

Extent and limits of cooperation in animals

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Individuals in many animal species are strongly motivated to form close social bonds and to attend to the social interactions of others. Some animals may also recognize other individuals' intentions and simple mental states. Such curiosity appears to be adaptive, because it enables observers to learn about others' status and relationships and to anticipate future events without direct participation. However, many questions remain unresolved. In particular, it remains unclear whether animals keep track of favors given and received when interacting with others, and whether they rely on memory of past cooperative acts when anticipating future ones. Primates appear to possess many of the cognitive abilities required for human-like contingent cooperation. However, most investigations of captive primates have indicated that cooperation is seldom contingency-based, and that interactions are not influenced by inequity aversion or sensitivity to cheaters. In contrast, several experiments with nonprimates have found that animals can take into account recent interactions when supporting others, suggesting that the apparent rarity of contingent cooperation in primates may not stem from cognitive constraints. Instead, individuals may tolerate short-term inequities in favors given and received because most cooperation occurs among long-term reciprocating partners.

reciprocity | mental state attribution | baboon | chimpanzee

An anthropomorphous ape, if he could take a dispassionate view of his own case, . . . might insist that they were ready to aid their fellow-apes of the same troop in many ways, to risk their lives for them, and to take charge of their orphans; but they would be forced to acknowledge that disinterested love for all living creatures, the most noble attribute of man, was quite beyond their comprehension.

Charles Darwin, *The Descent of Man*, 1871, p. 105

Humans have for centuries sensed that we share with animals the motivation to form close, enduring social bonds. Recent research has not only confirmed these intuitions but has also begun to uncover the many fitness benefits of such bonds (1). Nevertheless, despite many similarities in patterns of cooperation between humans and other animals, there are also important differences in its quality and scope. The reasons for these differences remain topics of debate, in large part because we still do not understand the full range of animals' cognitive abilities, in what ways these abilities differ from humans', and how these abilities contribute to the formation of cooperative bonds. Many animals share with humans the ability to monitor other individuals' friendships and animosities, to remember the nature of recent interactions, and perhaps also to recognize other individuals' motivations and intentions. Whether they recognize more complex mental attributes like the intent to deceive, however, remains unclear, as does the extent to which animals share humans' sometimes hyperbolic motivation to engage others in cooperative ventures.

Recognition of Other Animals' Relationships

Many social animals live in groups containing both kin and nonkin, in which interactions are simultaneously competitive and cooperative and in which individuals maintain differentiated relationships with a subset of group members. To navigate through this complex network of relationships, it seems essential

to be able to monitor not only one's own interactions but also the interactions of others. The ability to acquire and use information about other individuals' social relationships permits individuals to assess the strength of allies and opponents, to reconcile with opponents, and to choose mates, and it appears to be under strong selective pressure. Indeed, there is now an extensive literature indicating that animals are highly motivated to learn about other individuals' relationships and competitive abilities. Knowledge of other individuals' dominance ranks has been demonstrated in a variety of species, including not only primates and other social animals like pinyon jays [*Gymnorhinus cyanocephalus* (2)] and hyenas [*Crocuta crocuta* (3)], but also in less social territorial birds and fish (e.g., refs. 4–6). When joining a coalition, for example, hyenas and monkeys selectively recruit or support the higher-ranking of two combatants (e.g., refs. 7, 8; reviewed in ref. 9). Capuchin monkeys (*Cebus capucinus*) selectively recruit allies who both rank higher than their opponents and have a closer bond with themselves than with their opponent, indicating that they are able to compare the bond between the ally and themselves with the bond between the ally and their opponent (10). In playback experiments involving wild baboons (*Papio hamadryas ursinus*), a sequence of calls that mimics a higher-ranking opponent threatening a lower-ranking animal elicits little response from listeners, but if the individuals' roles are reversed, the response is significantly stronger—presumably because the rank-reversal sequence violates the listener's expectations (11–13).

The ability to eavesdrop on the social interactions of others enables individuals to acquire knowledge about another's competitive ability and probable allies without directly challenging him. In nonsocial birds and fish, males use information acquired through eavesdropping when deciding whether to challenge an intruder (e.g., 4 and 5; see ref. 14 for similar data on rhesus macaques, *Macaca mulatta*). Similarly, female chickadees (*Poecile atricapillus*) assess their mate's relative dominance status by attending to his singing contests with neighboring males. Females mated to males who are dominated in such contests are subsequently likely to solicit extrapair copulations from apparently more dominant neighbors (15).

