categories:

1. Children who are categorized as secure (B) have developed a trust in their caregivers' availability and responsiveness and react to the stress of the SS in ways that highlight their positive expectations. In particular, secure infants seek proximity when reunited with caregivers and can return to play when comforted.
2. Children who are categorized as avoidant (A) have developed a belief that they cannot turn to their caregivers for comfort, and during the SS, avoidant infants typically avoid the caregiver upon reunion and control – but do not regulate – their negative emotions.

3. Children who are categorized as resistant (C) have learned that care will be unpredictable, and during the SS they seek comfort inconsistently often switching from clingy and sobbing to withdrawing and angry. They cannot be comforted upon reunion and do not return to play with the available toys.
4. The disorganized category was added by Main and colleagues who expanded the examination of parent-child attachment to high-risk samples. Children who are categorized as disorganized (D) are often in the care of parents who are abusive (physically, emotionally, and/or sexually), and in response to the extreme stress of their home life, these children do not present a coherent attachment strategy during the SS (e.g., freezing rather than proximity seeking).

The SS procedure provided the impetus for considerable research (well over 7,000 citations for Ainsworth et al. 1978), and over the past 50 years, it has been well established that one of the negative consequences of poor parenting is the development of insecure attachment. Insecurely attached individuals, by definition, tend to have childhood experiences that are characterized by lack of care and high control. Insecure children develop a sense of the world as inconsistent (resistant) or rejecting (avoidant), and it is well established that insecure attachment negatively influences child development. Considerable work has explored attachment beyond infancy into childhood. For example, research has demonstrated that insecure children are less socially competent, are more likely to have emotional and behavioral problems, are more likely to have medical problems, and score lower on tests of achievement than secure children. Secure children report pleasurable interactions with their parents; avoidant children, although often non-confrontational, will minimize interactions with parents; anxious-ambivalent children describe difficult relationships mixed with hostility, sadness, and immature proximity-seeking attempts; and disorganized children display negative, punitive behaviors, rejection and/or embarrassment of the parent, and sometimes overly bright, although inappropriate, affect.

Measurement and Development of Adult Attachment

A

From the beginning, Bowlby asserted that attachment representations were important “from the cradle to the grave” (1969/1991, p. 208) and noted that in adolescence and adulthood, there would be a “change of the figures towards whom the [attachment] behavior is directed” (1969/1991, p. 179). Although several scholars wrote about the importance of attachment across the lifespan, it was not until the mid- to late 1980s that two groups of researchers independently began to explore the measurement of adult attachment. Their work focused on somewhat different approaches to assessing adult attachment, and the two areas of adult attachment research remain, somewhat, at odds with each other. Main and colleagues developed an interview-based assessment of adults’ attachment of their family of origin which focused on the coherence of their representations (Main et al. 1985), whereas Hazan and Shaver (1987) introduced a simple three-paragraph forced-choice self-report questionnaire that focused on adult romantic relationships. Not surprisingly, since they both modeled their assessment from Ainsworth’s work, both originally proposed three categories and, it is well known that both measures of attachment have proved to be powerful predictors of adult behavior.

Main et al.’s (1985) adult attachment interview (AAI) continues to be the primary method of assessing adult attachment in developmental and clinical fields despite the time-consuming training and coding of attachment interviews (see Hesse 2016 for a summary). The interview coding protocol which assesses individuals’ coherence of their current state of mind with respect to their families of origin (past-focused) results in one of four attachment categories: autonomous (secure), dismissing, preoccupied, and unresolved/disorganized. Bakermans-Kranenburg and van IJzendoorn (2009) summarized the data from over 10,000 AAIs addressing issues of baseline proportions in clinical and nonclinical samples, gender distributions, as well as differences in distributions for adolescents and individuals from

low SES samples, ethnic minorities, and non-Western countries. Using the four-category classification of a sample of nonclinical mothers ($n = 700$) as their baseline, their findings indicated that nonclinical fathers, adolescents and students, individuals from at-risk samples, and individuals from clinical samples were more likely to be classified as dismissing than mothers from nonclinical samples. Individuals from at-risk samples were also more likely to be classified as unresolved, and individuals from clinical samples were also more likely to be classified as unresolved or preoccupied.

Hazan and Shaver introduced a simple three-paragraph forced-choice self-report measure of adult attachment modeled from Ainsworth's three infant categories focusing on adult romantic relationships. Their three categories – secure, avoidant, and anxious-ambivalent – proved to be quite productive, but the categorical measurement was met with some concern by personal relationship researchers. Although the three-category measure did not stand the test of time, this seminal article provided the impetus for the next few decades of work on adult attachment.

Although the self-report methodology assessing attachment of close peer relationships is controversial – some would say that peer relationships are not attachment relationships (see below for discussion and van IJzendoorn and Bakermans-Kranenburg 2010 for a recent example) – research exploring the importance of adult peer attachment relationships continues to be prolific, and the effects of adult peer relationships on adult social behavior are well documented.

In 1990, Bartholomew published a paper which merged the work of Main et al. (1985) and Hazan and Shaver (1987) as well as Bowlby's original descriptions of the self- and other-models. Specifically, Bowlby had proposed that throughout childhood, individuals develop a sense of whether they are worthy of love and support (or not) and a sense of whether others can be trusted and relied upon to provide care and support (or not). By adulthood, these views of the self and the other are well established and have developed into sophisticated internal working models of what to expect from close others,

and these internal working models guide behavior over the lifespan. Bartholomew suggested that the intersection Bowlby's proposed dimensions of the self-model and other-model resulted in a four-category model of attachment. Secure individuals were defined to have developed a positive model of both the self and others, and considerable research has supported that secure individuals have high self-esteem and self-confidence as well as high trust and support with others. Preoccupied individuals were defined to have developed a negative model of the self and a positive model of others; similarly, considerable research has supported that preoccupied individuals tend to have conflicting views of the self and others which tends to negatively impact their relationships. Bartholomew noted that her definitions of secure and preoccupied prototypes were consistent with both Main et al. and Hazan and Shaver. Although the previous researchers had each proposed one type of avoidance, Bartholomew expanded this definition of avoidance by proposing that avoidance could be either fearful (similar to Hazan and Shaver's description of avoidance) or dismissing (similar to Main et al.'s description of avoidance). Fearful individuals were defined to have developed a negative model of both the self and others and tend to consistently report higher levels of depression, neuroticism, marital conflict, and interpersonal sensitivity. Dismissing individuals were defined to have developed a positive model of the self and a negative model of others and reported high levels of self-esteem and self-confidence but low levels of trust and warmth in their relationships. Researchers have indicated that both types of insecure-avoidant adults deny symptoms of distress (dismissing) or are afraid to ask for help (fearful) as they believe that others will reject their attempts at proximity seeking or challenge their feelings of distress.

In her early work, Bartholomew presented both interview and survey measures to assess the four-category model (see Bartholomew and Horowitz 1991; Griffin and Bartholomew 1994). Although the interview proved to be the most reliable method, researchers tended to gravitate toward the less time-consuming, albeit less reliable, self-report surveys. The four-paragraph measure (RQ,

Relationship Questionnaire) was modeled from Hazan and Shaver's three-category measure with an additional paragraph describing the dismissing category (see below). Participants were typically asked to rate each of the four categories on a Likert scale from "not at all like me" to "very much like me" and then choose the one category from the four that was "most like them." The Relationship Scale Questionnaire (RSQ) was simply a list of the 17 statements from the RQ, and participants were asked to rate each of the items on a Likert scale from "not at all like me" to "very much like me." The four scales were computed by averaging the items. The paragraphs from the RQ categories (Griffin and Bartholomew 1994) are as follows:

Secure: It is easy for me to become emotionally close to others. I am comfortable depending on others and having others depend on me. I don't worry about being alone or having others not accept me.

Fearful: I am somewhat uncomfortable getting close to others. I want emotionally close relationships, but I find it difficult to trust others completely or to depend on them. I sometimes worry that I will be hurt if I allow myself to become too close to others.

Preoccupied: I want to be completely emotionally intimate with others, but I often find that others are reluctant to get as close as I would like. I am uncomfortable being without close relationships, but I sometimes worry that others don't value me as much as I value them.

Dismissing: I am comfortable without close emotional relationships. It is very important to me to feel independent and self-sufficient, and I prefer not to depend on others or have others depend on me.

Personal relationship researchers were concerned with the reliability of early measures, but they were also drawn to the concept of adult attachment, and the early 1990s saw a wave of studies proposing new measures of attachment. Brennan et al. (1998) collated the items from these attachment measures (323 items which assessed 60 attachment constructs from

14 different scales) and proposed a new measure the Experiences of Close Relationship scale (ECR). The ECR has two orthogonal dimensions (attachment anxiety and attachment avoidance) and improved reliability over the RSQ. The ECR-R (Fraley et al. 2000) attempted to correct some of the limitations of the ECR; however, both the ECR and the ECR-R proved to be inadequate measures of security and imprecise assessments of Bartholomew's four-category model (see Mikulincer and Shaver 2007) – both scales are imperfect due to the limitations of the existing item pool. Although these measures – Bartholomew's RSQ, the ECR and ECR-R – continue to be well used in the literature, researchers continue to work on improving questionnaire measures of adult attachment (see Scharfe 2016).

Are Adult Close Relationship Attachment Relationships?

Despite the fact that Bowlby asserted that attachment representations were important across the lifespan and that a change of attachment figures would be observed in adolescence and adulthood, there is some controversy about who serves as attachment figures in adulthood. Personal relationship researchers have insisted that adult romantic partners and friends as well as family members may serve as attachment figures. Considerable work has provided empirical support that lovers, friends, and family members serve as attachment figures for adults. This line of research began with a listing of reasons why adult love relationships may be attachment relationships in Hazan and Shaver's (1987) seminal article. Since that time, personal relationship researchers have demonstrated that one can observe attachment behaviors in adult relationships (i.e., proximity seeking, proximity maintenance, safe haven, secure base), similar to infants and children there are consistent, measurable individual differences in adult attachment; that adults express anxiety if their attachment figure is not accessible; and that adults experience distress if separations from their attachment figures are prolonged.

Attachment Internal Working Models and Hierarchies

Bowlby (1969/1991) highlighted specific developmental changes in attachment relationships over the lifespan, and the various measures of adult attachment have allowed researchers to begin to explore this feature of his theory more fully. For example, Bowlby proposed that attachment representations started from one primary attachment relationship in infancy, but he acknowledged that early on, often soon after attachment to the primary caregiver was evident, infants would begin to establish the development of attachment relationships to other caregivers. Specifically, infants were proposed to develop a primary attachment with the caregiver who satisfied their basic needs – this primary attachment relationship was the most intense regardless of the number of secondary attachment relationships. Infants and children, however, do receive care from other caregivers, within and outside of their family of origin, and they may also develop secondary attachment bonds to these individuals. Considerable work has provided support that infants and children will develop attachment relationships with adults who are not their primary caregiver.

During these early years, attachment relationships are typically unidirectional – the caregiver fulfills the attachment needs of the child. By the time we reach adolescence and adulthood, most individuals have multiple attachment relationships which are organized into a “state of mind” or internal working model, and these relationships can be reciprocal (i.e., both individuals fulfill and provide attachment needs). Furthermore, Bowlby proposed that in adulthood, there would be a “change of the figures towards whom the [attachment] behavior is directed” (1969/1991, p. 179) and that adolescents and adults tend to organize their attachment relationships into a hierarchy.

Bowlby (1969/1991) proposed that during adolescence, the child’s attachment to their parents would change due to the importance of other adults in the child’s life as well as the sexual attraction to their peers. There has been considerable research exploring the change of attachment from parents to

peers initiated by Hazan and Zeifman (1994). They reported that, between the ages of 8 and 14 years, adolescents reported that they approached peers for proximity and safe haven functions and parents for secure base functions (see also Nickerson and Nagle 2005). They also noted that during late adolescence (15–17 years), those individuals who had formed peer romantic relationships were less likely to approach their parents for attachment functions (see also Mayseless 2004; Nickerson and Nagle 2005), although research findings have not been consistent on this point. Consistent with Bowlby’s suggestion that, for most individuals, the bond with parents would continue throughout life, researchers have found that one’s mother, in particular, continues to be an important attachment figure throughout the lifespan (Pitman and Scharfe 2010).

Bowlby (1969/1997) also proposed that individuals, regardless of age, would organize their attachment relationships into a hierarchy and would demonstrate a preference for a primary attachment figure. Over the past two decades, several researchers have found support that individuals do tend to organize their attachment relationships into hierarchies, and these findings have been found across the lifespan in several diverse samples (e.g., Doherty and Feeney 2004; Pitman and Scharfe 2010; Trinke and Bartholomew 1997). Interestingly, mothers tend to be listed at or near the top of the attachment hierarchy across the lifespan.

Attachment Stability

Paradoxically, Bowlby (1980/1991) proposed that once formed, attachment representations would remain stable but could also change over the lifespan. Specifically, he proposed that once formed, internal working models of attachment would remain relatively stable in adulthood; however, he highlighted that changes may occur during development (see Del Giudice 2009; Del Giudice and Belsky 2010 for an evolutionary explanation for these changes) but may also change in adulthood in reaction to particularly traumatic events (see Scharfe 2003 for a summary of the lifespan research). Researchers have demonstrated that parent-infant attachment shows

moderate-to-high stability (e.g., Waters 1978) and that change is likely when infants' caregiving environments change (e.g., Thompson et al. 1982; Vaughn et al. 1979). In particular, there is some evidence that it is important to determine how sensitively changes were managed (e.g., NICHD Early Child Care Research Network 2001). Similar findings have been reported exploring stability of attachment throughout childhood (e.g., Howes and Hamilton 1992).

Bowlby (1973/1991) proposed that by adulthood, attachment representations would be well developed and more "constrained" and less adaptive to change. Over the past few decades, researchers have reported moderate-to-high stability of adult attachment representations regardless of the method of assessment (e.g., Scharfe and Bartholomew 1994). To date, several studies have examined the stability of attachment from infancy to adulthood and have found moderate stability when social environments remain relatively stable (e.g., Waters et al. 2000).

Conclusion

Bowlby's theory of attachment includes several important foundational constructs including the proposal that attachment behavior was instinctual and important across the lifespan. He also described characteristic attachment behaviors and individual differences in attachment as well as both adaptive and maladaptive care environments. Finally, he outlined the development of multiple attachments and hierarchies of attachment as well as the development of internal working models of attachment and proposed conditions to expect both stability and change of attachment. Considerable research over the past 40 years has provided empirical evidence for these foundational constructs.

Cross-References

- Attachment in Adulthood
- Early Attachment Experiences and Romantic Attachment

- John Bowlby
- John Bowlby: Pioneer of Attachment Theory
- Measurement: Categorical Versus Continuous
- Sex Differences in Attachment

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Attack

► Aggression

Attention

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Synonyms

Awareness; Concentration; Consciousness; Focus; Mindfulness

Definition

The cognitive and behavioral process during which one becomes actively, and consciously, aware of one or several stimuli, while cognitively suppressing irrelevant stimuli. Attention is an executive function.

Introduction

George is 8 years old and he is attending the third grade of elementary school. During his first year

of elementary school, when he was 6 years old, he was diagnosed with Attention Deficit Hyperactivity Disorder (ADHD, predominantly inattentive presentation) as he was meeting the diagnostic criteria of the fifth edition of the Diagnostic and Statistical Manual (DSM-5; American Psychiatric Association 2013). Specifically, George met six of the seven DSM-5 criteria for inattention, namely:

- (a) He was failing to pay good attention and made careless mistakes
- (b) He could not focus for long periods of time
- (c) He was often failing to listen when others were speaking to him
- (d) He would not pay good attention to directions or instructions
- (e) He would easily be distracted by trivial stimuli in his environment (e.g., in the classroom or during homework)
- (f) He would fail to organize his belongings and actions or plan ahead for activities

As it is evident by the criteria that George was meeting for ADHD, his difficulties are interfering with his everyday activities, functioning, and cognitive processes. His difficulties are mostly evident in the classroom when he has to pay attention to the teacher, concentrating in writing and reading or solving mathematics, and follow instructions or directions that he receives verbally or in writing, such as in tests. At home, George cannot sit for long periods of time to complete his homework as his attention cannot be maintained longer than 20 min. His parents complain that he often appears to be daydreaming instead of following conversations that they would like to have with him. Finally, teachers and parents were immensely concerned about George's inability to inhibit trivial stimuli out in order to concentrate to an action that he is supposed to complete. For example, he tends to play with his pencils or erasers instead of completing a written assignment that only needs his full attention for 30 min. In other words, he finds it difficult to suppress irrelevant stimuli (i.e., things on the desk) and focus on the most important stimulus (i.e., his assignment).

Attentional Process: Selective Attention, Divided Attention, Sustained Attention, and Alternating Attention

Selective Attention

Neuroscientists, psychophysicists, and cognitive psychologists' experiments revealed that we solve our problems of sensory overload (the abundance of large numbers of stimuli at a given point) by choosing the most important/relevant sensations or stimuli that are important at any given time, while suppressing irrelevant sensations or stimuli that are simultaneously present in our environment (Zhong-Lin 2008). This could be a good definition for attention, especially selective attention (focusing on the most relevant stimulus). This of course has evolutionary value, as humans (and other animals) need to be selective in an environment of numerous stimuli and attend to the stimulus that is most likely to have the highest survival value. For example, paying attention to a dangerous animal in your immediate surroundings, while ignoring a beautiful butterfly on a flower next to you that you would normally enjoy watching.

