

Clever animals and killjoy explanations in comparative psychology

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From the process of organic evolution to the analysis of insect societies as self-organizing systems, biology is full of awe-inspiring examples of complexity arising from simplicity. Yet in the contemporary study of animal cognition, demonstrations that complex human-like behavior arises from simple mechanisms rather than from 'higher' processes, such as insight or theory of mind, are often seen as uninteresting and 'killjoy', almost a denial of mental continuity between other species and humans. At the same time, however, research elsewhere in psychology increasingly reveals an unexpected role in human behavior for simple, unconscious and sometimes irrational processes shared by other animals. Greater appreciation of such mechanisms in nonhuman species would contribute to a deeper, more truly comparative psychology.

Complexity from simplicity in biology and behavior

The extremes of higher-level traits may at first appear to have a life of their own, one too complex or fragile to be reduced to their basic elements and processes by deductive reasoning and experiment. But such separatist holism is in our opinion a delusion, the result of still insufficient knowledge about the working parts and processes.

Thus Holldobler and Wilson ([1] p. 60) on how the amazing construction of a perfectly air-conditioned termite nest is explained by the local responses of myriads of individuals. Incredible as it seems, there is no termite architect. Similarly, honeybee societies, schools of fish, and other group phenomena in animal behavior are increasingly well understood as self-organizing systems [2]. It is hard not to be in awe of how such complexities arise out of simplicity. The concluding paragraphs of *On the Origin of Species* [3] are eloquent expression of such an attitude toward organic evolution: "There is grandeur in this view of life" as the inevitable product of variation, selection and inheritance. But when it comes to clever-looking animal behaviors such as communicating, using tools, solving novel problems or preparing for the future, a contradictory attitude often prevails: explaining behaviors that seem to require human-like thought in terms of simple processes such as associative learning and species-typical predispositions is 'killjoy' [4], tantamount to denial of mental continuity between humans and other animals.

Justification for valuing anthropomorphic explanations of animal behavior can be traced to Darwin. Nowadays support for them is sometimes based on limited understanding of the alternatives offered by contemporary experimental psychology and ethology and on outdated folk psychology. Contemporary human social and cognitive psychology is revealing that folk psychology is often misleading, and the very sorts of simple, unconscious mechanisms that explain much animal behavior are more important in human behavior than intuition suggests. Consistent with this trend, comparative psychologists are beginning to appreciate that sweeping anthropomorphic questions such as 'Do animals have insight?' (Box 1) or 'Do animals count?' are best answered by dissecting broad abilities into elements, some of which are phylogenetically widespread, others confined to species with specific ecologies or evolutionary histories, and some perhaps unique to humans.

The evolution of comparative cognition

Interest in proving animals are clever in human-like ways goes back at least to Darwin. Chapters 2 and 3 of *The Descent of Man and Selection in Relation to Sex* [5] Darwin outline a program for comparing 'mental powers' of other species with those of humans that is still being carried out. Because proof that other species are mentally as well as physically similar to humans seems to be key evidence for evolutionary continuity between humans and other

Glossary

Anthropomorphism: The attribution of human qualities to other animals, usually with the implication it is done without sound justification.

Extinction: As a procedure, discontinuing reward for a previously rewarded (reinforced) behavior; as a phenomenon, the reduction in rate of the behavior subject to the extinction procedure.

Functional generalization: (also known as mediated generalization). This refers to the well-established finding [71] that events associated with the same response, stimulus or outcome come to be treated as equivalent. Functional or mediated generalization thus contrasts with stimulus generalization [72], in which cues are responded to in the same way if they are perceptually similar. Thus it is in effect a mechanism for classifying together perceptually dissimilar things.

Lloyd Morgan's Canon: Formulated by the early comparative psychologist C. Lloyd Morgan [7] and commonly taken as forbidding unsupported anthropomorphism or as a form of Ockham's Razor, this precept states, "In no case may we interpret an action as the outcome of the exercise of a higher psychological faculty if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale."

Scala naturae: The linear arrangement of animals from 'lower' to 'higher' or from less to more highly evolved. Although this is manifestly incorrect, in that evolutionary theory shows species are related as branches on a tree, the language of 'low' vs. 'high' is still too often used when meaning something like elementary and phylogenetically widespread vs. complex and confined to relatively few species.

