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Social scripts as drivers of primate cooperation

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QUESTION

Why do primates help non-relatives?

ABSTRACT

Humans have a reputation for being 'hyper-cooperative', as they occasionally behave altruistically when they should not, for instance when helping strangers with no prospect of reciprocity or reputational benefits. Although intriguing, human behaviour is also accountable to evolutionary theory, which predicts that altruism is only adaptive if it benefits close genetic relatives. One way to explain maladaptive helping is that humans and primates experience reality to various degrees as part of social scripts - mental representations of how social events normally unfold. As a consequence, decisions about helping are no longer about kinship but about anticipating the cooperation enforcement strategies of others, particularly negative reciprocity. Social scripts thus extract altruism from the evolutionary confines of kin-biased helping to enable non-kin cooperation with all its partner-control mechanisms. A review of the primate literature suggests that social script theory may explain the often inconsistent results in great ape prosociality experiments as well as puzzling findings of altruism towards non-relatives in the wild. Cognition may enable humans and some animals to behave altruistically towards non-relatives because social scripts make them perceive the need of others as a cooperation problem.

Keywords: cognition, evolution, primates, altruistic behaviours, cooperation, social scripts

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INTRODUCTION

Humans are extraordinary primates. Over the last million years, average brain sizes nearly tripled [1], which caused unprecedented cultural progress and a massive, ongoing population expansion. Larger brains undoubtedly permit more complex cognition, which is particularly useful in the social domain with its constant altercations between competition and cooperation [2]. Indeed, humans cooperate in virtually all aspects of life, both dyadically and polyadically, and regardless of whether interactions are with kin, friends or strangers [3]. Moreover, the behavioural economics literature is full of examples where humans act irrationally altruistic, for instance, by being overly generous to anonymous partners from whom they can never expect any reciprocity [4]. This has led to the conclusion that humans have evolved an ability to be 'hyper-cooperative' [5], as if somehow having evaded the confines of the laws of fitness and evolutionary theory more generally. Another relevant issue is that cooperation and altruism are common in species that do not have large brains [6], to the effect that the relationship between complex cognition and cooperation has remained obscure.

The argument here is that brain expansion endowed humans with a qualitatively different way of representing reality, with profound implications for the ability to cooperate. Humans do not appear to perceive real-life events in simple terms of agents acting in the here-and-now (as prevalent in animals [7][8]), but in terms of events belonging to larger social scripts, which prescribe how events can and cannot unfold in the future [9]. A key element of social script theory is that, in any given situation, the number of possible developments is rather limited, which simplifies the decision space for individuals in their trying to maximise positive outcomes. Perceiving events as belonging to social scripts allows humans and possibly other animals to use their altruistic propensities, evolved to unilaterally help relatives, for bilateral cooperative endeavours. This is particularly likely in species that have evolved cooperation via partner control, i.e., social systems in which individuals repeatedly interact with each other with an ability to remember past events. In such cases, individuals can no longer

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rely on simple situation-specific payoffs when taking social decisions, but need to take into account the ongoing social script of which the ongoing event is part of, as well as the consequences of cooperating or defecting. Since social scripts are broad they will occasionally lead to irrational decisions, in the sense that they are at odds with evolutionary theory, especially when participants interact in artificial settings, for which they do not have a social script available and therefore need to revert to neighbouring scripts.

In the following, the evolutionary theory of helping is reviewed and linked to recent empirical work on primate cooperation. The overall goal is to identify cases where primates behave in evolutionarily maladaptive ways, for instance by acting prosocially when they should not, to explore the hypothesis that non-human primates may operate with social scripts, as suggested for humans [9]. The prediction is that species vary in the complexity of their social scripts (in particular how ongoing events are perceived as having future consequences) and that reliance on scripts will sometimes lead to decisions that go against optimal payoffs of the moment.

Evolution of helping

Cooperation and altruism are challenges for evolutionary theory. Why should an organism devote time and resources to help another rather than pursuing its own selfish goals? Yet, helping is widespread in the living world, distinguishable as either altruistic or cooperative [10]. It is important to keep in mind that terms such as cooperation, altruism or mutualism have been used with different meanings, with no agreed terminology. Here, mutualism is reserved for interspecies interactions (not reviewed), whereas the term altruism is used in a restricted indirect fitness sense, i.e., as unilateral costly helping [10] in contrast to, for example, Trivers [11], who used the term for any kind of helping, both unilateral and reciprocal.