Cognitive scientists found that our selective attention enhances the subjective (individual perception) physical qualities of stimuli that we concentrate on, while it could do the opposite to stimuli that remain outside our immediate focus. For example, a red flower appears brighter (stimulus enhancement) when we select to pay attention to it and all other nature around it becomes duller (noise reduction) or stays completely out of our perception (noise exclusion). Our selective attention applies to all of our senses (auditory, tactile, gustatory, visual, and smell) and very pertinent to our memory (e.g., attending to a specific piece of information that you learned) and other cognitive processes.

Divided Attention

Divided attention is also an attentional process. During this process, we pay attention to more than one stimulus or action (e.g., multitasking). For example, in dichotic listening (Ingram 2007), we could be able to pay attention to a person we are having a conversation with, while at the same time

paying attention to the train announcements in the arrival hall.

Sustained Attention

Sustained attention is the ability to focus on a stimulus (or stimuli) or action for a period of time without being distracted by other stimuli or actions (Oken et al. 2006). Neuropsychologists using norm referenced tests assess a person's sustained attention in order to extract conclusions about a person's ability to remain focused on an action or stimulus, at least as long as the average of the population. In our introductory case study, George most probably faces difficulties in maintaining his concentration on tasks that take a long time to be completed (e.g., writing a 2000 word essay on a topic).

Alternating Attention

Our ability to alternate our focus (attention) between stimuli or actions is another aspect of our attention that is crucial to our survival and is often measured in neuropsychological assessments (Sohlberg and Mateer 2001). For example (using the example with the person paying attention to a dangerous animal), a huntergatherer could be very vigilant and pay attention to a dangerous animal in his surroundings, but at the same time he could be switching his attention at times to collecting mushrooms for dinner. Good alternating attention exhibits cognitive flexibility that allows you to go back and forth on different activities or switch from one important stimulus to another. Cognitive flexibility is highly positively correlated with intelligence measures. The ability to shift our attention (mental shift) as needed, and not perseverate on certain stimuli, is learned early in life and is part of our educational systems.

Attention Disorders

Deficits or impairments in attention are not only evident in ADHD, but also in frontal lobe (or other brain areas) damage, schizophrenia, memory disorders, anxiety, depression, or as a side effect due to substance use or medical treatments (Gitelman 2003). Attention disorders could be rehabilitated

with medication, behavioral and cognitive therapy, relaxation techniques, and/or combination of these and other treatments.

Conclusion

Attentional resources could be voluntarily allocated to stimuli or actions (Pinto et al. 2013); this is also called a top-down process, where the brain decides what calls for our attention (e.g., deciding that it is time to pay attention to my teacher in the classroom and forget about a discussion I had before class). Alternatively, Pinto et al. (2013) state that our senses could direct us to a stimulus or action in a bottom-up process where a sense alters the brain to allocate its attention to a particular stimulus or action (e.g., a sudden noise turns our head towards the source of sound).

Attention, whether bottom-up or top-down, is a process that is crucial to our everyday functioning and ultimate our survival. Therefore, scientists are constantly improving the assessment methods and rehabilitation techniques for attentional deficits, while certainly the improvement of attention and its aforementioned components is pertinent in individuals without attentional disorders, as well. This is evident by the invention of medications or substances and development of methods for attention and concentration improvement.

Cross-References

- [Interference](#)
- [Personal Memory](#)
- [Self-Observation](#)
- [Working Memory](#)

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Attention and Memory

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Synonyms

Awareness; Cognition; Consciousness; Inquisitiveness; Recall; Recollection; Reminiscence; Selection

Definition

Attention and memory are a set of linked, cognitive processes. Attention refers to a number of processes – some deliberate, others unconscious – where a discrete aspect of information is selected over other, ignored information. Memory involves reproducing or recalling what had previously received attention and priority. These are related processes, as information maintained and attended to then becomes a more durable memory.

Introduction

In both humans and the animal kingdom, attention and memory have functional relevance. Both groups rely on these cognitive processes, in similar ways. Attention describes the “who” and “what” of our conscious experience, as it helps keep something “alive” longer. This is the case for all animals, as they must encode and understand their dynamic environment, with the complexities associated with locating food and water, protecting their young, and so on. These aspects of their environment are then prioritized in memory, as well. Todd et al. (2005) had previously suggested that several topics from traditional cognitive psychology are at odds with evolutionary theory. However, recent research from both the attention and memory literatures would largely disagree with this suggestion. The current review discusses recent findings from these literatures, with an emphasis on humans’ natural tendencies to attend to and remember (1) dangerous and fear-relevant stimuli, (2) attractive and other positive aspects in their environment, and (3) self-relevant information. Each of these emphasizes the role of evolutionary priorities driving cognitive processes.

Dangers and Fear-Relevant Stimuli

Fear exists to inform and respond to someone or something perceived as dangerous or a potential threat. However, it is also a very normal reaction to danger, and researchers can agree that fear is an adaptive emotion (i.e., a fight or flight response) which in turn is self-protecting (Slobounov 2008). Fear can be expressed through physical reactions and/or behavioral expressions (e.g., sweating, rapid heartbeat, shortness of breath). Individuals that are faced with fear generally tend to either avoid the danger or use defense mechanisms against it. Along with fears, phobias can provoke exaggerated responses that are also in line with avoidance behaviors, the key component in the disorder. Isbell’s (2006) theory suggests that evolutionary fear-relevant stimuli, when compared against neutral stimuli, should activate threat responses, particularly those related to attention;

however, this effect should not be dependent solely upon the stimuli and task materials, such as the often used snake- and spider-detection task using neutral backgrounds (though predators are often prioritized in both attention and memory systems; Kazanas and Altarriba 2017, 2018).

In one such example, LoBue and Rakison (2013) showed that compared against other objects and animals, snakes are detected more automatically. When compared against spiders, studies have found that the fear and threat of snakes are higher (Shibasaki and Kawai 2011), though spiders can be recognized faster (Öhman et al. 2012). Quick detection displayed by non-human primates is limited to snakes, so it is unclear as to whether spiders hold a significant status in human perception (Shibasaki and Kawai 2009).

Research on emotion and retrieval have shown that, while negative information drives attention and memory, this often comes at the expense of missing positive and neutral information. For example, Kensinger et al. (2007) have shown that younger adults tend to remember the details for negative stimuli more so than for neutral stimuli, but there is also the thought that young adults may not be as able to correctly identify the visual aspects of positive objects. Multiple studies have shown that negative items tend to benefit from enhanced vividness (Dewhurst and Parry 2000; Kensinger and Corkin 2003; Kensinger and Schacter 2006; Ochsner 2000). Because of this, individuals tend to claim that they *recognize* a positive stimulus when it was first introduced, but do not *commemorate* the details of its presentation (Dewhurst and Parry 2000; Ochsner 2000). Storbeck and Clore (2005) also noted that positive information can be incorrectly retrieved when compared alongside negative information (Kensinger and Schacter 2006; Levine and Bluck 2004). Kensinger et al. (2007) note that negative stimuli are prioritized in memory, suggesting that emotion effects may depend on both the valence and arousal of the stimuli.

Negative experiences – and their resulting memories – can have their consequences, including post-traumatic stress disorder (PTSD), where

fear is known as the most important emotion in this disorder. PTSD is a pathological response to trauma that may develop after exposure to an event or ordeal in which death, severe physical harm, or violence occurred or was threatened. Traumatic events that could potentially trigger PTSD include but are not limited to violent personal assaults, natural or unnatural disasters, accidents, or military combat. A large amount of the PTSD literature is based on conspecific research (e.g., war veterans), and the results may not be representative of other PTSD populations. Cantor (2009) asked whether predator-induced PTSD differs from conspecific-induced PTSD. He found that one way to examine this could be to use shark attack file data sources. Cantor (2009) also asked whether shark attack victims display less generalized avoidance, particularly less fear of conspecifics, along with a more specific thalassophobia (i.e., a fear of the ocean). PTSD studies to date have not examined the predator question, though the rates of conspecific-induced PTSD (the result of assaults) tend to be higher than rates of environmental PTSD. Generally, the literature relevant to PTSD and evolutionary psychology helps us to understand that what is adaptive for one environment might not be for other environments. Cantor (2009) concluded by stating that:

Fear motivates the defensive behaviors, the chief of which in mammals are deployed according to distance from the source of threat and other contextual variables. Those defensive behaviors are avoidance, attentive immobility, withdrawal, aggressive defense, appeasement, and tonic immobility, operating in conjunction with vigilance and risk assessment. The origin of PTSD may have involved an enduring heightened defensive reorientation that has become adaptive. This evolutionary perspective brings together psychological, social systems, and neuro-scientific research findings. (p. 1046)

Quite often, negative information carries a higher value than positive information, which then attracts more attention and other cognitive processing. This higher value is noted by various physiological responses, automatic detection and recognition, increased memorability, and, in extreme circumstances, psychopathology.

Attraction and Other Positive Aspects in the Environment

On the other hand, positive qualities and characteristics can also drive attention and memory processes. The attraction literature provides many relevant examples. Individuals observe various things about each other upon their first encounter, but the most common is generally the physical appearance of the other's face. Faces are typically categorized into what is attractive and what is considered less attractive. Attractiveness can be measured using scales (i.e., 1 = low attraction and 7 = high attraction) or simply making a choice (i.e., *A is more attractive than B and C*), etc. These seemingly automatic decisions translate into a number of interesting outcomes. For example, the attraction literature finds more attractive males reporting a larger number of short-term sexual partners and more attractive females reporting a larger number of long-term sexual partners (Rhodes et al. 2005).

Why are attractive individuals more likely to grab our attention? From an evolutionary perspective, perhaps, symmetry can signal one's overall health; preference for such symmetry is in line with by-products of the way brains process that information. Averageness and sexual dimorphism (femininity in female faces, masculinity in male faces) also factor into sexual behaviors within and outside of relationships (Rhodes et al. 2005). Researchers have hypothesized that if attractiveness is such an important feature for mate selection, then attractive people should have a higher success rate with their partners than that of their peers. Rhodes et al. (2005) found that a male's facial attractiveness correlates with their number of short-term sexual partners and the opposite is true for a female's facial attractiveness, which correlates with their number of long-term sexual partners. They also tested the impact of body attractiveness, finding that male body attractiveness correlated with the number of short-term sexual partners. Importantly, this was not the case for female participants, as there was no correlation between their body attractiveness and sexual behaviors.

In another line of investigation, researchers have explored memory with emotional distractors and manipulated focused and distributed attention. For example, Srinivasan and Gupta (2010) found that happy faces were acknowledged more so than sad faces when the conditions were lower and attention was more distributed. They also noted that identification of either sad or happy faces was contingent upon how the attention was distributed. Furthermore, recognition of happy faces when they were preceded by neutral stimuli was greater than recognition of happy faces preceded by sad faces. This conclusion suggests that happy faces rely on distributed attention or fewer attentional resources when differentiated from sad faces. In a similar study, Srivastava and Srinivasan (2010) found that happy faces were also recognized better, even under a limited attention manipulation, when compared against sad faces. They went on to discuss that better recognition of happy faces could be related to the commonality of happy faces. Their results are also consistent with other arguments that assume individuals have more previous experience with happy faces in photographs (Gupta and Srinivasan 2009; Jackson and Raymond 2006). Srivastava and Srinivasan (2010) further discussed that because humans are skilled at recognizing faces with emotion, they are not certain why there would be a tendency to more correctly identify happy versus sad expressions in faces. With that, familiarity may not be responsible for differences in the time course of attention across happy and sad faces.

Research suggests that as individuals age, how they commemorate emotionally important information changes, too. For example, Mather and Carstensen (2005) suggest that older adults might have a memory bias toward positive and self-relevant information because they typically remember stimuli that are connected to positive emotions rather than negative emotions. Eppinger et al. (2010) have found results consistent with these predictions, as older adults showed better memory performance for positive stimuli than for negative stimuli. One explanation for these results is that older adults tend to have a more difficult time differentiating between the information that is being presented (Eppinger and Kray 2011).

Together, these findings show the attention biases and memorability of positively-valenced information, such as the finding that happy faces can be more easily recognized than sad ones. Positive qualities can also result in interesting behavioral outcomes, as is the case with attractive individuals having a greater number of sexual partners.

Self-Relevant Information

Humans, like animals, are particularly sensitive to events that can have an impact on their value and even social standing (Weisbuch et al. 2009). They tend to examine their environment for indications that are relevant to their said relational value, even on a pre-attentive level. The “cocktail party effect,” for example, is when an individual focuses their attention toward a particular voice in the commotion of a party or environment, often when their name or other salient information can be heard among that commotion. Individuals tend to think a great deal about what other people evaluate and perceive of them and also try to gain insight into how, in future endeavors, others will respond to them (Leary and Guadagno 2011). However, some of these evaluations are idle imaginings, while others stimulate deep distress when they suggest that one’s past, present, or future relational value is lower than desired. This additional focus, or prioritization, underlies the self-reference effect.

The self-reference effect – a mnemonic benefit for information processed for its self-relevance – has been most often observed with noun stimuli (see Klein 2014 for a review of this literature). In a relevant vein of the self-reference literature, researchers have also found a mnemonic benefit for information processed for its survival value. In this paradigm, participants rate a list of words according to the following prompt:

In this task, we would like you to imagine that you are stranded in the grasslands of a foreign land, without any basic survival materials. Over the next few months, you’ll need to find steady supplies of food and water and protect yourself from predators. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be for you in this survival situation. Some of the words

may be relevant and others may not – it’s up to you to decide. (Nairne et al. 2007, p. 264)

Researchers from a number of independent laboratories have replicated a “survival advantage”: a mnemonic benefit for words, pictures, and locations encoded this way (Kazanas and Altarriba 2015). Klein’s (2012, 2014) work has suggested self-reference as a potential mechanism underlying this effect, as participants consider their very survival as they encode the to-be-remembered information. Or, self-reference and survival processing may benefit from similar, elaborative encoding mechanisms (Kroneisen and Erdfelder 2011), as self-preservation is a highly salient adaptation.

Conclusions

The adaptive value of attention and memory cannot be overstated. Researchers have noted the attention-grabbing nature of a number of self-relevant stimuli: dangers in the environment, attractive individuals, and, most commonly, an individual’s name or other interests. Research supports the enhanced memorability of these objects and individuals, as well. Findings supporting these attention and memory enhancements are numerous, with researchers using both physiological and behavioral measurements. Each of these findings contributes to our understanding of the cognitive underpinnings of evolutionary psychology.

Cross-References

- ▶ [Different Functions of Memory](#)
- ▶ [Evolved Physiological Reactions](#)
- ▶ [Facial Attractiveness](#)
- ▶ [Fears](#)
- ▶ [Fears and Phobias](#)
- ▶ [Mate Choice Effects](#)
- ▶ [Mate Preferences](#)
- ▶ [Predators as Attention-Grabbing](#)
- ▶ [Selective Attending](#)
- ▶ [Universal Human Fears](#)

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Attention and Perception

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Synonyms

Observation; Selective focus; Sensitivity; Understanding

Definition

Before information can be used in a meaningful way, it must first be attended to within the perceiver's environment. Once information is attended to, how it is interpreted by the individual based on current goals, drives, and motives determines how it is perceived. Humans have an automatic tendency to focus their cognitive resources on stimuli that convey messages of potential danger (threat to survival) or mate prosperity (reproductive success). However, how these stimuli are perceived must be examined in the context of its evolutionary function in order to understand their adaptive relevance to the human cognitive system.

Introduction

The ability to efficiently attend to information within one's environment is a vital cognitive skill that allows an organism to appropriately interact with the world. However, not all information (particularly fitness-enhancing information)

is processed equivalently nor do all varieties of stimuli garnish the same attentional response (see Öhman et al. 2012 for a review). Attention can be understood as the prioritizing of a select set of information within one's environment, as deemed pertinent by the individual based on one's goals, deemed importance, salience, and past practices (Jiang and Sisk 2019). It allows an individual to focus their cognitive resources on a subset of all available information. From an evolutionary perspective, the types of details that become automatically and most readily directed by this attentional focus are thought to be those most relevant to the survival and success of the individual's genetic longevity.

Furthermore, information in the environment can be interpreted from a variety of standpoints based on the context of interaction. This susceptibility of stimuli to be perceived in different fashions can be understood as a crucial adaptation of human cognition. The research discussed in this entry will highlight the various ways in which human attention and perception influence each other and demonstrate an attunement toward evolutionarily relevant problems within the modern era.

Capture by Predatory Threat

Threats to the physical health of primates have existed in a variety of capacities causing them to develop methods of protection. For example, a quick and accurate detection of potential predators and harmful objects would facilitate one's ability to procure a safe escape or position of self-defense. In modern society, the occurrence of human predation (e.g., attacks from tigers and pythons) in many cases is not as eminent as it was for our Paleolithic ancestors. However, the residual adaptations of our cognitive system to respond to such potential threats remain present and are activated through heightened attention toward dangerous stimuli allowing for an assessment of the level of imminent threat. To test this assertion, Yorzinski et al. (2014) recorded the eye movements of individuals as they viewed evolutionarily dangerous (snakes, lions) and benign

(lizards, impalas) animals. Photo arrays were created so that there was one dangerous animal intermixed with seven non-dangerous animals, as well as the reverse. Participants viewed the arrays, one at a time, with the task of locating the unique photo (i.e., target) as quickly as possible. Regardless whether the photos were presented in vibrant, full color or in reduced quality, black-and-white format, the visual scan paths (eye movements) illustrated a clear pattern of attentional capture by the dangerous animal photos. When a dangerous animal was the target, participants were faster at locating the image than when a non-dangerous animal was the target. Conversely, when dangerous animals were the to-be-ignored photos, participants demonstrated difficulty in disengaging from these images. The authors concluded that the presence of evolutionarily threatening predators both grabs and maintains human attention due to the innate features of these animals, even when task-irrelevant (see Calvillo and Hawkins 2016 [on animacy effects] and Shabbir et al. 2012 [on pattern repetition] for additional factors in attentional superiority toward predators).