Monkeys also recognize the close bonds that exist among others. In vervets (*Chlorocebus aethiops*) and macaques, an individual who has just been involved in an aggressive interaction will often redirect aggression by attacking a close relative of her opponent (16, 17). Similarly, if a female baboon hears a call sequence that mimics a fight between one of her own close relatives and the close relative of a more dominant female, she will subsequently avoid that female (18). Playback experiments have also demonstrated that low-ranking male baboons monitor the status of other males' sexual consortships to take advantage of opportunities to mate “sneakily” (19).

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If a baboon receives aggression from another and then, minutes later, hears a “reconciliatory” grunt from a previously uninvolved animal, the listener’s response to the grunt depends on the relationship between the calling animal and the listener’s opponent. If the caller is a close matrilineal relative of the opponent, the listener is subsequently more likely to approach her recent opponent and to tolerate her opponent’s approach than she is if she hears the grunt of an animal unrelated to her opponent. Subjects act as if they infer that they are the target of the vocalization even though they have not recently interacted with the signaler, but with her relative. They therefore treat the call as a reconciliatory signal that functions as a proxy for reconciliation with the opponent herself (20). They could do so only if they recognize the close bond that exists between the two females. A similar phenomenon occurs among chimpanzees (*Pan troglodytes*), whereby the behavior of bystanders and victims following aggression depends both on their own relationships with the combatants and on their perception of the relationship between the other animals involved (21).

To cite another example, chimpanzees often scream when involved in aggressive disputes. Victims produce acoustically different screams according to the severity of aggression they are receiving. In playback experiments, listeners responded differently to the different scream types (22). In cases of severe aggression, victims’ screams sometimes exaggerated the severity of the attack, but victims gave exaggerated screams only if their audience included at least one listener whose dominance rank was equal to or higher than that of their opponent (23). Victims seemed to alter their screams depending upon their perception of the relationship between their opponent and their potential allies.

Some progress is beginning to be made in identifying the neural mechanisms underlying knowledge of others’ social relationships. In male zebra finch (*Taeniopygia guttata*), for example, hearing another male’s song induces activation of a specific group of immediate early genes (24). These genes are activated rapidly and transiently by even brief social experiences, and they influence the transcription of other genes. The genes’ expression is linked to the social significance of the song and may function to enable the brain to keep track of the ever-changing social environment (24). Unfamiliar songs elicit a stronger response than familiar songs, and the response is enhanced if the listener is in the presence of another bird. Similarly, when a female cichlid fish (*Astatotilapia burtoni*) observes a preferred mate win a fight against another male, areas in the brain associated with reproduction are activated. If, however, the preferred mate loses a fight, areas in the brain associated with anxiety are activated instead (25). These changes occur even though the female is only observing the interactions. Such eavesdropping may permit observers to anticipate changes in the social environment without having to experience them first.

Further supporting the hypothesis that social skills have been under strong selective pressure across taxa, there is some indication in mammals that more social species show higher degrees of encephalization than less social species (26). Sociality may even affect relative brain size within species. In paper wasps (*Polistes dominulus*), for example, there is a significant increase in the size of the antennal lobes and collar in females that nest colonially with other queens, as opposed to solitary breeders (27). This increase in neural volume may have been favored because sociality places increased demand on the need to discriminate between familiar and unfamiliar individuals and to monitor other females’ dominance and breeding status.

In sum, knowledge of other individuals’ relationships has been widely documented in many species by using many different techniques (see ref. 28 for review). There appears to have been strong selection pressure for passive observational learning in the context of social interactions and for the acquisition of knowledge about other individuals’ social relationships. The repre-

sentations that underlie such recognition undoubtedly differ from one species to the next, and certainly differ from humans’ more explicit representations, but there is no doubt that animals acquire and remember information about other animals’ relationships and that this knowledge affects their behavior. In principle, this information can be acquired through relatively simple associative processes. The degree to which animals proceed beyond simply recognizing the association between two other animals, however, remains poorly understood. We still do not know, for example, whether a baboon distinguishes among different types of relationships, like “sister” or “daughter,” or whether she imbues these relationships with motives and emotions—for example, like “love.”

Attribution of Intentions

In the more than 30 y since Premack and Woodruff (29) posed the question “Does the ape have a theory of mind?” much progress has been made in the study of mental state attribution in animals. Many questions, however, are still unresolved.