Altruistic helping

Altruistic helping is here defined as having negative direct fitness consequences for the altruist, suggesting it can only evolve if it has positive direct fitness consequences

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for a genetic relative, which results in indirect fitness benefits for the altruist, according to Hamilton's rule [12]. Parental behaviour is the classic example, with biological parents willing to risk their lives to protect their offspring [13]. Altruistic helping bestows the genotype as the future beneficiary, which can also include kin groups, as per 'modern' multilevel group selection models [14]. Like many species, primates live in social groups with closed memberships, which leads to elevated levels of within-group relatedness, a possible facilitator for the evolution of (low-cost) altruistic behaviour, beyond what is seen in parent-offspring interactions. For example, chimpanzees and bonobos live in male philopatry, which has been linked to higher within- than between-group male relatedness [15][16]. However, helping behaviour in primates is unlikely caused by kin selection alone, as genetic relatedness is generally low [17].

Altruistic helping is psychologically interesting because it presumably requires an ability to recognise genetic relatives and also a motivation to help when help is necessary. Some form of kin recognition is therefore needed, either directly via phenotypic markers or, probably more common in mammals, via bonds amongst maternal kin [18]. Indeed, male chimpanzees prefer to cooperate with their maternal brothers (which may thus qualify as altruistic helping), but they also maintain cooperative relationships with unrelated males, which require other explanations [19].

In terms of the underlying motivation, an interesting candidate mechanism is empathy, a state-matching operation that ranges in scope and complexity across animals, with possibly deep phylogenetic roots [20]. In humans, empathy involves understanding how others feel and a concern for their welfare. Empathy has been addressed with research on 'prosociality', defined as "…behaviours that are intended to benefit others" (as opposed to unintended by-products of selfish pursuits) [21], a definition that is challenging by presupposing intention [22][23]. Apart from this, most researchers work under the assumption that prosociality emerges from empathy. In humans, prosocial behaviour is linked to measurable physiological reactions and emotional experiences of happiness or gratitude [24][25]. Similarly, Hepach et al. [26] found that chimpanzees who helped a conspecific to obtain food had decreased pupil diameter soon after they had helped, while watching third party provide the needed

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help had no effect, unlike in children. Interestingly, as noted by [21], the ability to empathise also appears to be responsible for negative, antisocial sentiments, such as jealousy or malicious joy, both aimed at decreasing the welfare of others [27], suggesting that empathy is more basic than an evolved mechanism for helping.

Cooperative helping

Voluntary vs enforced cooperative helping

Helping amongst unrelated individuals is in accordance with evolutionary theory if it somehow concurs a positive direct fitness outcome for the helper, which can either be unenforced ('win-win situations') or enforced by means of a partner control mechanism. Examples for unenforced cooperation are cooperative hunting, group travel or mutual grooming in chimpanzees, which confers direct benefits to all participants, provided their momentary priorities are compatible. But more often than not, cooperation does not come naturally because helping only benefits one participant, either due to the nature of the task or due to other incompatibilities. In such situation, cooperation is only possible if it can be enforced, either by increasing the benefits of cooperating (positive direct reciprocity) or, perhaps more commonly, by increasing the costs of not cooperating (negative direct reciprocity). The key point is that, whenever cooperation is not intrinsically beneficial for both, the helper must deploy an enforcement strategy to keep the partner from defecting [28].

Enforced cooperative helping via positive or negative direct reciprocity

Direct reciprocity has been interpreted as a first form of enforced cooperation, which can be either positive ("I help you, so you help me") or negative ("I aggress you, so you help me"). For both forms, an individual's social interactions with another are embedded in prior history, such that social interactions become endowments that can or cannot be reciprocated. Direct reciprocity requires partners to keep track of past events in order to reciprocate by helping (positive direct reciprocity) or increasing the costs for not cooperating (negative direct reciprocity).