This attentional priority for evolutionarily dangerous creatures has also been found to extend into unconscious perception. Because humans are not naturally equipped with physiological resistance to counteract dangers such as venom and suffocation, having the ability to quickly detect animals that have the possibility of being a threat is a lifesaving adaptation of human visual cognition. Using an inattentional blindness paradigm that allows for the examination of the types of information that are given attentional superiority, New and German (2015) tested participants' ability to detect threatening images presented unexpectedly. While completing a computer task requiring participants to focus on the center of the screen, an image appeared in the corner of the screen that resembled either an evolutionarily threatening (spider) or a non-threatening shape (housefly, hypodermic needle). When probed to identify the surprise image, participants were most accurate in detecting and indicating the location of the image when it resembled a spider, as compared to an evolutionarily non-threatening

shape. Similar results indicating early, automatic, and sustained attentional capture by fear-inducing images have also been shown using event-related potential (brain wave recordings) techniques (Leutgeb et al. 2015).

The results from New and German (2015) suggest attention is not equally allocated to all types of threatening information, but rather natural and evolutionarily based dangers produce a bias for immediate processing. The authors concluded that the human visual system is designed with a preparedness toward detecting information that has been deemed evolutionarily important, regardless of explicit awareness. However, other researchers have suggested that all threat cues, both modern and historically relevant, are efficient at automatically capturing attention. Spatial attention (i.e., focus in a visual scene) is facilitated by the presence of threatening images, particularly when the threat is directed toward the self (e.g., a gun pointed toward the observer; Carlson et al. 2009). Notably, this eliciting can occur even when conscious perception of the threat is diminished. Objects and creatures that can pose a threat to one's survival are processed with a particular advantage to allow for rapid detection, even in the absence of observer perceptual awareness. It appears that humans have an automatic drive to detect and gather information about potential dangers within their visual field.

Attunement Toward Fearful Messages from Others

Besides the viewing of natural predators, threat can be detected through observing the facial and emotional expressions of others. Emotion-evoking stimuli have been shown to be effective at capturing attention by instilling a particular value, such as a fearful face indicating a threat alert. This value can, in return, convey a message of urgency toward action to increase survival likelihood when it is of a threatening nature (see Öhman et al. 2012). A threatening message that can be quickly conveyed with urgency allows for a greater chance that the receiver can distance themselves from danger.

While assessing the role emotional faces play in facilitating risk avoidance, Becker et al. (2014) demonstrated that memory is prioritized toward remembering and detecting threatening faces. Participants were tasked with memorizing photos of male and female faces, with half of each gender making a slightly angry facial expression. When presented with a series of faces that included all of the studied faces as well as additional unstudied faces, participants were more efficient at identifying the faces that had been a part of the original study set if they were *males* displaying an angry facial expression, regardless of participant gender (Experiment 1) and outgroup status (race; Experiment 2). In line with evolutionary accounts of men holding more aggressive social roles than women, male participants displayed faster response times to the threatening male faces than female participants indicating men have a particularly heightened vigilance for identifying signs of physical threats in other men.

The authors interpreted this pattern of results to indicate robust support for automatic sensitivity toward angry faces, particularly for men with social goals relevant to identifying the motive of potential mate stealing and physically threatening individuals (also see Sulikowski and Burke 2014 for heightened attention to objects related to social roles). This capturing of attention by valenced faces has also been found in young children, indicating that the significance of an emotional message is understood early on and has a genetic component in allocating spatial attention (Elam et al. 2010). Once a threatening face has been detected, it remains in a position of privilege in memory. This readiness to encode fear-inducing messages helps to facilitate identification of information that can be used to garner the safety level of a face when it is encountered at a later point. Thus, the heightened awareness of potentially dangerous stimuli not only enhances the immediate survival of the organism but also its future success.

Besides visual cues, auditory indications of distress and danger are effective at automatically directing attention. Vocalization patterns can be used to convey messages to others about one's internal state. For example, whines, particularly when used by infants toward caregivers, tend to indicate a sense of helplessness through an

increased pitch, slowed speech production, and amplified loudness (Chang and Thompson 2010). These special acoustic characteristics have been shown to capture diverted attention in adults and increase attentiveness toward the source of the whines. Ultimately, this attention-grabbing vocalization has the possibility to naturally elicit the help the individual needs from others.

As in the case of fear-filled messages, throughout the literature emotion has repeatedly been shown to play a key role in directing attention, influencing memory, and, consequently, manipulating conscious perception (Pessoa 2005). However, results from these studies must be interpreted within their individual contexts. Emotion-inducing information is generally processed in a rapid manner that overrides attention to simultaneously ongoing processes so that the message conveyed by the stimuli is prioritized (e.g., Elam et al. 2010). Under these circumstances, attention is diverted from its intended focus thereby adding to the pressures of attentional load capacity. When unattended information of an emotional nature demands attention, an emotion processing advantage is demonstrated. Therefore, individuals with varying sizes of attentional reservoirs may not display the same degree of responding to emotional information. In addition, individual differences in sensitivity to label a stimulus as fearful or threatening (Pessoa 2005), past experiences (Jiang and Sisk 2019), and contextual framing of a situation (Wang 1996) could influence how attention is directed. For example, if an angry face is perceived as a neutral expression, a threat response may not be activated for that individual and no enhanced attempts at self-preservation will occur. In other words, visual and verbal messages intending to convey a sense of urgency by directing attention toward a threat identified by one individual may not be perceived in the same fear-induced fashion by the receiver.

Relationship Maintenance and Procurement

An understanding of the world is not based solely on the direct information that is picked up by one's sensory organs. Rather, the types of information that make it into one's attentional focus

and how that information is interpreted can lead to various outcomes of perception (Carrasco and Barbot 2019). The evolutionarily relevant goals of finding viable mates and proper survival resources have been shown to be supremely influential in dictating the type of stimuli one will notice in a scene and how those stimuli will be evaluated.

One such example of how the object of an individual's attention can influence their perceptual experience of the world is found in the misattribution of ambiguous noises and sights to an illogical source that aligns with the object of one's attention. White and Fessler (2013) looked at this phenomenon in bereaved pet owners. Long-term pet owners who recently (within the past 2 years) lost a cat or a dog were surveyed for their frequency of falsely attributing sounds (e.g., another dog barking), visualizations (e.g., mistaking another pet as one's own), and compulsions (e.g., urge to look for or feed the pet) to the presence of their late pet. Grieving individuals who most frequently viewed the deceased pet's photos (taken while alive) were more likely to commit instances of false pet recognition, and this occurrence decreased as the time elapsed since the loss increased. Forming an emotional relationship requires a significant amount of time and effort that, if successful, can have a benefit to fitness or, if unsuccessful, be resource depleting. Following the death of a person or pet, the surviving party may feel reluctant to abandon the expensive investment and continue to search for cues that the lost agent remains a viable relationship partner. The authors suggest that misattributing ambiguous sensory information during the grieving process may serve to direct the bereaved's attention toward definitive evidence as to the possibility of rectifying the lost relationship bond. Namely, when attention is focused on a lost pet via frequently viewing photographs, the cognitive systems are readied to perceive ambiguous stimuli in a way that aligns with the desire to maintain the connection.

Due to the intense benefits associated with creating bonds, the desire to do so encompasses a large portion of the evolutionary literature. From an evolutionary perspective, there is an innate drive in humans to identify and secure viable mates so as to prolong and pass on one's genes

to the next generation. For men, this revolves around the desire to find healthy, fertile females who can successfully carry offspring. For females, the search for a strong, resourceful protector and provider to assist in child-rearing is at the forefront. When individuals' motivations related to the likelihood of mating success are manipulated, visual attention is also influenced (Chang and Lu 2012). Specifically, while viewing images of the opposite sex, men tend to focus their attention on a female's waist/hip area (indicative of fertility status) when motivated by a short-term relationship potential but focus on the face area (provides age and nurturing capacity information) when faced with long-term relationship motives. However, when information pertaining to the social status and resource acquiring success is present, both males and females tend to demonstrate early attentional persuasion toward attractive men (DeWall and Maner 2008). This attention toward males with a perception of a high social status aligns with females' adaptive preparedness to identifying resource-rich mates and males attending to threats of potential mates. The shift in visual attention based on one's reproductive goals supports the notion that perceptual attention has evolved in a sex-specific manner.

Attention to Nutritional Resources

How information pertaining to nutritional needs of an individual is perceived can also be influenced by where attention is directed. Repeated exposure to high-calorie food options has been linked with increases in observer desire to obtain and consume unhealthy nutrient options and poor body health (Alblas et al. 2018). In particular, individuals who do not have practiced self-regulation skills and also maintain a mentality of food restriction (i.e., chronic dieting) are easily primed to acknowledge the presence of food-related information. Having food-related thoughts readily in mind leads to an increased ease of perception for relevant environmental cues. This preparedness to orient toward satiating, high-calorie food has also been demonstrated by individuals in a state of hunger (Sänger 2019) as well as those experiencing stress (a response to

perceived threat; Klatzkin et al. 2019). While rapid detection and ingestion of food can be a valuable asset for individuals with a deficit of nutrition availability, such as our hunting-gathering ancestors, it can also be dangerous to the physical health of those living in a resource-enriched modern environment. Yet, an enhanced attentional and perceptual sensitivity to this necessary resource remains a crux of our cognitive processing system. The ability to quickly detect food sources as they become available in the environment allows for the option to encode and obtain or leave the food item, depending on one's most relevant goals and the amount of additional cognitive resources available (e.g., working memory capacity, self-regulation, attentional focus).

Food selection quality has also been shown to be influenced by a diner's mating goals. When dining in a public setting, individuals may manage their personal appearance through the nutritional quality of meal selection. In a recent study, Baker et al. (2019) asked a large sample of individuals to imagine themselves on a dinner outing accompanied by a new classmate who was either attractive or unattractive. When asked to make hypothetical food selections to eat in front of their assigned partner, heterosexual males and females dining with the opposite sex tended to order options with fewer calories the more attractive they perceived the dining partner. However, only individuals *not* currently in a romantic relationship demonstrated this indication of a personal desire to improve or maintain one's health via nutrition conscious choices. In other words, individuals with the potential to secure a mate attempted to display signs of fitness and increase personal likeability. Social context and personal mating motives, both food-irrelevant aspects, can be used to portray a positive image to viable mates through behavioral choices.

Conclusion

The literature reviewed briefly demonstrated a natural, innate attunement of human cognitive processing toward obtaining evolutionarily

significant goals. Attention is captured and maintained by information relating to the detection and avoidance of danger, procurement of viable mates, and obtaining nutritional resources. How this information is interpreted and dealt with by the individual can be influenced by the observer's motivations, goals, and evolutionary drives. While attention and perception often coincide in allowing an individual to explore and understand the environment, it is paramount to consider how the mechanisms driving these processes have adapted and evolved to shape their priorities.

Cross-References

- [Adaptations: Product of Evolution](#)
- [Associative Learning](#)
- [Attention and Memory](#)
- [By-Products of Adaptations](#)
- [Communication, Cues, and Signals](#)
- [Emotions](#)
- [Evolution of Mammalian Vision, the](#)
- [Evolutionary Cognitive Psychology](#)
- [Evolutionary Hierarchy of Needs](#)
- [Face and Object Recognition](#)
- [Fundamental Motives](#)
- [Identifying Adaptive Functions](#)
- [Predators as Attention-Grabbing](#)
- [Problem Solving](#)
- [Response Bias](#)
- [Selective Attending](#)
- [Selective Attunement to Adaptive Problems](#)
- [Sex Differences in Same-Sex Aggression](#)

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A

Attentional Capture

► Predators as Attention-Grabbing

Attire

► To Afford Protection Against Climate and Weather

Attitude

► Prejudice

Attraction

► Evolution of Desire, The ► Facial Disfigurement

Attraction During High Fertility

► Attraction During Ovulation

Attraction During Ovulation

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Synonyms

Attraction during high fertility; Ovulatory shifts in attraction

Definition

Shifts in attraction, in both men and women, during ovulation.

Introduction

Although women typically benefit most from engaging in long-term mating strategies (i.e., attaining and maintaining long-term, committed romantic partners), women can benefit from engaging in short-term mating strategies during ovulation – the short window of time in which the likelihood of conception is most probable. Recent research has suggested that in order to simultaneously reap the benefits associated with both short- and long-term mating, women have evolved dual-mating strategies. Consistent with this idea of dual mating, women's attraction to short-term mates who may offer genetic benefits to potential offspring increases during ovulation. Notably, these ovulatory shifts manifest through (a) changes in women's mate preferences such that women more strongly prefer traits associated with high genetic quality, (b) changes in behaviors such that women more frequently engage in behaviors aimed at attracting high-quality, short-term mates, and (c) changes in men's attraction to women that coincide with women's ovulation. In this chapter, we review each of these ovulatory shifts in turn.

Ovulatory Shifts in Women's Mate Preferences

Heterosexual women are attracted to men's physical and psychological traits that are associated with the willingness and ability to invest in future offspring (e.g., intelligence, access to resources, dependability, trustworthiness, willingness to provide paternal care). Indeed, they demonstrate consistent preferences for these traits across their ovulatory cycles (for a review, see Gildersleeve et al. 2014). In addition to these investment-signaling traits, heterosexual women are attracted to men's physical and psychological traits that are associated with high genetic quality (e.g., masculinity, muscularity, social dominance, intrasexual competitiveness). Men that possess such traits, however, often pursue short-term mating strategies, which are associated with higher rates of infidelity, less warmth and agreeableness, and lower levels of commitment (see Cantú et al. 2014). Accordingly, such men are often risky long-term mates. Evolutionary perspectives suggest that in order to minimize these risks while also maximizing the genetic benefits (for potential offspring) that such men have to offer, women evolved an ovulatory shift in mate preferences such that they more strongly value traits associated with high genetic quality in potential short-term mates during ovulation. That is, women temporarily adopt short-term mating strategies such that they are more attracted to cues of genetic quality in potential short-term mates (because a short-term sex partner's genetic quality could directly influence the genetic quality of any potential offspring) during peak fertility compared to less fertile phases of their ovulatory cycles.

Consistent with this notion, a growing body of research has demonstrated an ovulatory shift in women's attraction to physical cues indicative of high genetic quality. Indeed, women demonstrate a greater preference for indicators of masculinity such as facial masculinity (for review of this work and other similar work, see Gangestad et al. 2005), body masculinity and muscularity (specifically when evaluating potential short-

term mates; Gildersleeve et al. 2014), and vocal masculinity (for review of this work and other similar work, see Gangestad et al. 2005) near ovulation compared to less fertile phases of their ovulatory cycles. Likewise, high (compared to low) fertility women report stronger attraction to the scent of men who possess higher levels of testosterone, presumably because testosterone leads to facial masculinity and increased musculature (Thornhill et al. 2013).

Research has also demonstrated ovulatory shifts in women's attraction to men's nonphysical cues indicative of high genetic quality (e.g., social dominance, competition, riskiness, genetic diversity). One study, for example, demonstrated that women are more attracted to aggressive, arrogant, and socially respected (i.e., intrasexually competitive) men as short-term partners near ovulation compared to less fertile phases of their ovulatory cycles (for review of this work and other similar work, see Gangestad et al. 2005). Likewise, high (compared to low) fertility women are more attracted to men who appear less faithful (for review of this work and other similar work, see Gangestad et al. 2005), which is likely due, at least in part, to the notion that such men are pursuing short-term mating strategies – strategies that only high genetic-quality men can successfully pursue. Moreover, women report increased attraction to outgroup men near peak fertility compared to less fertile phases of their ovulatory cycles (Salvatore et al. 2017), which is likely due, at least in part, to the genetic diversity that such men can offer any potential offspring. Finally, women are more attracted to men who display multiple indicators of genetic quality (i.e., charisma, confidence, and social dominance) as potential short-term mates when they are near peak fertility compared to less fertile phases of their ovulatory cycles (Cantú et al. 2014). Notably, supporting the robustness of this growing literature, a recent meta-analysis examining women's preferences for multiple cues of genetic quality demonstrated that high (compared to low) fertility women had an overall stronger attraction to cues of genetic quality when evaluating potential short-term mates, but not

when evaluating potential long-term mates (Gildersleeve et al. 2014; cf. Wood et al. 2014).