Nonhuman primates and other animals are acutely sensitive to other individuals’ direction of gaze. When attempting to engage another individual’s attention—for example, when recruiting an alliance partner—primates will actively attempt to engage their partner’s gaze (30). In competitive contexts, rhesus macaques are more likely to attempt to steal food from a human whose eyes are averted than from one whose eyes are not (31), and captive chimpanzees are more likely to approach food that a competitor cannot see than food that the competitor can (32). Similarly, when potential competitors are present, ravens (*Corvus corax*) and scrub jays (*Aphelocoma californica*) are more likely to cache food in sites that are out of view or hidden behind barriers than in more open sites (e.g., refs. 33–35).

Primates also appear to attribute simple mental states, like intentions and motives, to others. In captivity, apes distinguish between intentional and accidental actions, and they also recognize other individuals’ goals (36). Under natural conditions, the recognition of others’ intentions is most evident in the context of vocalizations, when animals must make inferences about the intended recipient of someone else’s calls. Monkey groups are noisy, tumultuous societies, and an individual could not manage her social interactions if she interpreted every vocalization she heard as directed at her. Inferences about the directedness of vocalizations are probably often mediated by gaze direction and relatively simple contingencies. Even in the absence of visual signals, however, monkeys are able to make inferences about the intended recipient of a call based on their knowledge of a signaler’s identity and the nature of recent interactions. For example, when female chacma baboons were played the “reconciliatory” grunt of their aggressor within minutes after being threatened, they behaved as if they assumed the call was directed at themselves, as a signal of benign intent. As a result, they were more likely to approach their former opponent and to tolerate their opponent’s approaches than after hearing either no grunt or the grunt of another dominant female unrelated to their opponent (37). Call type was also important, because subjects avoided their recent opponent if they heard her threat-grunt rather than her reconciliatory grunt (38). By contrast, if subjects heard a female’s threat-grunt shortly after grooming with her, they ignored the call and acted as if they assumed that the female was threatening another individual. Thus, baboons use their memory of recent interactions to make inferences about the caller’s intention to communicate with them.

In primates, faces and voices are the primary means of transmitting social signals, and monkeys recognize the correspondence between facial and vocal expressions (39). When rhesus macaques hear one of their own species’ vocalizations, they exhibit neural activity not only in areas associated with auditory processing but also in higher-order visual areas, including superior temporal

sulcus (40). Ghazanfar et al. (41) explored the neural basis of sensory integration using the coos and grunts of rhesus macaques as stimuli. They found clear evidence that cells in certain areas of the auditory cortex are more responsive to bimodal (visual and auditory) presentation of species-specific calls than to unimodal presentation. Although significant integration of visual and auditory information occurred in trials with both vocalizations, the effect of cross-modal presentation was greater with grunts than with coos. The authors speculate that this may occur because grunts are usually directed toward a specific individual in dyadic interactions, whereas coos tend to be broadcast generally to the group at large. The greater cross-modal integration in the processing of grunts may therefore have arisen because, in contrast to listeners who hear a coo, listeners who hear a grunt must determine whether or not the call is directed at them.

When deciding “Who, me?”, then, upon hearing a vocalization or observing an approaching group member, monkeys must take into account the identity of the individual, its direction of gaze (if visible), the type of call given, the nature of their prior interactions with the signaler or her relatives, and the correlation between past interactions and future ones. Learned contingencies doubtless play a role in these assessments. However, because listeners’ responses depend on simultaneous consideration of all of these factors, this learning is likely to be both complex and subtle.

Attribution of Knowledge

Although baboons and other monkeys may be able to recognize other individuals’ intentions when inferring, for example, whether or not they are the target of another individual’s call, the extent to which animals attribute knowledge, ignorance, and beliefs to others remains controversial. For example, baboons often give “contact” barks when separated from others. When several separated individuals are calling simultaneously, it often appears that they are answering each other’s calls to inform each other of their location. Playback experiments suggest, however, that baboons call primarily with respect to their own separation from the group, not their audience’s. They “answer” others when they themselves are separated, and they often fail to respond even to the calls of their offspring when they themselves are in close proximity to other group members (42, 43). In this respect, the vocalizations of monkeys are very different from human speech, in which we routinely take into account our audience’s beliefs and knowledge during conversation.

Some investigators have suggested that animals’ attentiveness to gaze direction is an indication that animals recognize what other individuals can and cannot see and hence what they can and cannot know. These arguments are confounded, however, by the possibility that animals use gaze direction to assess not what others know but what they intend to do. As a result, they recognize, for example, that other individuals are motivated to defend food that they are looking at, and less likely to defend food when they are looking away.