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Box 1. Deconstructing insight

Recent studies of possible animal insight (e.g. [48,49]) revive a line of research dating from Thorndike [8] and Köhler [34]. In human problem solving, insight is equated with experience of an ‘aha moment’, suddenly ‘seeing’ a solution [50], but whether these solutions are arrived at by a process distinct from mental trial and error or analysis is still debated [22,23]. It is clear, however, that a problem is solved more readily after experience with its elements [23]. With animals, the most thorough analysis of how experience generates apparently insightful behavior is the famous demonstration [51] that pigeons can solve the same novel problem as Köhler’s [34] chimpanzees, by moving a box to reach a hanging (toy) banana. The birds that ‘insightfully’ solved the problem had been trained not only to climb and peck but also, in sessions without the banana, to push the box toward a spot at varying locations on the wall. They were also extinguished for jumping and flying toward the banana when the box was absent. When confronted with banana and displaced box, they first seemed confused, but then approached the box and pushed it toward the banana; to uninformed observers their behavior seemed human-like.

A basic principle of ethology is that significant cues in a situation can control incompatible behaviors, the relative strengths of which change dynamically with behavior. Here, when the pigeons first confronted the banana and the displaced box, ‘confused’ looking back

and forth expressed two learned behaviors that could not be completed. Because the birds had been extinguished for flying and jumping at the inaccessible banana, approach to the box soon predominated, followed by pushing. The banana became the target of pushing in the absence of the spot through functional generalization because both banana and spot had been associated with food. Finally, by pushing the box toward the banana, the ‘insightful’ pigeons produced the situation in which climbing was reinforced. Epstein [52] claims that such *interconnection*, combining old behaviors in new ways, underlies human and animal creativity.

Students of animal tool use are beginning to take Epstein’s claim seriously by deconstructing situations in which animals use tools in novel ways and examining the contributions of experiences with their elements. For example, New Caledonian crows given experience operating an apparatus by pecking or using a stick became more likely to operate a similar apparatus by dropping a stone onto it [53]. Related analyses have begun with string pulling [54] and metatool use [55,56]. The extent to which the solving of novel problems is entirely explained by this approach remains to be seen. For instance, it is a mystery what specific experience, if any, prompts a bird that has seen stones drop and release food to collect and bring stones itself [49,53,57]. Whatever the answer, one can only speculate about the ‘aha moments’ of crows and chimpanzees.

animals, Darwin’s supporters, as well as Darwin himself, were enthusiastic purveyors of anecdotes seeming to show that animals could think and solve problems as humans do [6]. The unsupported anthropomorphism characterizing many of these efforts soon stimulated a backlash: formulation of Lloyd Morgan’s Canon [7] and development of an experimental approach by Thorndike [8] and others. In studies of imitation, Thorndike showed how to test the behavioral implications of anthropomorphism by putting naïve chicks in a maze where they could either copy a trained demonstrator (imitation) or choose randomly (individual learning, the observed outcome). With this research together with demonstrations that behavior like opening latches that looks clever in human-like ways develops through trial and error learning, Thorndike helped drive anthropomorphic interpretations of animal behavior underground.

A century later they have resurfaced in an outpouring of studies directed toward demonstrating previously unsuspected human-like abilities in other species: episodic memory, creative manufacture and use of tools (Box 1), teaching, theory of mind (Box 2), planning (Box 3), empathy and so on (for comprehensive critical reviews see [9–12]). Much of this research is integrated in a more sophisticated way than in the past with evolutionary thinking and comparative neuroanatomy, ecology, human cognitive and developmental psychology, cognitive neuroscience, and other biological and cognitive sciences (see [10]). Much of it relies on scrupulous behavioral criteria for testing mentalistic predictions [13,14]. Nevertheless, although the extent of human–animal cognitive similarity is undoubtedly a key issue for comparative psychology, it sometimes seems the agenda is to support anthropomorphic interpretations rather than to pit them experimentally against well-defined alternatives. The enthusiasm of the popular and even scientific press for clever animal stories nourishes this tendency: killjoy explanations are less likely to make headlines than stories about how octopi or birds are unexpectedly human-like.

The label ‘killjoy’ originated in Dennett’s [4] analysis of levels of intentionality in cognitive ethology. In his principal example, a monkey’s alarm call might reflect wanting its fellows to move away, wanting them to know a predator

Box 2. Reading minds or only behavior?

Theory of mind is the understanding that other individuals have minds: beliefs, desires, intentions and so on. A creature with theory of mind represents behavior not simply as ‘He takes the apple’ but ‘He wants the apple’, ‘He intends to eat the apple’, or the like. Species tested for theory of mind include primarily chimpanzees but also dogs, food-storing birds, and others. The results are controversial [58,59,60]. Because inferences about another’s mental state are inevitably based on their behavior, a fundamental issue is how to distinguish reasoning about another’s mind from responding to behavioral cues alone.