It is worth noting that these ovulatory shifts in mate preferences are not unique to single women. Even partnered women who are actively engaged in long-term, committed relationships experience increased attraction to cues of high genetic quality during ovulation. Interestingly, however, the implications of such increased attraction differ depending on the genetic quality of women's current long-term partners. Specifically, ovulatory shifts in attraction to cues of genetic quality can have negative implications for women whose long-term partners exhibit low genetic quality but positive implications for women whose long-term partners exhibit high genetic quality. For instance, ovulating women with less (versus more) symmetrical long-term partners, an indicator of genetic quality, are less sexually attracted to their current partners and more sexually attracted to alternative partners outside of their current relationships (i.e., extra-pair partners; for review of this work and other similar work, see Gangestad et al. 2005). In contrast, ovulating women with more (versus less) symmetrical long-term partners report increased sexual attraction to those partners (for review of this and similar work, see Gangestad et al. 2005). It is likely that there are numerous implications of accumulated drops and spikes in sexual attraction over the course of long-term relationships. We are not aware, however, of any research that has explored such long-term implications. Future research may benefit from doing so.

Ovulatory Shifts in Women's Behavior

Women's behaviors also shift during ovulation, which likely function to increase their ability to attract high genetic-quality partners. For instance, women's clothing choices fluctuate across their ovulatory cycles. Indeed, women dress in more attractive and sexy attire (for review of this work and other similar work, see Haselton and Gildersleeve 2011) and are more likely to wear

red clothing, which men find particularly attractive, during the fertile phases of their ovulatory cycles compared to the luteal phases (Eisenbruch et al. 2015). Likewise, in an effort to enhance their appearance and thus attract high genetic-quality mates, women are more likely to restrict their caloric intake (Meltzer et al. 2015) during the fertile phases of their ovulatory cycles compared to the luteal phases. Finally, evidence demonstrates that women's flirtatious behaviors fluctuate across their ovulatory cycles. One study, for example, demonstrated that heterosexual women displayed more flirting behaviors when interacting with men who exhibit cues of high genetic quality near peak fertility compared to less fertile phases of their ovulatory cycles (Cantú et al. 2014). Notably, women were no more or less likely to display increased flirting behaviors when interacting with men who lacked such high genetic-quality cues. Moreover, high (compared to low) fertility women report greater interest in attending social gatherings where they are likely to meet available men, and are more likely to agree to dance with men when at a nightclub (for review of this work and other similar work, see Haselton and Gildersleeve 2011).

Ovulatory Shifts in Men's Attraction to Women

Such ovulatory shifts do not appear to be unique to women – men have demonstrated similar shifts in attraction that coincide with women's ovulation. That is, some research has demonstrated that men are more attracted to women who are in the fertile phases of their cycles compared to their luteal phases, which is seemingly adaptive given that ovulation represents women's brief window of reproductive opportunity. For instance, men report increased attraction to high (compared to low) fertility women's voices and scents (for review of this work and other similar work, see Haselton and Gildersleeve 2011; also see Gangestad et al. 2005). Notably, such ovulatory shifts in attraction also emerge among partnered men. One study, for instance, demonstrated that heterosexual men are more attracted to their current long-term female partners when they are near peak fertility

compared to less fertile phases of their ovulatory cycles (Cobey et al. 2013).

Why do such shifts occur in men? Although research has not yet uncovered a clear explanation, it is possible that women experience physical changes during ovulation that men perceive either at an automatic or explicit level. Another possible explanation may be that women emit pheromones that men receive via olfactory communication. Future research would benefit from further examining these and other potential explanations for shifts in men's attraction that coincide with women's ovulation.

Conclusion

Compared to most primates, women's ovulation is relatively concealed. Nevertheless, there are notable shifts in (a) women's mate preferences, (b) women's behaviors aimed at attracting high genetic-quality partners, and (c) men's attraction to women that coincide with women's ovulation. Among women, such ovulatory shifts in mate preferences and behaviors appear to be aimed at procuring a high genetic-quality mate, which would in turn increase the genetic quality of any potential offspring. Among men, such ovulatory shifts in their attraction to women appear to be aimed at procuring women with high likelihoods of conception, which would in turn increase their likelihood of successfully reproducing. Taken together, these ovulatory shifts carry important implications for both women and men, regardless of whether they are seeking new partners or maintaining current relationships.

Cross-References

- [Ovulation](#)
- [Reproductive Strategy](#)
- [Women's Preferences During Ovulation](#)

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Attractive

- Hollywood Actors

Attractiveness

- Appearance/Beauty in Girls
- Male Counter Strategies to Cyclic Shifts
- Male Qualities and Likelihood of Orgasm
- Sex Differences
- Sex Differences in Attractiveness of Humor
- Sexual Signaling During Ovulation

Attractiveness and Anger-Proneness

A

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Synonyms

Aggression; Strength; Weight

Definition

Perceived positive physical characteristics influence aggression.

Introduction

Evolution asserts that physical markers and superior traits will endure generations of breeding to absolve undesirable traits from remaining. In this process, it is argued that attractiveness remains a desirable trait among the population. Examination into evolutionary psychology and its influence on attractiveness has established how physical and psychological traits influence human behavior. The development of research into attractiveness and human behavior claims that individuals who are considered attractive have a higher predisposition to anger. In this new area of research into attractiveness and anger, it explores how certain physical characteristics of an individual are perceived as attractive, but also how having these characteristics influence behavior, such as anger.

Attractiveness

Attractiveness can be considered subjective to individuals who are observing individual's physical characteristics and it's considered to be a disadvantage to be unattractive (Griffin and Langlois 2006). For different sexes, attractiveness can be measured using several physique markers on the human body. One notable physical marker of attractiveness remains body structure. It is

believed that individuals who are considered attractive place a higher regard to weight as a measure of their attractiveness (Horvath 1981). Females who have larger curvature compared to females with less curvature in their body types were seen as more attractive by both males and females (Horvath 1981). Therefore, females who are considered “full-figured” or fat have a higher likelihood to be viewed as an unattractive individual. With this view as a prominent indicator of the perception of attractiveness for individuals, females are inclined to believe that they are overweight when they remain within the healthy weight range, but also neglect to perceive themselves as underweight when they were (Connor-Greene 1988). Females are more likely to be within a healthy weight range, but still perceive themselves as overweight (McCreary and Sadava 2001). The perceptions of body physique for females continue to influence human behavior by having females diet in unhealthy ways, such as using laxatives and vomiting as an effective weight-loss strategy, to manipulate others’ perceptions for a positive response to their attractiveness. (Connor-Greene 1988). Females who were underweight for a healthy body structure continued to perceive themselves as more attractive (McCreary and Sadava 2001). Weight as the measure for body structure impacts the perceptions of attractiveness for females which can influence their behavior to obtain a higher level of perceived attractiveness.

Females are usually the focus of research regarding body structure and attractiveness. However, males have similar perceptions from their body structure to influence their behaviors. Contradictory to females, males tend to rather gain weight rather than lose weight when they felt dissatisfied with their bodies (Connor-Greene 1988). Gaining weight for males shows that males have muscle and strength as their body structure and is perceived as a valuable trait among women. Men who were considered overweight still perceived themselves lighter than they were, but still considered themselves more attractive and healthier than overweight females (McCreary and Sadava 2001). Body structure can also be perceived using smaller facial characteristics that help others perceive their body as attractive. In face structure, women

associate a man’s face shape, specifically prominent jaws, with their perceived masculinity and strength perceiving them as attractive individuals (Windhager et al. 2011). Thus, if a male has certain facial characteristics that manipulate females to believe that their body structure is muscular, then they will be considered attractive. One reason why women may perceive certain masculine features of males as attractive is because they consider these features to be a sign that these males are healthy (Fink et al. 2006). If females are more likely to believe that males are healthy individuals, then there is a possibility for a desirable relationship between the pair that creates the potential for future offspring. Perceived attractiveness between sexes shows that there remain significant differences between what is considered attractive for females and for what is considered attractive for males. Thus, females are perceived as attractive when they have a lower weight, while males are perceived as attractive when they have more weight.

Attractiveness and Anger

Anger is a fundamental part to human behavior that appears in infancy and remains throughout the life course across cultures and individuals (Sell et al. 2009). Since anger appears early on in one’s life, examining aggression in children has shown that attractiveness and anger remain correlated with one another. Teachers of preschoolers report that aggressive children are perceived as some of the most physically attractive individuals (Hawley et al. 2007). Using others to measure the perceived attractiveness of children show that other’s perception of attractiveness does not influence the internal feelings that can lead to anger. Rather, physically attractive children are more anger-prone than unattractive students. Examining the overall physical attractiveness of children and adolescents shows that more physical attractiveness leads to a higher likelihood of anger-proneness.

Anger is asserted and expressed differently between the two sexes, similar to how the perceptions of attractiveness vary significantly between the two sexes. Females’ perceptions of their own attractiveness are correlated with their proneness

toward anger, even when controlling for the strength of the female (Sell et al. 2009). Thus, controlling for a physical indicator of attractiveness that is seen in males (i.e., strength), females who are considered attractive using the standards set by other females act aggressive when they are being measured using their stereotypes. Being physically attractive is a fundamental predictor in popularity and superiority for females and in order to maintain the social position females engage in covert aggression against others (McBride 2011). Therefore, females who are considered more physically attractive are more likely to engage in anger and aggression.

Females that are perceived to be physically attractive are prone toward anger. However, unlike the differences in measuring physical attractiveness between sexes, males are also more prone to anger when they are perceived as physically attractive (Sell et al. 2009). Since musculature is an important predictor of physical attractiveness in males, as an indicator to his strength often determined by body weight, both strength and attractiveness are highly correlated with one another (Sell et al. 2009). Hypermasculine males, or macho men, are more likely to respond with anger when they are faced with threats to their sense of perceived attractiveness by a woman (Downs and Gold 1997). Similar to females, males who are perceived as physically attractive are more prone to anger.

Conclusion

Attractiveness is considered a subjective trait and is “in the eye of the beholder.” However, individuals who are perceived as being physically attractive are more likely to respond with anger to stimuli. Attractiveness is a perceived quality of human life that varies between the sexes. While females want to be skinnier as an indicator of attractiveness, males tend to want to gain more weight as an indicator of strength which influences perceived attractiveness. Females who are perceived as being more physically attractive are more prone to the emotion of anger compared to females who are unattractive. Similarly, males who

are considered physically attractive are also more prone to anger compared to males who are not considered attractive. Overall, attractiveness leads to anger-proneness among individuals throughout the life course and across cultures.

Cross-References

- ▶ Hollywood Actors
- ▶ Sex Differences in Aggression
- ▶ Strength and Anger-Proneness

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Attractiveness Effort

- ▶ Desire to Be Included Among Desirable Women

Attribution of Human Traits

- ▶ Anthropomorphism

Attribution of Intentionality

- ▶ Agency-Detection

Audition

- ▶ Hearing

Auditory Cerebral Cortex

- ▶ Primary and Secondary Auditory Cortex

Auditory Cortex

- ▶ Auditory Neurobiology

Auditory Nervous System

- ▶ Auditory Neurobiology

Auditory Neurobiology

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Synonyms

Auditory cortex; Auditory nervous system

Definition

The physiology of the auditory system of the brain

Introduction

It is noteworthy to state that the physiology of the auditory nervous system has been studied mostly in experiments with animals rather than with humans (Moller 2013). Next, the physiology of the nervous system is briefly discussed, along with frequency selectivity being the main property of the auditory nervous system. As parts of the auditory system, the primary and secondary auditory systems are involved in a higher processing and analysis of sound information. Finally, the mechanosensors are briefly discussed, as they contribute to a process known as mechanotransduction – a physiological process which living cells sense and respond to mechanical stimuli by transducing them into electrochemical signals which, in turn, elicit cellular responses (Bavi et al. 2017).

Structure of the Auditory System

Anatomically, the auditory nervous system consists of ascending and descending systems that create a link between the ear and the auditory cerebral cortex. The axons from the ear connect to neurons in the cochlear nucleus, which in turn connect to other nucleus in higher locations in order to reach the cerebral cortex. The neurons from these systems descend from the

central structures to the nuclei located in a surrounding distance, including the area of the ear (Moller 2013).

There are two separate pathways called classical ascending pathways, also known as the tonotopic system, and nonclassical, or adjunct systems, which are known as the extralemniscal, diffuse, or polysensory systems. There are specific nuclei (Demanez and Demanez 2003) between the auditory nerve and the primary auditory cerebral cortex, which are located in the classical ascending pathway. These nuclei are the cochlear nucleus (CN), where the auditory nerve fibers are divided into dorsal, anteroventral, and posteroventral fibers; the central nucleus of the contralateral inferior colliculus (ICC); the lateral portion of the ventral division of the contralateral medial geniculate body (MGB); and the superior olivary complex which are made by three main nuclei: the superior lateral, medial, and trapezoid body nuclei. These nuclei handle the acoustic information based on the synaptic transmissions and their position in the brain (Moller 2013; Velluti 2008). The neurons in the ventral MGB connect to the primary auditory cerebral cortex (AI) and other auditory cortical areas (Moller 2013).

The auditory nerve (AN) in humans has around 30,000 fibers and it is part of the eighth cranial nerve (CN VIII). It also includes the superior and inferior vestibular nerve (Moller 2013). The majority of the fibers in the auditory nerve help to innervate inner hair cells (Pickles 2012). In order for the auditory nerve to achieve action potential, certain events must take place. Firstly, the sound waves create sound vibrations that reach the tympanic membrane, which in turn trigger the movement of the middle ear's ossicles. As a result, the sound vibrations travel from the ossicles to the oval window membrane, which elicits movement of the cochlear fluids and the basilar membrane. The motion of these structures bend the hair cells' cilia which determine the excitation of the hair cells and finally action potential is generated (Velluti 2008).

There is the so-called frequency selectivity as the main property of the auditory nervous system.

The frequency selectivity of the basilar membrane is responsible for the frequency tuning of the auditory nerve cells and cells in the classical ascending auditory pathways. Nerve fibers of the auditory nerve, cells of the auditory nuclei, and those of the auditory cerebral cortex are anatomically arranged on the basis of their characteristic frequency. This structure is known as the tonotopic organization (Moller 2013; see Polley et al. 2014 for a review on topography and tonography).

Primary and Secondary Auditory Cortex

The auditory cortex involves a complex organization of connections that lead to the processing of auditory information (Moller 2013). The auditory cortex is responsible for the perception of sound and aids with the understanding and production of sounds (Hackett 2015). The complete anatomy of the human auditory cortex is not completely known, nor completely understood, as there is yet an exact consensus between the scientists concerning the exact anatomic positions of the auditory components of the auditory brain (Moller 2013).

Specifically, the primary auditory cortex occupies the cortex of the supratemporal plane and is surrounded by auditory association areas in circular sulcus and the superior temporal gyrus (Pandya 1995). Based on information taken with the use of MRI, the location of the primary auditory cortex seems to be located on a region on the medial two thirds of Heschl's gyrus, linked to Brodmann's area 41 (Pickles 2012; Wasserthal et al. 2014; Moller 2013). There have been efforts to create a tonotopic mapping of the auditory cortex, but this has been a challenging process. The small size of the auditory cortical fields and the lack of a common consensus in regards to the specific locations of the auditory cortex made the process of the tonotopic mapping difficult (Saenz and Langers 2014). However, efforts to topotopically map frequency has proven to be successful (Isaa et al. 2017; Wolak et al. 2017). Equally mapped is the modulation rate (Lithari and Weisz 2017), sensory tuning bandwidth

(Saenz and Langers 2014; Wang and Eliades 2017), and sound intensity (Bilecen et al. 2002).

The Secondary Auditory Cortex

Some neurons from the secondary auditory cortex respond to other stimuli, besides sound. These stimuli are somatosensory, such as touch and vision (Moller 2013). Based on recent research, there is a structural connectivity between the visual and the auditory cortex (Chen et al. 2013) and a multimodal sensory interaction between the sensory cortices (Hosokawa et al. 2017). Both primary and secondary auditory cortices occupy only a small fraction of the neocortex, which is composed of association cortices (see Moller 2013, p.103).

Mechanosensor

These are molecules that interact with other molecules and are affected by mechanical forces. In certain cases, these molecules engage in biological reactions (Shen et al. 2017).

In the cell, these molecules are responsible for a process known as mechanotransduction. This is a physiological process which living cells sense and respond to mechanical stimuli by transducing them into electrochemical signals which, in turn, elicit cellular responses (Bavi et al. 2017).

Furthermore, mechanosensors work as molecular reporters inside the cells that connect external mechanical stimuli at the surface of the cell to intra cellular signaling events and downstream effectors through mechanosensory proteins (Bavi et al. 2017).

In eukaryotic cells, there are three main mechanosensors: (1) the caveole, microvilli, and cilia; (2) intra- or extracellular elements such as the actin cytoskeleton, a cadherin rich cell to cell junction, glycocalyx; and (3) mechanosensitive ion channels. There is a possibility that a combination of these mechanosensors contribute to the mechanotransduction (Bavi et al. 2017).

Certain studies have attempted to study the exact role and structure of the mechanosensors

using sophisticated techniques such as magnetic nanoparticles and magnetic fields (Shen et al. 2017; see Kita et al. 2013, for the birth of a mechanosensor).

Fritsch, Beisel, Pauley, and Soukup (2007) suggest that the evolution of the mechanosensors is interpreted as different mechanosensory organs which where developed in different phyla. Structural designs of ion channels were also found, suggesting that the evolution of mechanosensors took place independently (Delmas and Coste 2013).

Moreover, Kung (2005) in his study described a unifying principle for mechanosensation based on the use of mechanosensitive ion channels. He suggested that channel proteins sense forces from the lipid bilayer involved in opening and closing the mechanosensitive ion channels.