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'Friendships' (social bonds) have been interpreted as a form of positive direct reciprocity, a kind of 'social insurance'. Here, it often looks like friends are 'trading' services, such as grooming for tolerance during feeding or support during aggression (e.g. [29][30][31][32]). In bottle-nosed dolphins, for example, social bonds are the best predictor for future dyadic cooperation ('first-order alliances'), irrespective of kin relations [33], suggesting that social bonds - and the trust and tolerance that emanates from them - operate as facilitators of cooperation. It may be important to consider that what is interpreted as 'friendships' is little more than social tolerance. If an animal requires help, it may be more likely to persuade someone nearby (i.e., individuals with a benign attitude) than other group members (who would respond in the same way, but are not nearest neighbours). Also, 'true' friendship by reciprocity would require a tracking or accounting mechanism, beyond the predictions of basic tolerance and proximity. Another key prediction for true reciprocity is that individuals should adjust their efforts in maintaining social bonds depending on a partner's record in cooperative acts. Whether such book-keeping takes place in animals has largely remained unclear and important topic for future research.

Regarding negative direct reciprocity an interesting example is aggressive responses to individuals that fail to cooperate (i.e., retaliatory aggression or 'punishment'; [34]). Food calls are a particularly interesting example, produced in relation to feeding opportunities [35]. Here, it has been claimed that rhesus macaques that failed to produce calls when encountering food attract aggression from others, an apparent example of negative direct reciprocity [36][37]. In chimpanzees, food calls are also produced when individuals find food but also in response to others' arriving at food trees, particularly to high-ranking or aggressively motivated individuals [38][39]. Again, such behaviour is consistent with the interpretation that food calls are part of enforced cooperation via negative direct reciprocity, i.e., concerns about retaliatory aggression when failing to announce the location of food (i.e., not being cooperative). Retaliatory aggression may be a driver of cooperation in non-related animals, although this strategy is obviously only available to dominant individuals. Here, more targeted research is needed to investigate the distribution of retaliatory aggression in natural situations.

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Enforced cooperative helping via positive or negative indirect reciprocity

In group-living animals, social interactions almost always take place in front of audiences. Bystanders observe others' social interactions and, if they can remember content and outcome, this may add another feature by which to classify partners as 'cooperative' or 'selfish' [40] in addition to standard social categories, such as kinship [41], rank [42] or friendship [43].

For cooperative activities, the two main possibilities of altering an individual's reputation are by 'image scoring' [44] or judgments of 'good standing' (standing strategies: [45][46]). Image scoring is said to be cognitively less demanding, as each helpful act simply adds a point to the co-operator's image, whereas each deceitful act removes a point. In contrast, standing strategies are more complex as scoring is partner-dependent. For example, if a co-operator interacts with a defector, then failing to help is considered the right response, which raises the co-operator's standing as much as when a co-operator helps another co-operator. In sum, 'good standing' reputation not only depends on the act but also on the recipient, whereas 'image scoring' only depends on the act [47].

There is evidence that chimpanzees and other animals indeed assess each other in terms of cooperative/selfish proclivities, although this appears to be mainly based on personal experience (direct reciprocity) and not from observing third-party interactions (indirect reciprocity). In particular, Schmelz et al. [48] found evidence for preferences for prosocial individuals but only from direct reciprocity interactions and not from general (indirect) reciprocity. Generally, the topic is not so well researched in animals, apart from work on cleaner fish [6].

Humans evidently care much about their reputation and may even engage in proactive 'reputation-building', by actively displaying their cooperative inclinations in front of others, in order to confer an image of a valuable community member, a form of indirect reciprocity [44]. Importantly, however, the term 'reputation' has a limited meaning in the cooperation literature, confined to helping behaviour. But humans care much about their own and other's reputation in all sorts of social domains (courage, knowledge, reproduction), as evident from the spread of social media platforms. Hence, reputation building may have more to do with displaying one's social style, with more general goal of establishing a social network compatible with one's personality and current situation.