Consider an example not usually discussed in this context. Breeding male songbirds learn who their neighbors are while fighting for territories in spring and later ignore them. But even then, a territorial male attacks if he hears a familiar neighbor’s song from an unaccustomed direction. This behavior is normally explained by sensitivity to cues of individual identity in species-specific songs, ability to memorize and associate them with spatial cues, and habituation to familiar song-location combinations [61]. But we can imagine a territory owner with theory of mind reasoning, ‘That neighbor is on the move and wants to take some of my territory.’ He might even represent the other’s theory of mind (higher-order intentionality): ‘I want him to know that I know he is trying to take over and I will fight.’ Such anthropomorphisms might seem plausible for apes on the *assumption* their minds are human-like, but arguably no data yet collected demand them [58]. Explaining, for instance, why chimpanzees or corvids treat an individual who saw food being hidden as a competitor [58,59] requires discriminative and learning abilities qualitatively no different from those of the songbirds in our example.

In studies training animals to use artificial cues such as human gestures, transfer tests with novel cues are used to distinguish inferences about human knowledge or intentions from learned responses to specific cues. Because such tests provide opportunity to learn about the new cues, conclusions must be based on the first such trial [60,62]. But even these data could be as consistent with generalization over behavioral cues as with theory of mind [58]. All the same issues bedevil studies with young children [63]. An important new proposal [39] is that human adults use both a quick, efficient ‘behavior reading’ system shared with other species and a more cognitively demanding, gradually developing, theory of mind.

Box 3. Do animals have representations of the future?

Rather than being dismissed out of hand as untestable, the claim that animals do not travel mentally into the future and hence do not plan as humans do [64] led to a rash of attempts to prove the contrary (see [37,65]). With the related phenomenon of episodic memory or 'backward time travel', established paradigms for humans have been adapted for animals [36], but in the absence of comparable research on human planning, experiments with animals often seem guided by a folk psychology of what behavioral evidence for imagining the future looks like. For example, if apes only occasionally save a tool for future use [66], are they planning? Criteria for acceptable evidence are still evolving [65,67], encouraging an occasional return to the anthropomorphism and single-subject anecdotes of the late 19th century. For example, the chimpanzee in a zoo who piled up stones in the closed hours and threw them at spectators when the zoo was open is said to plan [68]. But, among other reasons, because the piles of stones were apparently not documented until after stone-throwing became a problem for the zoo keepers, it is not entirely clear that gathering stones was done in anticipation of throwing them [65].

Another difficulty with demonstrating future planning is that, much as termites construct elaborate nests without knowing what they are doing, most animals are superbly equipped with mechanisms, from associative learning to innate programs for migration, that allow them to prepare for the future without representing the future as such [69]. Thus although recent research has uncovered fascinating new examples of future-oriented behaviors, it is debatable whether any depend on future time travel [10,65].

is approaching, or even higher levels of intentionality. In support of Griffin's [15] proposals for a cognitive ethology concerned with such processes, Dennett argued that these 'exciting' possibilities can be distinguished experimentally from the killjoy alternative: the sight of a predator reflexively elicits calling. Dennett's analysis helped encourage ethologists to join experimental psychologists (e.g. [16]) in bringing the cognitive revolution to animal behavior. However, using behavior as a window onto the mind does not mean forgetting the lessons of Tinbergen and Skinner about the importance of species-typical predispositions, past history, and present cues in controlling it. For example, using theory of mind implies responding to observable cues of eye gaze, companion's identity and the like, and a test with novel cues is necessarily a learning trial (Box 2).

Darwin upside down

The tendency in comparative cognition to emphasize the human-like in animals is curiously out of step with an important trend in cognitive and social psychology toward uncovering what is essentially the animal-like in humans. Of course emphasis on the elementary processes we share with other species is entirely Darwinian, the topic of Darwin's great book on human behavior, *The Expression of the Emotions in Man and Animals* [17], on the evolutionary roots of human emotional expressions. Contemporary research tracing the origins and functions of social and emotional responses (e.g. [18]) is connected with a wide-ranging literature showing that, more often than is commonly acknowledged, human behavior expresses unconscious responses to simple cues similar to those that influence other species. In effect, 'anthropomorphic' explanations are not always correct even for humans. "Classical" evolutionary psychology provides many examples. Broad shoulders in men and the waist-to-hip

ratio in women can influence mate choice much as loud songs, bright plumage and other sign stimuli influence mate choice in other species [19]. In an example of unconscious response to other simple social cues, when images of eyes 'watched' the box for contributions to a coffee pool (kitty), average payments more than doubled over weeks with flower images [20]. And as further possible evidence that the reasons for our behavior are not always what intuition suggests [21], not all researchers agree that an "aha" experience (Box 1) is indicative of a special insight mechanism, different from routine problem-solving [22,23].