Conclusion

The anatomy and complexity of the auditory nervous system was briefly discussed, which is involved in the processing of acoustic information. The auditory system is divided in the primary auditory system and the secondary auditory system. The mechanosensors contain living cells which are sensitive to mechanical stimulation, leading to biological responses - a process called mechanotransduction.

Cross-References

- [Mechanosensor](#)
- [Primary and Secondary Auditory Cortex](#)

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Auditory Perception

► Hearing

Auditory Properties of Rooms

► Cathedral Acoustics

Auditory System

► Hearing

Auditory System, The

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Synonyms

Inner ear; Middle ear; Outer (external) ear;
Peripheral auditory system

Definition

The structures of the outer (external) ear, middle ear, and inner ear.

Introduction

The auditory system is responsible for hearing and is consisted of the peripheral and central auditory system. The peripheral auditory system includes the structure of the outer ear, middle ear, and the inner ear (Romand and Ehret 1997; Velluti 2008). The cochlea and otoliths are also involved into the inner ear structure, and are briefly discussed as well.

The Outer Ear

The outer ear consists of the pinna, the ear canal, and the ear drum (Pickles 2012; Munir and Clarke 2013). The function of the pinna is to receive sound in order to transmit it to the cochlea – where all acoustic information is processed – through the ear canal (Seikel et al. 2010; Moller 2013). The sound then travels to the middle ear through the ear canal, otherwise called the external auditory meatus. The ear canal secretes cerumen (wax) which has a minor antibacterial function and protects the ear from minor injuries. The skin of the ear canal is covered with various nerves responsible for the heart rate, blood circulation, and fainting (Moller 2013).

The Middle Ear

The middle ear is an air-filled space and is located behind the tympanic membrane which contains the bones of hearing (ossicles) called malleus, incus, and stapes (Munir and Clarke 2013). These ossicles constitute the ossicular chain which help with the transmission of sound to the tympanic membrane and then to the inner ear (Seikel et al. 2010). Another part of the middle ear is the Eustachian tube which occupies the air space between the nose and the throat (Balkany and Brown 2017).

In the middle ear there are two tympanic muscles that are connected to the ossicles. These are called the stapedius and the tensor tympani. The function of the stapedius is to rotate posteriorly the footplate of the stapes stiffening the ossicular chain. The function of the tensor tympani is to pull the malleus anteromedially, thus reducing

the movement of the tympanic membrane. These two muscles stiffen the transmission system of the middle ear, monitoring the acoustic signal in the lower frequencies, thus protecting the ear from high intensity sounds (Seikel et al. 2010).

An additional part of the middle ear is the Eustachian tube, which forms a link between the nasopharynx and the middle ear. The cranial nerve VII passes runs through this pathway (Munir and Clarke 2013). The function of the eustachian tube is to allow mucous flow away and oxygen run through and out of the tube. It, also, works as a way to equalize the pressure levels in situations where pressure is changed such as under the water or in high altitudes (Balkany and Brown 2017).

Reichert's (1837) hypothesis on comparative morphology has contributed to the evolutionary understanding of the middle ear's ossicles, the malleus, and incus. According to his study, these ossicles were derived from the cartilages of the upper and lower jaw elements of the articular and quadrate amniotes. Further evidence was found to support this hypothesis based on fossil records in South Africa and Russia (Takechi and Shigeru 2010).

Furthermore, Manley (2010) has noted that the tympanic middle ears were developed independently and that their origin is unique. He further explained that evolution takes place independently in similar groups, and that the results developed from the same structures could be similar. He also mentioned of the possibility of a random evolution and that the developments of the middle and inner ear were essential for hearing in high frequencies. With the enlargement of the brain, the tympanic middle ear in therian mammals was developed, subsequently creating a secondary palate that helped with the development of a pressure system in the middle ear (Manley 2010).

The Inner Ear

The inner ear is sectioned into the cochlea and the balance system (the vestibular system). The first representation of the human and mammalian cochlea was discovered in 1561 (von Bekesy 1948) and the phenomenon of resonance was

proposed by Duverney in 1683 (Mudry 2000) who based his observation on the resonance of two piano strings in tune with each other. The careful drawings of Magnus Gustaf Retzius (Jelliffe 1920) who depicted the cytoarchitecture of the organ of Corti has given an elaborate description of the membranous labyrinth, cross sections of the cochlea, and the surface of the organ of Corti based on different stages of development (Johnsson and Hawkins 1967).

The balance system, otherwise called vestibular system, is made up of a vestibule, located between the cochlea and the semicircular canals. A structure called the osseous labyrinth (or bony labyrinth) is consisted of the cochlea, the vestibule, and the semicircular canals. The membranous labyrinth lies in the osseous labyrinth; it can be described as a sac filled with fluid (Boulpaep and Boron 2005). Both the bony and the membranous labyrinth are complex balance organs of the inner ear (Hain and Helminsky 2007).

Cochlea

The cochlea has a snail shape and has compartments filled with fluid. These compartments are in a form of a spiral and contain the organ of Corti, which is the receptor for acoustic information (Chang and Khana 2013). The organ of Corti and the vestibular organ are enclosed in the temporal bone (Moller 2013). There are more than 15000 hair cells in each cochlea which yield electrical signals based on the vibrations of the inner ear fluid; consequently, these electrical signals are perceived by the brain as hearing (Balkany and Brown 2017).

The cochlea distinguishes the sounds based on their frequency in order different sounds activate different auditory nerve fibers. This takes place in the inner hair cells. The outer hair cells help to reduce the friction on the basilar membrane and increase its vibration breadth. They also increase frequency selectivity, according to the intensity of sound, and frequency selectivity is decreased when the intensity of sound is increased, which causes the cochlea to function in a nonlinear way in order to compress the sound before the innervation of the auditory nerve. This process helps to

distinguish the sounds in the auditory nerve based on their intensities (Moller 2013).

The organ of Corti, as a part of the cochlea, is composed of a specialized structure consisted of hair cells, and is located on the basilar membrane. In essence, this structure organizes the auditory transduction (Pickles 2012, pp. 28–33). It is covered with a gelatinous and fibrous fold called the tectorial membrane, consisted of molecules and collagens known as tectorins, which play a significant role for the hearing process (Pickles 2012, pp. 28–33; Richardson et al. 2011). The organ of Corti generates sharply tuned traveling waves by the process called mechanotransduction based on electrochemical reactions in the cochlear scalae (Pickles 2012).

Otolith

Otoliths are describes as tiny carbonate particles that compose the otolithic membrane. The otolithic membrane accommodates the utricle and the saccule inside the vestibule (Chang and Khana 2013; Seikel et al. 2010). It, also, covers the utricular macula which is a sensory organ consisted of hair cells and cilia. The saccule is located near the scala vestibuli in the vestibule and is consisted with macula and the otolithic membrane. The linear motion or the tilting of the head creates a movement force between the otolithic membrane and the macular surface, which result in the bending of the hair cells (Oghalai and Brownell 2012).

Conclusion

The main structures of the peripheral auditory system were discussed, namely, the outer ear, middle ear, and inner ear, along with the structures of the cochlea and the otoliths.

Cross-References

- [Cochlea](#)
- [Inner Ear](#)

- ▶ Middle Ear
- ▶ Organ of Corti
- ▶ Otolith
- ▶ Vestibular System

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Aunt Care

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Synonyms

Adjunct mother; Almomothering

Definitions

Aunts, paternity Uncertainty, Kin caregiving, Matrilateral, Patrilateral, Asymmetric kin investment

Introduction

Despite being forgotten in research, maternal or paternal aunts are highly invested and play an essential role of an “adjunct mother,” thereby providing childcare, guidance, support, and affection to their nieces and nephews (Milardo 2009, p. xvi). The aunt-child relationship can be consanguineous or formed through marriage and therefore includes the sisters of a father (paternal aunts) or mother (maternal aunts) or the wives of father’s brothers (paternal aunts) or mother’s brothers (maternal aunts).

One of the most decisive factors in the degree of investment in nieces and nephews is a sense of solidarity or the relationship between parents and their siblings’ family, which can be further

influenced by contextual factors listed here. For instance, higher “associational (frequency of contact between parents), consensual (the similarity of attitudes and emotions between parents), functional (perception of support), normative (sense of obligation) and a structural (residential proximity) solidarity” (Milardo 2009; p. 12) can remarkably moderate ideas of kin-keeping and investment in nieces and nephews.

Laterality and Gender Effects

Notably, the scholarly examination of above listed contextual factors brings into light the concept of asymmetric kin investment or the laterality effect. Studies in favor of laterality effect suggest the occurrence of higher investment in nieces and nephews by a maternal aunt than a paternal aunt. To elaborate, in matrilateral societies, blood-related maternal aunts perceive a stronger sense of genetic relatedness and emotional closeness in comparison to paternal aunts. These perceptions are further influenced by paternity uncertainty, opportunities for frequent contact, stronger relationships between sisters, and young female's (in this case maternal aunt's) interest in learning maternal behaviors (Salmon 1999; Parent et al. 2013). Additionally, Tanskanen (2015), in the Finnish sample, showed that childless aunts are more likely to invest in their nieces and nephews, perhaps because they have more time and resources.

On the contrary, studies from patrilateral societies conclude otherwise. Patrilateral societies mandate higher associational, structural, and normative solidarity to the husband's family to ensure higher perceptions of genetic relatedness and a lower uncertainty of paternity. Consequently, patrilateral societies have more significant investment by paternal aunts than maternal aunts (Pashos 2000; Milardo 2009; Euler and Weitzel 1996).

Despite cultural variations on the laterality effect, aunts being females and therefore normed kin-keepers undoubtedly provide more intense and frequent caregiving to their nieces and nephews than uncles. To further

investigate, Gaulin et al. (1997) compared their US sample with Euler and Weitzel (1996). The authors reported that in the US sample, aunts invested more regardless of whether they are paternal or maternal. Therefore, unlike Euler and Weitzel (1996) study of German families, laterality played a smaller role than gender in the US sample.

Impact of Aunt Care on Development in Minority Families

After grandparents, aunts contribute the most in all domains of development. Aunts can be a role model, teacher, friend, or an allomother and provide meaningful family connections that can have a lasting and valuable effect on the development trajectory during adversity (Ellingson and Sotirin 2006) to strengthen families (Davis-Sowers 2012).

As noted, these positive effects are particularly relevant and distinct in minority families. Parent et al. (2013) found that among African American families in the USA, the warm relationship between maternal aunt and their nieces and nephews was negatively associated with internalizing and externalizing behaviors. Cross-cultural comparison studies in the USA and Finland reproduced similar results. Erola et al. (2018) found that resources at an extended family level, particularly of uncles and aunts, are positively associated with socioeconomic attainment among nieces and nephews. Likewise, Allen et al. (2008) concluded that among Latino families, extended family members such as aunts are untapped resources that bridge the intergenerational gap between parents and adolescents.

Aunt Care and Aunts

Davis-Sowers (2012) examined the determinants of the aunts' decision to care for their nieces and nephews in Black families. He found that aunts have little to no authority in denying/accepting care. The participants reported that decisions to parent are deeply rooted in gendered norms,

sense of obligation to the family, an occurrence of crisis-like situation, and religious values that promote kin-keeping. Despite the lack of agency, aunts were inclined to caregiving as it offers opportunities to build a personal identity, a higher sense of self-efficacy, and satisfaction of making a difference in the lives of their family.

The above article Davis-Sowers (2012) alludes to feminist criticisms of gendered caregiving. Strong-Boag (2009) agrees that after grandparents, aunts are first in line to provide care. Nevertheless, this reliance at the time crisis contributes to unpaid emotional and physical labor for women and undue pressure of being responsible for children's future.

Conclusion

Currently, we have a handful of research that solely pertains to the impact of aunt care on lifespan development. In extended family care literature, aunts are lumped together with grandparents and uncles, and therefore examining their role is challenging. The research supports the positive and vital role of aunts on individual development. Since many aunts are expending time, energy, and effort in maintaining or supporting relationships with their nieces and nephews, scholarly examination of their role is warranted.

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Aural Perception

► Hearing

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Definition

Aurelio José Figueredo is an evolutionary personality psychologist who has made significant contributions to research on sexual violence, environmental harshness and unpredictability, and on psychometric approaches toward measuring human life history.

Aurelio José Figueredo is an Evolutionary Personality Psychologist from the University of

Arizona in Tucson, who serves in the Departments of Psychology and Family Studies and Human Development. In addition to his full professor appointments, Professor Figueredo directs the Ethology and Evolutionary Psychology (EEP) graduate program. His most notable contribution to the field of evolutionary psychology was to more fully develop the *psychometric approach* to the assessment of human life history strategy by discovering the *K-Factor*, a latent higher-order construct of psychological, behavioral, and cognitive traits that are theorized to comprise a cohesive and comprehensive life history strategy. Since its inception in the early 2000s, the psychometric approach has generated much derivative research as well as controversy (see Copping et al. 2014). The sections below briefly discuss Professor Figueredo's private life, education, and a selection of his contributions to the field of evolutionary psychology.

Private Life

Aurelio José ("AJ") Figueredo was born in Victoria de las Tunas, Oriente, Cuba, on 27 December 1955 to Yolanda Fulgencia Rodríguez and Alfredo Odón Figueredo. He had two older siblings at the time, Alfredo Ezequiel Figueredo and Yolanda Inocencia Figueredo. Most notably, AJ's older brother became an Anthropologist who eventually achieved the status of world expert in Caribbean Archaeology and Territorial Archeologist for the US Virgin Islands. When he was only 3 years old, AJ's parents had to flee their native country under threat of execution by the newly established communist dictatorship of Fidel Castro; 9 months later, AJ and his two older siblings emigrated to the USA to join their parents, escorted by their grandmother María del Pilar Lalana de Figueredo. His younger sister, Ana María Figueredo, was later born in Brooklyn, New York, and is the only original immediate family member besides AJ remaining alive at the time of writing. AJ has been married since 1983 to Maureen Jacobs Figueredo, and she gave birth to one daughter, Alyssa Mia Figueredo, in 1987.

Academic Education

Having spent most of his childhood on the east coast, AJ moved west and earned a bachelor's degree in Psychology at California State University, Los Angeles, in 1983. AJ was then accepted into the University of California, Riverside, earning his master's degree in 1985 and receiving his doctorate degree in 1987, specializing in comparative psychology, physiological psychology, and quantitative psychology. His graduate advisor was Lewis Petrinovich, a comparative psychologist who worked extensively on song learning in the white-crowned sparrow and, later in life, wrote several books on the evolution of human moral intuitions.

The breadth of AJ's early training involved ethological and comparative research mainly focusing on biologically prepared behavioral development in insects, specifically focusing on conditioned host selection in the parasitoid jewel wasp, as a function of changing ecological conditions during development (Figueredo 1987, 1989). He additionally extended his comparative work to include the conditioned response to sex pheromones in the oriental fruit moth (Figueredo and Baker 1992), the quantitative ethology of song learning in the zebra finch (Figueredo et al. 1992), and the latent structure of personality dimensions in both stump-tailed macaque and the zebra finch (Figueredo et al. 1995) as well as in the common chimpanzee (King and Figueredo 1997).

Major Contributions to Evolutionary Psychology

The Evolutionary Psychology of Sexual Violence. Professor Figueredo's early work focused on the cross-cultural examination of aggressive behavior, especially sex offending, intimate partner abuse, and family violence as well as sexually motivated interpersonal aggression in general. This body of cross-cultural research asserted that issues that precipitated intimate partner violence were primarily fueled by sexual conflict between men and women. Men in these situations sought to control and retain sexual access to women by

coercive and aggressive means (Figueredo and McCloskey 1993). Further, the men often engaging in these coercive strategies were found to be low in mate value (*Competitively Disadvantaged Male Theory*; Figueredo and McCloskey 1993) and to have fast life history strategies (Figueredo et al. 2012; Gladden et al. 2008). Another finding from this body of research is that aggressive individuals are abusive and conflictual across different social domains (Figueredo et al. 2012), including the abuse of women and children (Figueredo and McCloskey 1993; Gladden et al. 2013; McCloskey et al. 1995).