When interacting with third-party individuals, a distinction is also made between positive indirect reciprocity ("I help you so somebody helps me") and negative indirect reciprocity ("I aggress you so you will help somebody"). Negative indirect reciprocity has attracted attention because of its relevance in human societal functioning, i.e., cases where individuals aggress others who behave antisocially (third-party punishment), despite the fact that this generates only costs, with no obvious benefits. Such examples of 'policing', defined as impartial interventions by bystanders, have also been found in monkeys and apes [49] although it may have to be interpreted differently. In chimpanzees, a dramatic example is males interfering during female-led infanticide [50], but policing is typically seen in high-ranking individuals who may have selfish reasons to maintain social stability, without any human-like community concern or group-mindedness [51], in which case it might be better classified as (non-enforced) direct reciprocity.

The prosociality conundrum

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Prosociality research in animals has been inspired by behavioural economics, which finds that humans can be irrationally generous, showing patterns of helping beyond what is expected by evolutionary theory [52], for example by giving money to complete strangers without prospect of reciprocity or implications for their reputation, which has led to the hypothesis that humans are 'hyper-cooperative' [53]. In many ways, this is counter-intuitive conclusion as it presumes that humans are somehow exempt from the laws of evolution.

To study prosocial behaviour in animals, some version of the Dictator Game is often used [4][52][54], for instance by letting subjects operate a food dispenser that can deliver food to the subject only (selfish), the partner only (prosocial-altruistic) or to the subject and partner simultaneously (prosocial-cooperative). In an early study [55], chimpanzees did not deliver food to others, despite no extra costs. But when food was replaced with tokens chimpanzees showed a significant bias for the prosocial option, interestingly even without solicitation (i.e., without enforcement [56]). One explanation for these opposing findings is that food elicits a powerful competitive response in chimpanzees, which may impede further social decisions [57]. Interestingly, bonobos easily transferred food, but not non-food items, suggesting important species difference in how cooperation problems are perceived [58].

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When chimpanzees are allowed to interact repeatedly, patterns changed insofar as subjects made significantly more prosocial choices after receiving their partner's assistance than when no assistance was given, particularly if the partners assistance was costly and even if the prosocial option was costly to them [59]. Similar evidence for some form of book-keeping is available for capuchins, whose prosocial choices increased when both partners alternated making choices, although no contingency could be detected between an individual's choice and their partner's previous choice [60]. In a recent study [61], helping consisted of tool transfers, which was either altruistic (no benefit for the helper) or cooperative (food reward for the helper). Here, altruistic tool transfers was observed in chimpanzees, but only in one mother-offspring pair, in line with kin selection theory. In bonobos, however, both altruistic and cooperative transfers occurred consistently, but only in female-female and never male-female dyads, with no added effect of receiver behaviour in either species.

These overall inconsistent findings suggest that additional unknown psychological factors are at work and have yet to be discovered. A first issue is whether subjects really understood the nature of the tasks. For some studies, this was confirmed (e.g., tool transfers in chimpanzees [62]. However, Tennie et al. [63] targued that chimpanzees were as likely to help a recipient getting as preventing to get food, concluding that prosocial responses were meaningless by-products of specific task features, an interpretation not generally accepted [64]. The issue of task comprehension has recently been raised again in a comparative study between children and chimpanzees [65]. When helpers knew that the requesting help was ineffective, children ignored the request and gave what was needed, whereas chimpanzees gave what was requested, suggesting that chimpanzees simply respond to enforcement, rather than understand what was required to actively help.

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What can be concluded about animal prosociality? Laboratory experiments have shown that unrelated bonobos and chimpanzees help others by giving objects to recipients, opening locked doors for others and releasing rewards. Evolutionarily speaking individuals should only be altruistic in interactions with close genetic relatives, whereas with non-relatives, prosocial behaviour should occur only in response to some form of partner control. In chimpanzees, prosocial behaviour emerges mainly in response to recipients' signalling (i.e., a form of partner control), in line with evolutionary theory, but bonobos have also been observed to help without enforcement [66], raising questions about other mechanisms.

Cooperation as a process

In natural conditions, animals and humans navigate through daily life in pursuit of their selfish goals, occasionally encountering situations that are best solved with cooperation or altruistic helping. The range of problems is wide, from helping individuals in danger, engaging in joint cooperative activities or initiating group-level collective actions. In some instances, collaborations are natural because both partners gain net benefits, although this may vary depending on circumstances. A useful experiment here, if it has not already been done, would be to monitor partner choice and enforcement behaviour depending on the partner's current activity. The prediction is that individuals who do nothing should be preferred over others who are engaged in self-serving or other cooperative activities.