In memory and decision-making, implicit memory and automatic processing of some fundamental information [24] are already well studied. Other unconscious processes lead to more 'animal-like', less rational outcomes; examples include preference for immediacy and other irrational biases in economic decision making, arguably expressions of species-general evolved predispositions [25]. As another example, presented appropriately, abstract transitive inference problems are solved by human subjects in the 'stupid' associative way typical of pigeons [26]. Similar evidence that characteristically human ways of problem solving and conceptualization exist in parallel with processes shared with other species occur in same-different categorization. Baboons classifying arrays of images respond 'different' more often the more different images an array contains. For human subjects, a single discrepant image in an array makes it 'different'. But although humans classify the arrays categorically, the arguably more primitive continuous process shown by the baboons is evident in their latencies [27].

Recent comparative research also shows that some simple processes demonstrated first in nonhuman species can be revealed in humans with nonverbal tests. For instance, the propensity of disoriented rats to reorient using the geometry of surrounding space is shared not only with birds, fish, ants and monkeys, but also with young children and, under appropriate conditions, adults [28]. These findings, together with increasing understanding of other elementary spatial processes in animals, support suggestions that in human spatial cognition insights from animals should replace the anthropomorphic concept of the cognitive map [10,29]. In numerical cognition, the question 'do animals count?' has been replaced by analysis of component processes including fuzzy discrimination among numerosities that follows Weber's Law [10,30]. The signature pattern of data for this process is found not only in nonhumans and human babies but also in human adults prevented from verbal counting (e.g. [31]) or with limited number language [32]. Laboratory tests of chimpanzees' tool use have inspired parallel tests with humans, with some results that undermine the folk psychological assumption of rational human tool behavior against which chimpanzees' failures have been measured. For instance, people avoid choosing a rake-like tool for pulling in a reward if the reward will pass near a hole, even if it will not fall in [33]. Subjects who know the difference between connection and contact nevertheless select a rope that merely contacts a reward, a choice reminiscent of errors made by Köhler's [34] apes [35].

Concluding remarks

Darwin's argument for mental continuity cuts both ways. Recent arguments in comparative cognition for the human in other animals and evidence for the 'animal' in humans elsewhere in psychology converge in showing that in mental life, as in other things, people and other animals share many characters. Appreciation of the interplay of shared and unique characters is increasingly evident in analyses of specific capacities such as numerical cognition [30], episodic memory [36], planning [37], theory of mind [38,39], category learning [27], and other-regarding behavior [40,41] into behavioral and sometimes neural components, some of which are phylogenetically widespread. This 'bottom up' approach [10,42] also helps pinpoint the domains in which humans could be unique [12]. An outstandingly successful example of this approach is the study of language evolution, in which the old question, 'Can animals learn language?' has been replaced by appreciation that although human language is just that, *human*, other species share important components of it. For instance, highly social primates may have evolved hierarchical conceptual abilities contributing to language, and neural and developmental control of songbirds' vocal learning is instructively analogous to that of humans [43,44].

The deconstruction of 'insight' in Box 1 is both killjoy and illustrative of the power of elementary mechanisms to explain apparently complex behavior. Historically, Morgan's Canon [7] dictated favoring such accounts over those invoking 'higher' processes. In the 21st century, its *scala naturae* assumption of linear evolution has been replaced by an understanding that 'lower' processes are those basic phylogenetically general processes of memory and learning present even in snails and fruit flies [45,46]. In any case, however labeled, no sort of explanation of behavior should be accepted without good evidence [46,47], and good evidence comes only from imaginative, well-informed, and rigorous formulation and testing of alternatives [14].

A century ago, Thorndike showed how to replace anecdotalism with experiments, and although the appeal of explaining 'clever' behavior anthropomorphically without strong evidence has hardly diminished in the meanwhile,

understanding of the simple kinds of mechanisms first studied by Thorndike has increased immeasurably. At the same time, as sketched here, students of human psychology are increasingly appreciating the role of simple nonverbal processes unlike those assumed in folk psychology in controlling our own behavior. To quote the passage at the beginning of this article, modern "knowledge about the working parts and processes" of complex animal behavior could be converging with new conceptions of the processes in human cognition to replace outmoded controversies with a more deeply comparative cognitive science (Box 4).

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Box 4. Questions for the future

- What are the limits to explaining complex human-like behavior in terms of elementary phylogenetically widespread processes? Some have proposed (e.g. [70]) that apes (at least) are so similar to us that evolutionary thinking justifies the assumption that their behavior can be explained anthropomorphically unless proven otherwise. Is this ever correct?
- To what extent can the sorts of simple unconscious processes in human behavior discussed in the main text be identified with processes shown by other species?
- Numerical cognition and theory of mind are mentioned as areas in which integration of comparative and developmental research indicates that elementary nonverbal abilities shared with other species exist in humans alongside later-developing, more cognitively complex, capacities. To what extent does this view of human cognitive architecture apply in other domains?
- Will the high level of interdisciplinary communication and theoretical integration now characteristic of areas such as numerical and spatial cognition and language evolution develop and become productive in other areas?

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