The Hierarchical Latent Structure of Human Life History Strategy (the K-Factor). Briefly, life history theory posits that organisms are given a finite amount of bioenergetic resources that they must allocate across varying facets of development. These trade-off decisions are influenced by the local conditions of the environment in which the organism resides, with resource allocation occurring in developmental domains that best maximizes resources for survival and reproduction (see Life history theory or Fundamental Strategies, encyclopedia entries). Life history strategies reside on a continuum, whereby fast life history strategies are oriented toward short-term mating and low parental care, while slow life history strategies are oriented toward long-term mating and high parental care. While Professor Figueredo has contributed to many aspects of human life history theory, one of his most notable contributions to the study of human life history was to put forth and test the hierarchical latent structure of the *K-Factor*, a psychometric extension of Rushton's (1985) psychosocial life history model (see Figueredo et al. 2013 for a summary). Both models posit that life history strategies encompass a coordinated suite of traits and characteristics that range from reproductive history (e.g., age of puberty, number of births, etc.) to behavioral, cognitive, and personality traits. One of the most comprehensive measures of life history strategies (*K*) was developed by Professor Figueredo and his colleagues called the *Arizona Life History Battery* (ALHB; Figueredo 2007) and the short-form version called the *Mini-K* (Figueredo et al. 2006). Most recently, they have introduced a psychometrically superior short form

called the K-SF-42 (Figueredo et al. 2016a), having developed a novel method for creating cross-culturally valid and generalizable short forms. Empirical work using these and equivalent measures of life history strategies have found evidence that *K* is both a heritable (Figueredo and Rushton 2009) and temporally stable individual trait (Brumbach et al. 2009; Figueredo et al. 2014a); a recent meta-analysis has also shown that *K* influences a wide array of psychosocial traits (Figueredo et al. 2014b). According to Figueredo et al. (2013, p. 3), *K* has been empirically demonstrated to:

- (1) positively and significantly predict Executive Functions, Trait Emotional Intelligence, Mate Value Inventory, Mate Value Scale, Rosenberg Self Esteem Scale, Self-Adjective Checklist, Social Economic Exchange Scale, Collective Self Esteem Scale, Positive Assortative Mating, Female Physical Height, Long-Term Mating Sociosexual Orientation, Moral Intuitions, In-Group Loyalty, as well as Secure Attachment, Supportive Communication, and Long-Term Satisfaction in Romantic Relationships, both cross-sectionally and longitudinally; and (2) negatively and significantly predict the Mating Effort Scale, Short-Term Mating Sociosexual Orientation, Escalated Mate Retention Tactics, Affective and Punitive Responses to Sexual or Emotional Infidelity, Intimate Partner Violence, Interpersonal Aggression, Female Intrasexual Competitiveness, Disordered Eating Behavior, Negative Ethnocentrism, Negative Androcentrism, Levenson's Primary Psychopathy Scale, Levenson's Secondary Psychopathy Scale, Machiavellianism Scale, Buss-Perry Aggression Questionnaire, Proactive-Reactive Aggression Questionnaire, and General Social Deviance.

Controversies Surrounding the K-Factor The K-Factor has generated empirical interest across many substantive domains such as interest in babies (Zilioli et al. 2016) and across international contexts (reviewed in Figueredo et al. 2015). However, the K-Factor has also generated controversy from developmental life history researchers (Copping et al. 2014). Critics of the psychometric approach to life history are mainly concerned with statistical aggregation across measures, such as how ALHB is constructed (Copping et al. 2014), and are also concerned that these measures have not been adequately validated with biodemographic indicators of life history

(Copping et al. 2014). Critics have also asserted that statistical aggregation of higher-order life history factors may obfuscate developmental psychological sequences, obscuring possible inquiry into pathways that may shape the behavioral development of life history strategies across the life course (Copping et al. 2016). Professor Figueredo and his colleagues have defended the use of aggregated measures in cross-sectional samples as a “snapshot” of experiences and developmental milestones from that point in an individual’s life (Figueredo et al. 2015, p. 312). Accordingly, advocates of each position agree that both points of view indeed represent valid and complementary perspectives and have conceded to continue improving the measurement and development of measures that best accurately capture human life history strategies (Copping et al. 2016; Figueredo et al. 2015).

Environmental Harshness and Unpredictability Evolutionary models – particularly life history models – emphasize the important role the environment plays on intraindividual variation on different suites of traits (Stearns 1992). Extrinsic sources of illness, disability, and death in adulthood that are not accounted for by age or health status are purported to be major drivers in the evolution and development of life history strategies such that increases of extrinsic morbidity-mortality may accelerate life history strategies (Charnov 1991; Ellis et al. 2009). Professor Figueredo, along with Bruce Ellis and other colleagues (Ellis et al. 2009), examined the impact of adult extrinsic morbidity-mortality by proposing two distinct ecological constructs: environmental harshness and unpredictability. The American Psychological Association conferred the George A Miller Award for an Outstanding Recent Article on General Psychology upon this paper in 2010. According to this model, environmental harshness and unpredictability are independent drivers of life history evolution and development. Harshness at the population level is defined by increases in adult extrinsic morbidity-mortality and is usually often operationalized in modern human populations at the individual level by measures of low socioeconomic status (e.g., Simpson

et al. 2012) or exposure to violence (Brumbach et al. 2009). Unpredictability is defined at the population level as the amount of fluctuation in adult extrinsic morbidity-mortality and is operationalized in modern human populations at the individual level through measures of unpredictability such as the number of household or school relocations or family transitions (e.g., Simpson et al. 2012).

Current Research Activities Professor Figueredo and international team of collaborators are currently working on integrative models of social biogeography that follow the social *sequelae* of human life history at the population level in the achievement of higher levels of social harmony, macroeconomic complexity, aggregate productivity, and advanced cognitive development (Figueredo et al. 2016b). In addition, Professor Figueredo and colleagues have been developing a statistical model designed to disentangle the intrinsic gene-environment correlations in commonly used developmental data (such as parental, neighborhood, and economic sources of harshness and unpredictability) from truly extrinsic environmental influences.

Cross-References

- [Bruce J. Ellis](#)
- [Environmental Harshness](#)
- [Environmental Unpredictability](#)
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Australopithecus aethiopicus

► *Paranthropus aethiopicus*

Australopithecus africanus

A

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Definition

First African hominin discovered; The species has several historically important specimens

Introduction

Australopithecus africanus is an early fossil hominin known from several localities in South Africa, most notably Swartkrans Cave. It is one of the most well-represented hominin fossil species, with large numbers of associated cranial and postcranial elements. Dating has proven difficult, due to the complex cave geology and lack of volcanic sediments in the known localities, but current estimates for this species range from 3.0 to 2.0 Ma (e.g., Herries and Shaw 2011).

History

This species includes several historically important fossils, most notably the juvenile specimen known as the “Taung child.” As described by Raymond Dart in 1925, this specimen represented the first known early African hominin and was confirmation of Darwin’s hypothesis that the earliest humans would be found in Africa. However, cultural and scientific prejudice, notably the wide acceptance of the fraudulent Piltdown specimen, prevented its acceptance as a human ancestor in the wider scientific community for almost 20 years. Various fragmentary specimens were discovered over the next several decades (e.g., Broom 1936), but it was not until the discovery of more complete adult specimens such as Sts 5 (aka Mrs. Ples, see Figure 1) at Sterkfontein (discovered 1947) that *Australopithecus*



***Australopithecus africanus*, Fig. 1**

africanus was widely acknowledged as human (e.g. Clark 1950).

Anatomy

A. africanus is broadly similar to other known species of *Australopithecus*, in that it possesses several primitive apelike anatomical retentions, including, cranially, a projecting subnasal region, a notable canine root, a relatively flat cranial base, and a cranial capacity between 400 and 500 cc. There appear to be several anatomical specializations related to dietary adaptation in the face (the buttressing of the “anterior pillar” alongside the nasal aperture, Rak 1983) and teeth (overall large postcanine dentition, Broom and Robinson 1947), and a diet of relatively tough foods is therefore inferred. Postcranially, this species is also similar to other early hominins in the genus, with a body size ranging from 1.1 m (for inferred females) to 1.4 m (for inferred males), relatively long arms, a well-developed thumb, and clear evidence of bipedalism in the pelvis and lower limb. There is a sufficiently large sample to assign individual skulls to sex, and the range of known adult specimens (e.g., Sts 5 and Stw 505) indicates a relatively high degree of sexual dimorphism, consistent with other well-represented early hominins (e.g., *Paranthropus*, *A. afarensis*), and a gorilla-like social structure is therefore inferred.

Evolutionary Relationships

The phylogenetic position of *A. africanus* has changed over the last 50 years, as the fossil record, particularly from East Africa, has expanded dramatically. Until the 1970s, this species was seen as the best candidate for direct ancestry to all later human species, including both the genus *Homo* and the robust genus *Paranthropus* (e.g., Tobias 1978). However, currently, *A. afarensis* and *A. aethiopicus*, both from East Africa, are seen as the likeliest ancestors for those two genera, and *A. africanus* is typically relegated to a terminal side-branch of human evolution (Strait and Grine 2004). More recently, an analysis of dental morphology has proposed that *A. africanus* may be ancestral to the later South African species *A. sediba* (Irish et al. 2013).

Conclusion

Australopithecus africanus played a critical role in the acceptance of Africa as the location of the origin of human evolution. Anatomically, it is similar to other species in the genus, with many apelike retentions. The current consensus is that it represents a phylogenetic dead-end in the human tree, but the continued production of specimens at Sterkfontein and other sites means that this species represents a wealth of critical information on anatomical adaptations in early fossil humans.

Cross-References

- [Australopithecus Group](#)
- [Human Evolution](#)

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Australopithecus boisei

► *Paranthropus boisei*

Australopithecus garhi

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Definition

Early human ancestor from 2.5 million years before present.

Introduction

Australopithecus garhi is an extinct fossil hominin species identified from remains discovered between 1990 and 1998 at the Bouri locality, in the Middle Awash region of the Afar Regional State, Ethiopia. The remains of this species, which date to roughly 2.5 Ma based on argon-argon dating techniques, are composed of unassociated cranial and postcranial elements discovered over

some 9 sq. km. Hypotheses for conspecificity for some of these elements are based on proximity at the time of collection; the more distant remains are associated primarily based on discovery in the same or temporally similar geological horizons.

Anatomy

The cranium (as known from holotype specimen BOU-VP-12/130) is characterized by extremely large postcranial dentition, well within the range of the robust group, *Paranthropus*, and it possesses a notable sagittal crest. However, this species lacks several anatomical traits uniquely seen in *P. robustus* and *P. boisei*, including molarization of the premolars, reduced anterior dentition, and a concave to flat midface; in fact the anterior dentition is notably large in this species. Other than the dental dimensions, *A. garhi* shows primitive anatomy typical *Australopithecus*: a ~ 450 cc cranial capacity, an apelike protruding subnasal region, and prominent canine roots. Postcranially, known elements (which were not discovered in direct association with cranial elements) demonstrate the characteristic *Australopithecus* pattern of relatively long arms; bipedalism is inferred, although there are no articular ends (which would allow more direct inference of locomotor pattern) preserved on the published femur.

Evolutionary Relationships

Phylogenetically, the position of *A. garhi* is unresolved. The initial publication (Asfaw et al. 1999) suggested the possibility of ancestry to the genus *Homo*, noting the lack of alternatives in the fossil record between 2 and 3 Ma. However, formal phylogenetic analysis has generally failed to support this hypothesis (e.g., Strait and Grine 2004), and subsequent discoveries have identified more likely alternatives for the ancestry of *Homo*.

Contemporaneous with Cutmarked Bone

Cutmarked bone, from several localities across several square kilometers, was found in general

stratigraphic association with the holotype cranium, and stone tools are known from the 2.6 Ma horizon at the Gona location, some 100 km distant (de Heinzelin et al. 1999). However, whether *A. garhi*, or another contemporaneous hominin, is responsible for this material, is not currently possible to demonstrate.

Conclusion

Australopithecus garhi is a hominin discovered in Ethiopia and dates to 2.5 million years before present. It is characterized by anatomy generally similar to other species of *Australopithecus*, but with notably large postcanine teeth.

Cross-References

- [Australopithecus Group](#)
- [Human Evolution](#)

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Australopithecus Group

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Synonyms

Australopiths; *Kenyanthropus*; *Paranthropus*;
Praeanthropus

Definition

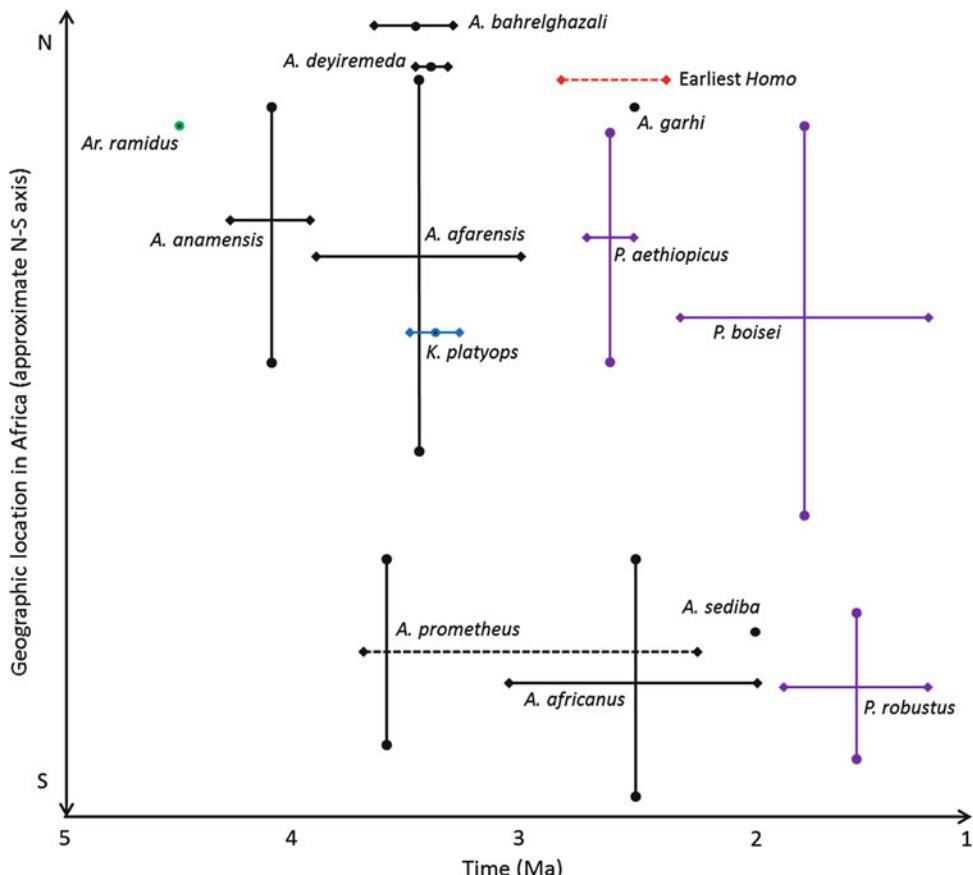
A genus (or group of multiple genera) of fossil hominins ranging in geological age from the Pliocene through the early Pleistocene (~4.2–1.2 Ma = Mega annum, or millions of years) of Africa, the name *Australopithecus* comes from Greek for “ape” (pithekos) and Latin “of the south” (australis), for the geographical location of the first material discovered, in South Africa.

Introduction

The *Australopithecus* group (“australopiths”) consists of up to twelve species of Plio-Pleistocene hominins (members of the human lineage following the phylogenetic divergence from chimpanzees and bonobos) mostly included in the genus *Australopithecus* (but several species are commonly included in a distinct genus, *Paranthropus*, and one species is named in a distinct genus, *Kenyanthropus*). Additionally, some researchers suggest that the earliest members of the genus *Homo* should actually be transferred to *Australopithecus*, leaving just *Homo erectus* and its descendants in *Homo*. The genus *Australopithecus* is almost certainly paraphyletic, meaning that it does not form a natural group; instead, one or more lineages are more closely related to members of other genera (e.g., *Paranthropus* or *Homo*). Australopiths were ape-like hominins that retained relatively small brains and probably some adaptations to the arboreal environment (i.e., long arms for tree climbing), yet were clearly upright bipeds (adapted to walking on two legs), some of which were primitive tool users. Determining which australopith lineage gave rise to later hominins (i.e., *Homo*) is a major area of focus and controversy in paleoanthropology (Fig. 1).

History

The genus *Australopithecus* was not the first hominin genus other than *Homo* to be named, but it is the oldest one that is still used (*Pithecanthropus*, for example, has been



Australopithecus Group, Fig. 1 Australopiths in time and space. Species are arranged according to their documented presence in the fossil record (x-axis; Ma = Mega annum: millions of years before present) and approximate geographic locality (y-axis; arranged from south to north). Species known from more than one locality or date, or when a range of dates are published, are shown with vertical and horizontal bars, respectively. Single points indicate that a species is known from one site and date; a dashed line indicates that the date is controversial

(as is the case with *A. prometheus*) or links material not currently assigned to a species to affiliated material (as is the case with the Ledi-Geraru mandible and the A.L. 666-1 palate, the earliest *Homo* material). *Homo* material <2 Ma is not shown but is represented in both East and South Africa and elsewhere outside Africa. Color codes indicate different genera: green *Ardipithecus*, black *Australopithecus*, blue *Kenyanthropus*, purple *Paranthropus*, red *Homo*

subsumed within *Homo* as *H. erectus*). Named in 1925 by Raymond Dart, *Australopithecus africanus* was immediately challenged by Dart's senior colleagues in England, largely due to the influence of the later-discredited Piltdown material and the early developmental age of the *A. africanus* type specimen, a juvenile skull from Taungs. Throughout the 1930s and 1940s, Robert Broom amassed a number of adult specimens that he initially attributed to a new species, *A. transvaalensis* (then later a new genus, *Plesianthropus* – “near man”), the most famous

of which is the Sts 5 cranium, nicknamed “Mrs. Ples.” Broom and his assistant John Robinson, who carried on work at Sterkfontein after Broom's death in 1951, also discovered Sts 14, the first partial skeleton of an early hominin that preserved numerous associated postcranial (below the skull) bones and therefore provided information on the way in which *A. africanus* walked. Robinson (1972) and later Owen Lovejoy and others (e.g., Lovejoy et al. 1973) studied this material to understand the anatomy and biomechanics of bipedalism in an early hominin. The new, adult material

attributed to *A. africanus* mostly put to rest the idea that Dart's "African ape of the south" (or "southern ape of Africa") was anything but a bipedal, early member of the human lineage.