For interactions with non-relatives, partners should be vetted in terms of their previous records and susceptibility to partner control, such as solicitation or retaliatory aggression, such that the payoff is favourable for both partners. Once cooperation has been initiated, it may need to be maintained because payoff matrices can change throughout cooperative interactions, requiring further enforcement (e.g. [67]). Finally, cooperative interactions have to be terminated, so that both partners understand that they are released from each other, in way that it makes future cooperation still possible (for a recent series of studies see [68][69][70][71][72]).

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Why are humans hyper-cooperative?

Melis & Semmann [73] argue that humans, in contrast to animals, employ a wider range of enforcement mechanisms, which allow higher levels of cooperation to evolve, both amongst unrelated individuals and in large groups. However, several of the studies reviewed here did not report any such evidence. In prosocial experiments, individuals should only altruistically help genetic relatives or, when with non-relatives, in response to partner control mechanisms, such as soliciting or past help. For instance, in the Horner et al. [56] study chimpanzees operated with tokens linked to selfish or prosocial outcomes, which led to a significant prosocial bias, without any sign of enforcing solicitation, something also shown for bonobos [61][66]. According to theory, such results should not occur although it is always possible that researchers overlooked subtle solicitation behaviour or they did not collect relevant social data before the experiment, i.e., may have missed evidence for negative or positive direct reciprocity.

Script theory offers an alternative explanation and may resolve some of the inconsistencies in the primate data. The fact that great apes occasionally behave prosocially when they should not, may be due to the fact that some experiments have obtained script character or became incorporated into already existing scripts. For instance, over trials and over experiments subjects may have learned something about the longer-term social consequences of behaving prosocially (or antisocially). Here, the predictions are clear: when subjects are unfamiliar with a task and its social ramifications, i.e., in the early parts of an experiment, selfish choices should prevail and then gradually be replaced by prosocial alternatives.

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Social scripts are not just learned associations; they consist of generalised knowledge of how events unfold, their internal causal structure and their serial alignments. Hence, subjects may have understood to integrate their social experiences during an experiment into pre-existing social scripts. For instance, in the Nolte & Call [61] study, female dyads (but not male-female dyads) acted consistently prosocial, suggesting that the females had already been engaged with each other in cooperative interactions and simply learned to integrate the constrained interactions available during the experiment. Also relevant are the findings of the Hepach et al. [65] study, showing that chimpanzees did not show evidence of what their partner needed, but simply complied to their requests, suggesting that their social scripts, if they had any, did not convey the key component of the task designed by the experimenters.

As mentioned at the beginning, humans often behave irrationally generous when taking economic decisions, beyond what is predicted by evolutionary theory [52] [53]. It is likely that such cases of hyper-cooperation and maladaptive altruism are the results of well-rehearsed social scripts used in daily interactions and simply imported into the unfamiliar situations of the experiments. When moved to laboratory conditions and faced with cooperative/competitive choices, subjects may have activated the nearest available script, which then produced seemingly maladaptive outcomes (such as giving money to strangers, i.e., out of a sense of fairness). Under natural conditions, however, such behaviour is usually adaptive, as people interact within the reality of cooperative enforcement strategies.

More difficult to explain are cases of third-party punishment - costly to the actor with no obvious benefit. But here again it is imaginable that subjects, when faced with antisocial behaviour, activate the more common cooperative alternative and act in response to the perceived discrepancy. Partly, this may be the result of proactive socialisation during infancy, common across human societies, which in adulthood remains as social scripts which hold a promise of a better society free from antisocial behaviour, something that is unlikely very relevant for non-human primates, including great apes.

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In conclusion, the evolution of effective enforcement strategies, mainly direct negative and positive reciprocity, combined with powerful social cognition, allowing humans to anticipate future outcomes of their current decisions, may have moved helping behaviour, originally evolved to benefit relatives, into the general arena of social behaviour. With bigger brains came better representational abilities, allowing humans to maintain more complex social scripts to make better decisions about whether or whom to help.

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