Some recent experiments have attempted to avoid this confound by eliminating the possibility that subjects are responding only to their rival’s direction of gaze when choosing among food items. Kaminski et al. (44) presented chimpanzees with the choice of three buckets, two of which contained food. The first bucket was baited in the presence of both the subject and the rival. The second bucket was baited in the presence only of the subject. In the test condition, the subject’s view of the apparatus was blocked while the rival was allowed to choose first. In the control condition, the subject chose first. When subjects chose first, they were as likely to choose the bucket that their rival had seen baited as the one he had not. However, when they chose second, they were more likely to choose the bucket that their rival had not seen baited, suggesting they inferred that the rival would have chosen the bucket that he had seen baited. In other words, they acted as if

they recognized what their rival knew, based on what he had seen. However, when subjects observed the experimenter mislead the rival by seeming to hide the reward in one bucket but actually putting it in another, they did not distinguish between the rival’s true belief and his false belief. The authors conclude that chimpanzees recognize what others know, but not what they believe.

If, as seems likely, chimpanzees and other animals cannot attribute false beliefs to others, this would provide one explanation for their apparent failure to punish cheaters who defect from risky cooperative ventures. If chimpanzees cannot recognize the intent to deceive, they will be unable to distinguish between a partner who fails to cooperate because he is unable to do so, and one who fails to cooperate because he intends to do so, and they will by definition be unable to impose sanctions against such individuals. I return to this question later.

Mechanisms Underlying Cooperation

Although it is now clear from a variety of animal species that strong, cooperative bonds enhance longevity and offspring survival (1), the mechanisms that motivate individuals to form such bonds are still far from well understood. Female baboons, for example, do not groom only with close kin and those with whom they share a close social bond; they also groom less regularly with other females. When a close partner dies, they may attempt to establish a close bond with a previously infrequent partner. We hypothesize that knowledge of other individuals’ relationships guides the formation of new relationships, but this hypothesis has not yet been tested. Indeed, we still know little about whether or how animals keep track of their social relationships, of cooperative and noncooperative interactions, or of favors given and received.

Furthermore, although it is now clear that both humans and other animals derive reproductive benefits from strong, predictable social relationships, at least some of the mechanisms underlying these relationships are doubtless very different. Human social relationships are imbued with inferences about others’ intentions and beliefs, and humans are at times also acutely aware of whether a favor has been returned, or whether a partner has deceived them. The extent to which any animal is capable of similar mental projections remains unknown.

There continues to be debate about the psychological mechanisms that underlie animals’ social interactions and relationships. Because we have no direct evidence that animals can plan or anticipate the benefits that might derive from a long-term relationship, a number of investigators have argued that animals’ cooperative interactions are motivated only by short-term rewards, such as the opportunity to handle an infant or gain access to food. According to these arguments, social interactions are not founded on long-term patterns of affiliation but are based instead on short-term byproduct mutualism or biological markets motivated by the current value of a potential partner (45). So, for example, when a female monkey grooms another, she may simply be engaging in a short-term negotiation with a trading partner who controls a desirable commodity, like a young infant (46).

There is no doubt that many social interactions vary with current conditions. Several studies have shown, for instance, that female baboons often groom lactating females to obtain immediate access to their infants (47, 48). Similarly, males groom estrous females at higher rates than pregnant or lactating females, and subordinate individuals groom dominant individuals in apparent exchange for tolerance at food sites (49, 50). In an experiment directly testing the hypothesis that grooming in vervet monkeys is motivated in part by the expectation of immediate reward, Fruteau et al. (51) manipulated a food container in such a way that it could only be opened by one low-ranking female. Consistent with biological market theory, the rate at which the female subsequently received grooming from others increased significantly. This initial gain, however, decreased after a second

subordinate female was allowed to open the container. Thus, grooming appeared to be adjusted according to the relative value of the provider.

Observations indicating that some social interactions are influenced by the current value and supply of alternative trading partners are not inconsistent with evidence that others reflect long-term patterns of affiliation. Female baboons, for example, form long-term bonds with only a small number of other females; many of their other social interactions may well be initiated or maintained by interactions that depend in part on the current value of commodities. Nevertheless, much grooming occurs in the absence of an immediate reward, and it is seldom evenly balanced between partners within single bouts (52). Despite short-term asymmetries, nonhuman primates form the strongest bonds with those individuals with whom they have the most balanced and reciprocal grooming interactions over extended periods of time (1).