Additionally, Broom discovered what he considered two species of a new genus that he named *Paranthropus*, meaning "alongside man" (*P. robustus* and *P. crassidens*; although a minority of researchers today still recognize material from Kromdraai and Swartkrans, respectively, as separate species, the latter material is generally subsumed within the former species). These cranioidentally (concerning the skull, including teeth) "robust" hominins were distinct from the more "gracile" *A. africanus*, which later led to the introduction and common use of "gracile and robust australopithecines" to refer to the two groups, the former later subsuming within it a new species called *Australopithecus afarensis* (see below). Today, the terms are outdated, both because neither *A. africanus* nor *A. afarensis* was particularly gracile in cranioidal morphology and because "australopithecine" invokes a taxonomic statement (subfamily designation) that is considered by many to be too broad and therefore inaccurate (i.e., "hominin" refers to a tribe, Hominini, whereas Homininae, a subfamily, includes all African great apes – hominins and members of the chimpanzee/bonobos and gorilla lineages). Therefore, the term "gracile" has been largely abandoned and "robust australopith" is preferred in colloquial reference to members of the genus *Paranthropus*. In the 1950s, Louis and Mary Leakey discovered Olduvai Hominid 5 (OH5), a cranium belonging to what they called *Zinjanthropus boisei* ("Boise's eastern African man"), a hyper-robust species clearly adapted to heavy/tough/repetitive chewing, and hence nicknamed "Nutcracker Man."

In 1962, Sherwood Washburn organized a Wenner-Gren Foundation-funded meeting of prominent paleoanthropologists, primate anatomoists, molecular anthropologists, primate behavioral ecologists, and the three primary leaders of the modern synthesis of evolutionary biology, George Simpson, Theodosius Dobzhansky, and Ernst Mayr, to discuss the current state of taxonomy in the human fossil record. While all of the

entries in what would become an edited volume (Washburn 1963) are now considered classic contributions, Mayr's paper on the taxonomy of fossil hominids had a particularly strong influence on what Washburn called the "new physical anthropology." Recognizing the surfeit of genera in the hominin fossil record, Mayr recommended that just two be recognized, *Australopithecus* (including *Plesianthropus*, *Paranthropus*, *Zinjanthropus*, and other genus names proposed for early hominins) and *Homo* (including archaic - e.g., Neandertals - and modern humans and a plethora of other genus and other species names now referred to as *Homo erectus*). Many paleoanthropologists followed suit, including Robinson, who sunk *A. africanus* into *Homo* but retained *Paranthropus*, thus adopting a distinct, two-genus system to that proposed by Mayr (Robinson 1972).

In the 1970s, discoveries in East Africa, specifically from Laetoli in Tanzania and Hadar in Ethiopia, led to the naming of a new species of *Australopithecus*, *A. afarensis* (although for taxonomic reasons some researchers prefer the genus *Praeanthropus* – "pre-man"). The material it was based on included the type specimen, a mandible from Laetoli (Laetoli Hominid 4; LH 4) discovered by Mary Leakey and her team, and a partial skeleton from Afar Locality 288 (A.L. 288-1) colloquially known as "Lucy," along with other cranioidal and postcranial material from nearby localities (e.g., A.L. 129), discovered by Donald Johanson and Maurice Taieb. Since the naming of *A. afarensis*, much more material has been discovered, including the A.L. 333 "First Family," a collection of cranioidal and postcranial fossils attributable to a group of individuals killed around the same time, A.L. 444-2, a large partial skull (Kimbrel and Delezene 2009), and DIK-1-1, the skull and partial skeleton of a young individual similar in developmental age to the Taung child, from Dikika, Ethiopia (Alemseged et al. 2006). *A. afarensis* is both geologically older (3.9–3 Ma) and morphology more primitive in some ways than *A. africanus* (3.0–2.1 Ma); thus, it was interpreted by Johanson and Tim White to be ancestral to an *A. africanus*-*Paranthropus* lineage on one hand, and the genus *Homo* on the other (Johanson and White 1979).

The discovery of the KNM-WT 17000 (“the Black Skull”) cranium from West Lake Turkana in Kenya can be interpreted as a challenge to Johanson and White’s phylogenetic hypothesis (Strait and Grine 1997). Initially named *Australopithecus boisei* (Walker et al. 1986), it was later subsumed into the species *Paranthropus aethiopicus* based on a unique combination of features that were in some ways primitive (*A. afarensis*-like: e.g., very small braincase and a prognathic, or jutting face, as opposed to the flat, “dished” face of *P. robustus* and *P. boisei*) and in others derived (*P. boisei*-like: “robust” features of the skull, including a wide face and a sagittal crest, a protrusion of bone along the midline of the skull). If *A. afarensis* was ancestral to *P. aethiopicus*, which was in turn ancestral to *P. boisei*, then *A. africanus* was freed from its phylogenetic position between *A. afarensis* and *Paranthropus*. An analysis of nasoalveolar (nasal and upper jaw) morphology also supports the monophyly (ancestral-descendant relationship) of all *Paranthropus* species to the exclusion of *A. africanus* (Villmoore and Kimbel 2011).

Multiple new species have been discovered and named throughout the 1990s and 2000s, falling geologically and phylogenetically on both sides of *A. afarensis*. White and colleagues discovered new crani dental and postcranial material at Aramis in Ethiopia and named a new species, *Australopithecus ramidus*, which was later transferred to a new genus, *Ardipithecus*, based on its distinct and more primitive traits. *Ardipithecus ramidus* is now known from a partial skeleton and a plethora of other specimens (White et al. 2009). Another new species, *Australopithecus anamensis*, is additionally thought to be more primitive and potentially ancestral to *A. afarensis*. Specimens later attributed to *A. anamensis* were initially discovered in the 1960s at Kanapoi in Kenya. New material discovered in the 1980s and 1990s, including both crani dental and postcranial fossils, led Meave Leakey and her team to name the species in 1995 (Leakey et al. 1995). White and his team working at Aramis and Asa Issie in Ethiopia discovered new material that they attributed to *A. anamensis*, including jaws and a femur

(White et al. 2006). *Ar. ramidus* and *A. anamensis* date to 4.4 and 4.2–3.9 Ma, respectively, and form what White and colleagues describe as an ancestor-descendant relationship (White et al. 2006). In South Africa, a nearly complete skeleton from Sterkfontein nicknamed “Little Foot” (StW 573) was recently re-dated to ~3.7 Ma (Granger et al. 2015); if correct, it represents the oldest material in South Africa and is contemporaneous with *A. afarensis*. Its discoverer, Ron Clarke, has resurrected Dart’s species name for *Australopithecus* material from the South African site of Makapansgat, *A. prometheus*.

Other new species, either contemporary with or post-dating *A. afarensis*, include *A. barelgazali* (Brunet et al. 1995) in Central Africa (Chad, 3.6 Ma), *A. garhi* (Asfaw et al. 1999) and *A. deyiremeda* (Haile-Selassie et al. 2015) in Ethiopia (2.5 and 3.4 Ma, respectively), and *A. sediba* (Berger et al. 2010) in South Africa. The latter species is the best known, represented by two partial skeletons from Malapa (Malapa Hominin 1, or MH1, and MH2, 2.0 Ma), along with additional material from multiple other individuals. Both *A. garhi* and *A. sediba* have been argued to be the sister taxon (most closely related and sharing an exclusive relationship) to the genus *Homo* but neither is universally supported. A third new taxon, *Kenyanthropus platyops* (“flat-faced man from Kenya”), was named by Meave Leakey and colleagues in 2001 and also proposed as a candidate for that phylogenetic position (Leakey et al. 2001). Represented by a nearly complete but damaged cranium from West Turkana (KNM-WT 40000), the cranium is argued to share derived traits with members of the genus *Homo*, including a flat face with a non-jutting jaw.

One major problem stems from the relative ambiguity of the genus designation and how to decide what defines a particular genus. Bernard Wood and Mark Collard (1999) suggested that the earliest members of the genus *Homo* (*H. habilis* and *H. rudolfensis*) should be transferred to the genus *Australopithecus* based on an adaptive zone model, where factors like body size, diet, and locomotion separate species into *Australopithecus*

and *Homo*. This requires both craniodental and postcranial fossils to assess, however, and adequate material is not available for most species. *A. sediba*, which is adequately preserved and argued to share derived traits of the skull, teeth, and postcranium with members of the genus *Homo*, retains relatively small body size and adaptations to climbing, so would be classified in *Australopithecus* under this system, whereas it might be subsumed in the genus *Homo* or placed in a new genus under a strict, cladistic (i.e., character and parsimony-based) analysis (Berger et al. 2010; Dembo et al. 2015).

Locomotion

One thing that is clear is that members of the *Australopithecus* group demonstrate unequivocal evidence for bipedal locomotion, unlike earlier potential members of the hominin lineage (e.g., *Sahelanthropus tchadensis*, *Orrorin tugenensis*, *Ardipithecus kadabba*). *A. anamensis*, *A. afarensis*, and *A. africanus* show derived features of the foot, knee, ankle, pelvis, spine, and cranial base consistent with adaptation to habitual bipedalism (Robinson 1972; Lovejoy 2005). These features include a non-grasping foot with an adducted hallux (in-line big toe) and a large calcaneus (heel bone), a flat ankle joint, a large plateau at the knee joint, valgus (inward) angle of the femora, short and curved blades of the pelvis, sigmoidal curvature of the vertebral column with both thoracic kyphosis (posterior curvature) and lumbar lordosis (anterior curvature), and an anteriorly positioned, horizontally angled foramen magnum (“big hole” at the base of the skull) through which the spinal cord passes. Additionally, the Laetoli footprints preserve trace fossil evidence of bipedalism in the probable hominin that made them, *A. afarensis* (Masao et al. 2016).

Much discussion has been devoted to the retention of primitive features in the postcranial skeleton of *A. afarensis* and its implications for climbing vs. terrestrial bipedalism in this species (see Ward 2002 for a review). Disagreement centers on the interpretation of these features as primitive, nonfunctional traits in a committed

terrestrial biped vs. retained adaptations to climbing. Suffice to say, it seems likely that *A. afarensis* was a committed terrestrial biped that could forage and take shelter in the trees (Ruff et al. 2016). Unexpectedly, *A. africanus* seems to be better adapted to climbing than *A. afarensis* (Berger 2002). This suggests that either *A. africanus* has become secondarily more arboreal or that it retains the primitive condition and *A. afarensis* is more derived toward terrestrial bipedalism, perhaps in convergence with later members of the genus *Homo*; recent work on early hominin calcaneal robusticity has been interpreted in support of the latter hypothesis (Prang 2015).

Brain Size, Body Size, and Sexual Dimorphism

The late Miocene putative hominin, *Sahelanthropus tchadensis*, and early Pliocene *Ar. ramidus* both have chimpanzee-sized brains, with cranial capacities ranging from 360 to 370 cc (cm^3) and 300 to 350 cc, respectively (Zollikofer et al. 2005; White et al. 2009) (chimpanzees average ~366 cc; Grabowski et al. 2016). Members of the *Australopithecus* group are characterized by an average cranial capacity of ~450 cc, ranging from ~400 to 500 cc (Falk et al. 2000). For comparison, early members of the genus *Homo* have slightly larger brains (624 cc in *H. habilis*, but as low as 509 cc; ~750 cc for early *H. erectus*, but as low as 546 cc) (Grabowski 2016); however, *H. floresiensis* and the recently discovered species *H. naledi* overlap with the australopiths (426 cc and 465–560 cc, respectively) (Berger et al. 2015; Grabowski et al. 2016).

Early hominins also vary in body size, again with overlap between australopiths and some members of the genus *Homo* (e.g., *Australopithecus* average ~32 kg; *H. habilis* average ~33 kg) (Grabowski et al. 2016). Relative brain size is probably more relevant than raw brain size because brain size and body size are evolutionarily correlated and therefore have coevolved (Grabowski 2016). When body size is taken into account and an encephalization quotient (EQ) is

calculated by comparing observed brain size relative to predicted brain size given regression estimates on body weight, the difference between chimpanzees (EQ = 2.4) and australopiths (e.g., *A. afarensis*, EQ = 3.2; *A. africanus* = 3.8; *A. sediba* = 3.9) becomes more pronounced, and members of the genus *Homo* (except *H. floresiensis*, EQ = 3.8) become more distinct from *Australopithecus* (e.g., *H. habilis*, EQ = 5.0; early *H. erectus* = 4.6; later *H. erectus* = 6.0; modern *H. sapiens* = 7.6 (Grabowski et al. 2016).

Sexual dimorphism, differences in morphology (size and shape) between sexes of a single species, can only be estimated for reasonably well-documented extinct species. *A. afarensis* meets this criterion, but researchers do not agree on the degree of sexual dimorphism in this taxon (see Reno and Lovejoy 2015 for a recent review and perspective on new material), although it is almost certainly greater than that observed in modern humans. Given this non-consensus and lack of a clear relationship between sexual dimorphism (in body size or canine size) and sociosexual system amongst primates, little can be said about australopith social groups at this time.

Tool Use

Darwin proposed that bipedalism evolved in the context of freeing of the hands for tool and weapon use; however, until recently, the oldest tools in the archaeological record (the Oldowan) were 2.6 Ma, greatly postdating the emergence of the hominin lineage and thought to be associated with either early *Homo* or *Paranthropus*. Newly discovered, more primitive stone tools from West Turkana, Kenya (Lomekwi 3), dated to 3.3 Ma (Harmand et al. 2015) suggest that earlier species of *Australopithecus*, or perhaps *K. platyops*, which was discovered nearby, were tool users. It is notable that bone tools may have been used by *P. robustus* for activities like digging (e.g., termite mounds; Backwell and d'Errico 2001); similarly, other non-stone materials such as wood and bamboo may have been used by early hominins but would be unlikely to preserve in the fossil record.

Conclusion

Australopiths are a group of Plio-Pleistocene hominins with a large temporal and geographic distribution, ranging over 3 million years (>4–1 Ma) throughout East and South Africa and into Central Africa. In addition to *Australopithecus*, other genera are often included in the group or even subsumed within *Australopithecus*, including *Paranthropus*, *Kenyanthropus*, and arguably *Ardipithecus*. The group is clearly paraphyletic, that is, it is not a natural group because at least some lineages are more closely related to the genus *Homo* (e.g., *K. platyops* or *A. sediba*). Future fossil and archaeological discoveries will undoubtedly both clarify and complicate our understanding of relationships amongst the *Australopithecus* group of hominins.

Cross-References

- [Ardipithecus Group](#)
- [Australopithecus africanus](#)
- [Australopithecus garhi](#)
- [Bipedal locomotion](#)
- [Homo floresiensis](#)
- [Homo habilis](#)
- [Homo heidelbergensis](#)
- [Homo neanderthalensis](#)
- [Homo rudolfensis](#)
- [Orrorin tugenensis](#)
- [Paranthropus aethiopicus](#)
- [Paranthropus boisei](#)
- [Paranthropus robustus](#)
- [Sexual Size Dimorphism](#)

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Australopithecus robustus

- [Paranthropus robustus](#)

Australopiths

- [Australopithecus Group](#)

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Autism

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A

Synonyms

[Autism spectrum disorder \(ASD\)](#)

Definition

Autism is classified as a neurodevelopmental disorder with three common characteristics: impairments in social functioning, impairments in communication, and restrictions in behavioral repertoire or repetitive behaviors. The definition of autism has changed over time and is still controversial. Currently, the DSM V calls for a diagnosis of “Autism Spectrum Disorder” (or ASD) for people who previously would have fallen into any of three categories in the DSM IV. Those categories included (a) autism, (b) Asperger’s Syndrome, and (c) Pervasive Developmental Disorder-Not Otherwise Specified.

Introduction

When the movie “Rain Man” came out in 1988, there was a scene in which a medical professional was so unfamiliar with the term that he assumed that Tom Cruise’s character Charlie Babbit had said “artistic.” Clearly, autism had not yet really penetrated the cultural consciousness. Since then, autism has been a topic of increasing interest to people in the areas of clinical psychology, behavioral therapy, governmental policy, behavioral genetics, and medicine. There has been a large push to understand the disorder and to improve the quality of life of people with autism spectrum disorders. To the cognitive and evolutionary psychologists, the study of autism has been an illuminating endeavor which is helping us to

understand the social functions of the typical and atypical brain. This entry briefly covers how autism is identified, how it has increased in prevalence, how it can help evolutionary and cognitive psychologists understand neural organization via theoretical models, and some current issues affecting the autism community today.

Identifying Autism

There is no single symptom that can be used to identify a person with autism, and the impairments are usually recognized as a somewhat idiosyncratic pattern within a person. No particular deficit associated with autism, be it social, communicative, or behavioral, is guaranteed to be clearly present in a given person with autism. Generally, the characteristics that are seen as typical in autism are not clearly or sharply demarcated from the behavior of neurotypical people, which often makes it difficult to identify whether a person is properly identified as having autism, or has more mild, autism-like social or communicative impairments.

Increasing Prevalence of Autism

In 1943, Leo Kanner was the first to describe autism as a distinct syndrome. It was referred to as “childhood schizophrenia” before being called “infantile autism” and then just “autism” before being replaced by “autism spectrum disorder.” Incidences of autism were quite rare for decades, and even by 1975 it was estimated that only 1 in 5000 individuals were diagnosed with autism. A great deal of attention has been paid to a so-called autism “epidemic,” since the number of diagnosed cases of autism have risen dramatically in the past few decades and rates currently stand at about 1 in 68 (Weintraub 2011). However, it is unclear that this indicates a difference over time in the actual rate of autism in the population. More individuals are being diagnosed thanks to looser diagnostic criteria, increased awareness and acceptance, and the presence of programs designed to help autistic individuals (Fombonne

2009; Wing and Potter 2002). While heredity certainly accounts for a great deal of the reason some people have autism while others don’t, the leftover environmental variance is largely unexplained. However, it is always important to note that vaccination, in any format or vaccination schedule, has failed to be linked in any way with autism (DeStefano et al. 2013).

Interest to Evolutionary Psychologists

Autism is of special interest to evolutionary psychologists because it highlights the modular nature of social cognition and its dissociation from other functions (including general intelligence). Asperger’s Syndrome, specifically, is a category of ASD in which development in communication is not delayed and general intelligence is often unimpaired. Nevertheless, the person with Asperger’s syndrome may report being confused and bewildered by the social world. While everyone else seems to know what to do based on subtle social cues contained in tone of voice, body language, or subtext, the person with autism is often oblivious to nonliteral messages and is unable to act in a way that someone might if they were intuitively responsive to those signals. Simon Baron-Cohen has termed this phenomenon “Mindblindness.”

Therefore, a person with autism who is intelligent and communicative can allow for a very revealing comparison to neurotypical populations. By comparing the tasks on which a person with autism is (and is not) impaired, psychologists can learn more about the modular structure of the neurotypical brain.

In general, people with autism show a deficit on traditional “false belief” tasks, where a participant is asked to predict what a person will do when that person is acting based on an untrue (or out-of-date) belief or assumption. Interestingly, this impairment seems to be specifically about the minds of others and not out-of-date information *per se*. In one task, Leslie and Thaiss (1992) demonstrated that children with autism performed on par with their neurotypical peers when predicting behavior based on an out-of-

date photograph. This led the researchers to the conclusion that there was something about the ability to appreciate representations *in the head* of other people that was specifically impaired in autism. The brain module responsible for such functions was later termed the “Theory of Mind Module” or ToMM.

If such a module exists, it is important to know what is included in the proper domain of that module. More recent evidence has indicated that people with autism do not necessarily struggle with interpreting eye gaze or appreciating the basic desires and intentions of others. However, more complex or “higher order” social calculations like interpreting more cryptic desires or reading an emotion from facial cues are likely to elude a person with autism.

Alternative Cognitive Models for Autism

In addition to theories that focus on the dysfunction of a module specifically for Theory of Mind, other researchers have proposed that at least some of the deficits observed in autism are the result of impaired executive function (Kenworthy et al. 2008), or perhaps a lack of ability to integrate sensory information into a cohesive view of the world (Happé and Frith 2006).

Current Issues

The search continues for environmental factors which contribute to cases of autism. Within the autism community, there is some disagreement regarding whether this search for a cause and cure is really the best use of resources, or whether the focus ought to be in helping those with autism lead the most productive and satisfying lives possible.

Conclusion

Autism (also known as “autism spectrum disorder”) is a diagnosis involving communication,

social, and behavioral deficits. Its origins are not well understood, nor are its causes. Autism awareness has grown immensely over the last few decades, as have rates of diagnosis, but it is as yet unclear whether this is because more people actually have the symptoms of autism, or whether awareness, acceptance, and changing diagnostic criteria are the reason why so many people meet the criteria for autism spectrum disorder.

Cross-References

- Evolutionary Psychiatry
- Executive Functioning
- False-Belief Test, The
- Mindblindness
- Simon Baron-Cohen (Darwinian Psychiatry)
- Theory of Mind

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Autism Spectrum Disorder

- ▶ Social Disabilities
 - ▶ Special Case: Autism
-

Autism Spectrum Disorder (ASD)

- ▶ Autism
-

Autistic Disorder

- ▶ Special Case: Autism
-

Autobiographical Memory

- ▶ Episodic Memory
-

Automatic Functioning

- ▶ Procedural Knowledge
-

Autonomic Nervous System

- ▶ Polyvagal Theory
-

Avenge

- ▶ Ability and Willingness of Victim to Retaliate
-

Aversion

- ▶ Universal Human Fears
-

Avian Clutch Size

- ▶ Bird Clutch Size
-

Avian Sperm Competition

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Synonyms

Post-copulatory sexual selection; Sperm competition in birds

Definition

Sperm competition arises when a single female mates with more than one male. In such cases, post-copulatory processes involving sperm-sperm competition may represent an important component of sexual selection.

Introduction

Social monogamy is the prevailing mating system among birds, with males sometimes providing a substantial proportion of parental care. Until quite recently, therefore, polyandry was believed to be rare or absent in birds. Over time, however, there were growing indications that genetic polyandry does indeed occur in birds. Evidence came from a range of sources, including behavior (female

pursuit for extra-pair copulations, direct observation of extra-pair copulations in the field, males guarding females during the fertile period) and/or sex-biased heritability of morphological traits or plumage coloration (Griffith et al. 2002). The advent of molecular tools for determining paternity has revolutionized our understanding of genetic mating systems in birds. It is now apparent that genetic polyandry is relatively common in this group.

Extra-pair Paternity in Birds

The first DNA-based molecular study on multiple paternity in a free-living organism focused on house sparrows (Wetton et al. 1987). Since the late 1980s, more than 30,000 offspring of around 200 avian species have been screened for paternity status. It soon became obvious that the risk of sperm competition (often measured as the level of extra-pair paternity; EPP) varies considerably among bird species. Despite being common in many populations, EPP is completely absent in at least 10% of avian species (Griffith et al. 2002). In a typical socially monogamous avian species, about 11% of offspring result from extra-pair behavior. It is worth noting that, although molecular determination of paternity helps assess the risk of sperm competition, this value may actually underestimate both the frequency of extra-pair copulation and the risk of sperm competition in avian populations as not all extra-pair copulations result in extra-pair fertilizations. Attempts to explain interspecific variation in EPP levels have identified phylogeny as an important factor determining the occurrence of EPP in birds. As an example, EPP appears to be comparatively common in passerines, a phylogenetic branch comprising more than half of all avian species, with the proportion of extra-pair offspring approaching 80% in some species (Griffith et al. 2002). Several other ecological (e.g., population density, migration status, latitude) or life-history correlates of EPP (often associated with phylogeny) have now been identified in birds.

Across species, the varying risk of sperm competition due to polyandrous mating by females is

associated with a number of morphological and behavioral adaptations. Although males generally lack external genitalia, in some groups (e.g., ducks and ratites) the phallus has evolved to transfer semen directly into the female reproductive tract. In songbirds, the cloacal protuberance (or promontory) appearing around male cloaca during the breeding season may provide a similar function. As in other groups, the size of the testes (measured during the breeding season) increases with increased levels of sperm competition across avian species, as does the proportion of sperm-producing seminal glomera within the testes (Birkhead 1998). These adaptations may provide an advantage over other males in terms of larger and more competitive ejaculates (particularly useful when sperm competition occurs). In general, ejaculates in highly promiscuous species (such as the polygynous Galliformes) are selected to be of high quality, whereas ejaculates in genetically monogamous species with relaxed or absent sperm competition (such as owls, falcons, or penguins) often contain a large proportion of abnormal or immature sperm. Mate guarding and frequent within-pair copulations are also typical of promiscuous avian species.

The morphology of the sperm itself is exposed to strong selection pressure after copulation. In birds, as in other internally fertilizing vertebrates, selection on sperm can occur through female choice ("cryptic female choice") or through male-male (sperm-sperm) competition. While the former remains little studied in birds due to obvious methodological issues, the latter has received much attention recently. There have been a number of studies on the evolutionary context of spermatozoa morphology and function in passerines, with results showing a positive association between extra-pair paternity, sperm speed, and sperm length across species (e.g., Kleven et al. 2009).

Female birds typically store sperm for some time (the duration often determined by the typical clutch size of the species) in sperm storage tubules (SSTs), located at the uterovaginal joint. For a given species, SSTs are typically three times longer than the sperm cell, indicating intimate coevolution between sperm length and SSTs (Birkhead

1998). As sperm must fit into the SSTs, balancing selection on sperm size should be stronger in species with a high risk of sperm competition. As a result, variation in sperm length around the species-specific sperm size optimum should be reduced. Indeed, there is a strong negative correlation between variation in sperm length across males of the species and typical EPP rate (risk of sperm competition) for the species, suggesting that this estimate can be used as a reasonable surrogate for sperm competition risk across passerine species (Albrecht et al. 2013).

Unfortunately, intraspecific studies are less convincing in identifying sperm traits associated with superior male fertilization success, although careful experimental studies have identified sperm length and velocity as traits affecting sperm fertilization performance in at least some species (Bennison et al. 2015). As mentioned above, female control over fertilization (cryptic female choice) remains a “black box” in studies of promiscuous mating systems in birds. A clear example of female control over fertilization has been demonstrated in waterfowl, however, where “cryptic anatomical mechanisms of choice” (dead-end sacs or fake vaginas) in females have evolved to control for the outcome of frequent forced copulations with unwilling males (Brennan et al. 2007).

One might ask how sexual promiscuity (sperm competition) evolved and how is it maintained in avian populations? The consensus is that EPP is adaptive for males in that, through promiscuous behavior, males may increase the number of sexual partners and their own fitness. The benefits of EPP to females are less obvious as an increase in the number of sexual partners typically has no effect on female fitness. Females may gain indirect benefits, however, in terms of high-quality offspring, which leaves open the possibility that EPP evolved to compensate for hasty or inaccurate choice of social mate. The potential indirect benefits of sperm competition in birds have been intensively studied over the past two decades, with mixed results and generally inconclusive evidence (e.g., Arnqvist and Kirkpatrick 2005).

On the other hand, promiscuous behavior also carries potential costs to one or both sexes. As an example, males may be able to reduce parental care in response to female infidelity, which could constitute strong selection pressure against female promiscuity (Arnqvist and Kirkpatrick 2005). Indeed, EPP is almost absent in avian clades where males are in largely responsible for food delivery to incubating females and growing offspring (e.g., in birds of prey or owls). Numerous other potential costs have been associated with promiscuous behavior, and these are reviewed in Forstmeier et al. (2014). This has led some to consider female promiscuity in birds to be a nonadaptive behavior evolving as a by-product of strong selection on promiscuous behavior in males (intersexual antagonistic pleiotropy or the “genetic constraint” hypothesis). Though a controversial idea, it has recently received solid experimental support (Forstmeier et al. 2011). Nevertheless, it remains difficult to explain why females in some species pursue extra-pair matings, despite the low strength of selection on male extra-pair paternity (contribution of EPP to overall male fitness) in these species. Despite intense research into this enigmatic behavior over the last three decades, there is still no general agreement as to whether promiscuity evolved as a male or female strategy in birds.

Conclusion

The risk of sperm competition varies substantially across avian species, making this group an ideal subject for studies on the evolution of behavioral, physiological, and morphological adaptations, as well as for assessing the potential benefits to female of genetic polyandry. Social monogamy is the prevailing mating system in birds and, from a sociobiological point of view, studies on the factors affecting postcopulatory processes in avian promiscuous systems could increase our understanding of human reproductive systems and behavior, particularly as most human cultures also promote social monogamy.

Cross-References

- Sperm Competition: Evidence in Nonhumans
- Insect Sperm Competition
- Non-Primate Mammal Sperm Competition
- Primate Sperm Competition
- Sperm Competition Theory

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Avoidance

- Facial Disfigurement

Avoiding Stigmatization

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Synonyms

- Ostracism; Rejection; Stereotypes

Definition

Humans have evolved strategies that helped them remove group members who hampered group efficiency. By labeling characteristics and behaviors, also known as stigmatizing, groups could identify and remove inefficient and undesirable group members. To avoid social rejection, our ancestors developed ways to avoid stigmatization.

Introduction

We all know him. The guy who wears unusual clothing, or maybe talks a little too loud. He gives innocent people dirty looks, leading others to reject him. Nobody wants to be “that guy.” No matter who it is, he has some characteristic that leads people to avoid or ignore him. People learn to identify this stigmatizing feature and, if they also have it, how to conceal it. Avoiding stigmatization helps people avoid numerous negative consequences, such as social rejection.

Stigmatization

In our evolutionary history, forming groups and lasting relationships gave our ancestors an upper

hand. By forming groups, our ancestors were able to rely on others for protection, resources, and reproductive needs (Kurzban and Leary 2001). Small groups provide tremendous advantages. However, as group numbers increase, so do the risks. Referring to living in groups, Alexander (1974) stated, “There are automatic and universal detriments, namely, increased intensity of competition for resources, including mates, and increased likelihood of disease and parasite transmission” (p. 328). To combat these threats, people need to identify inefficient and undesirable members in order to reduce the group to a manageable size.

The most desirable group is one in which group members equally contribute to shared goals. Those who do not contribute hurt the group and are viewed as a weak link (Turner 1982). To determine the weak links, a set of specific traits or characteristics are defined in order to segregate and remove those individuals. Anyone with that trait would be considered more of a cost than a benefit. This classification of individuals based on a characteristic is stigmatization (Kurzban and Leary 2001). Stigmatized characteristics can be based on whether an individual identifies with an outside group, such as racial, ethnic, or religious groups (Kurzban and Leary 2001).

The possession of a stigma informs group members that you lack the abilities required to perform the tasks necessary for group survival. Once marked, groups turn to denigration in order to look superior and force the lesser out (Turner 1982). In turn, the stigmatized individual will become rejected by the group. To avoid the stress and discrimination, stigmatized individuals will isolate themselves before rejection, only interacting with those in which they feel normal (Becker 1981). However, a stigmatization does not always mean instant rejection.

The amount of control a person has over a stigmatizing factor is correlated with negative attitudes and behaviors towards that individual (Mehta and Farina 1997). The more perceived control over the characteristic, the more the individual is discriminated against. For example, people often view obesity as something that people can control through diet and exercise. The

possibility of controlling one's weight adds to the ridicule and discrimination endured by obese individuals. Cancer patients, though stigmatized, do not face a similar fate due to the lack of control over developing the condition. Lack of control is not always a saving grace. The mentally ill and physically disabled are exceptions to that correlation (Mehta and Farina 1997).

Hiding Stigmas

Being linked to a stigma results in prejudice and discrimination (Kurzban and Leary 2001). To avoid ridicule and rejection, people try to hide the stigma. Some stigmas, like obesity, are difficult to hide. These individuals are forced to isolate themselves or attempt to cover their stigma to minimize the effects (Becker 1981). Once stigmatized, individuals will attempt to avoid further stigmatization. For example, because African Americans feel stigmatized, they show greater reluctance to seek medical attention for a stigmatizing medical condition (Anglin et al. 2006).

Some stigmas, however, are considered invisible. For example, some stigmas leave a psychological, rather than physical, mark on people, such as having a history of child abuse. An invisible stigma only becomes visible when people reveal it.

To try to keep stigmas invisible, there are three common tactics: counterfeiting, avoidance, and integration (Woods 1994). Counterfeiting involves pretending not to have the undesirable stigma. To make the cover story believable, individuals go to great lengths. For example, a diabetic child may eat and drink things that harm them in order to appear normal.

Counterfeiting involves creating a new identity. It also allows individuals to socialize with peers. On the other hand, avoidance entails telling half-truths, avoiding relevant topics, and censoring (Woods 1994). Though it is not an entirely new identity, individuals keep their distance from others, hiding their personal lives.

Both counterfeiting and avoidance shield people from being not being stigmatized, but they also come with consequences. Concealing a stigma

can lead to psychological strain, emotional stress, and stress-related illnesses (Smart and Wegner 2000). Fear and anxiety can increase these negative reactions (Smart and Wegner 2000).

The last tactic – integration – involves disclosing the stigma to peers. Disclosure can entail verbally informing everyone of the stigma, or even visually showing people the characteristic. For example, gay employees may tell their friends about their partner or bring their partner to work events. Though integration can provide relief, it also provides the risk associated with stigmatized people. That is, the reduction of stress through disclosure may lead to rejection. Because of these risks, individuals with invisible stigmas use varying strategies with different peers.

Controlling Stigmas

To avoid further stigmatization and rejection, people adapted the ability to control one's impulses, self-control (Baumeister et al. 2007). In a social interaction, controlling what one's says in order to hide their stigma requires a great deal of mental control. The stress and uncertainty of never knowing if your stigma will be discovered along with attempts to suppress negative stereotypes can be draining. For example, when African American students were primed with stigmatized thoughts, they showed lower self-control (Inzlicht et al. 2006). People placed in a stigmatizing situation for too long may become depleted, leading to poor self-control. Their poor self-control can lead to the discovery of their hidden stigma.

Conclusion

Nobody wants to be stigmatized. Being stigmatized can lead us to become socially rejected. Because we have a powerful need to belong, people evolved strategies to avoid stigmatization. Avoiding stigmatization is easier for some people than others. Visible stigmas often lead people to isolate themselves from the group, joining with others who make them

feel normal (Becker 1981). Stigmatized individuals will also do what it takes in order to avoid further stigmatization, even if it means avoiding doctor's visits (Anglin et al. 2006).

Other characteristics, such as AIDS or cancer, are easier to conceal. Though concealable, individuals are often left in a tough position. They risk rejection by disclosing it, but they also suffer from concealing their stigma. People avoid being stigmatized because they do not want to be rejected. Thus, we evolved the desire to avoid stigmatization.

Cross-References

- [Adaptations to Avoid Ostracism](#)
- [Stigmatization and Ostracism](#)

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Awareness

- ▶ Attention
- ▶ Attention and Memory
- ▶ Consciousness

Axons

- ▶ Early Stage of Brain Development at Birth