During the past decade, there has also been increasing skepticism about the relevance of contingent-based reciprocity in the social interactions of animals. Because most cooperative interactions like grooming occur between long-term partners (often kin) for whom any single altruistic act may be relatively insignificant, many investigators are now convinced that the sort of reciprocal altruism first proposed by Trivers (53) may be both rare and fragile in nature (54, 55). Although there is limited experimental and correlational evidence that animals sometimes rely on memory of recent interactions when behaving altruistically toward others, interpretation has been complicated by a paucity of convincing examples, the absence of important controls in some early tests, and a number of experimental studies seeming to indicate that animals lack the cognitive or empathetic ability to sustain contingent cooperative exchanges.

Cognitive Constraints

Doubts persist about whether animals possess the cognitive abilities to sustain contingent cooperation. These include the ability to remember specific interactions, to delay reward, to track favors given and returned, to plan and anticipate future outcomes, and to distinguish between cooperators and defectors (46, 56, 57). Some of these objections may be unjustified.

More than 100 y of research on classical conditioning have repeatedly demonstrated that animals are acutely sensitive to contingencies and to the predictive value of different stimuli on outcomes (reviewed in ref. 28). Animals also remember the nature of specific interactions with particular individuals. As already mentioned, for example, if a baboon hears another female's reconciliatory grunt shortly after being threatened by her, she behaves as if the grunt is causally related to the recent fight and directed specifically to her as a signal of benign intent. Her response appears to be guided by memory of the quality of a specific recent interaction. The extent to which this memory is explicit is as yet unknown.

Other purported cognitive limitations can also be questioned. There is now a large amount of literature on animals' numerical discrimination abilities suggesting that quantity assessments are widespread across many taxa (reviewed in ref. 28). Similarly, although many tests with primates have suggested a general failure to delay rewards beyond short time periods, there appears to be considerable interindividual variation in self-imposed delayed gratification. Moreover, the ability of primates and other animals to delay gratification in contexts that do not involve food rewards remains largely untested. Thus, contingent cooperation in animals is not necessarily constrained by the inability to delay reward or to quantify past cooperative acts.

It has also been assumed that animals are not capable of contingent cooperation because it demands the anticipation of future interactions. Leaving aside for the moment the question of whether mental projections of future outcomes are necessary

to sustain contingent cooperation, the assumption that animals are unable to anticipate future events may not be valid. There is a long history in experimental psychology of tests demonstrating that many animals accurately and predictably anticipate future rewards and outcomes (reviewed in ref. 28). Furthermore, a growing number of experiments suggest that primates are able to make prospective decisions based on certainty judgments about their past behavior (e.g., refs. 58–60). Indeed, some forms of cooperative behavior in animals—the boundary patrols of chimpanzees in particular (61)—are highly suggestive of shared intentionality, planning, and episodic memory.

It is also doubtful that nonhuman primates are unable to distinguish cooperators from noncooperators. In tests conducted in captivity that require two individuals to work together to obtain a food reward, both capuchin monkeys and chimpanzees are more likely to cooperate with partners with whom rewards are shared more equitably (62–65). Chimpanzees also recognize which partners are most effective (66) and show a limited ability to increase their rate of cooperation with partners who have cooperated with them in the past (67). They may also be able to resolve conflicts of interests when working together to achieve a common goal (64).

Emotional Constraints

In humans, inequity aversion, tolerance, and the motivation to engage in joint activities are important catalysts for cooperative behavior. Whether primates are motivated by these emotions, however, is a topic of much debate. Some experiments have suggested that primates reject food offered by humans if a rival is receiving a better reward (e.g., refs. 68). Other studies have failed to replicate these findings, and suggest that the food rejections are caused not by perceived inequality but by frustration at seeing, but not obtaining, a preferred food item (e.g., refs. 69, 70). In some experiments, chimpanzees have appeared to be generally indifferent to inequitable returns to themselves and others. When subjects have the opportunity to deliver food to a partner at no cost to themselves, for example, they show no sensitivity to the consequences for their partner (1). In other experimental paradigms, however, chimpanzees do help partners obtain food rewards, especially when the partner is attempting to reach for the food or soliciting help (71, 72). Thus, in some contexts, chimpanzees do seem motivated to help others and to take into consideration others' outcomes, even when they do not derive direct benefits from doing so.

It has also been argued that a lack of social tolerance may contribute to the low levels of cooperation displayed by chimpanzees in many experiments. Bonobos (*Pan paniscus*) achieve higher levels of success in some cooperative tasks than do chimpanzees, seemingly because their willingness to share rewards with their partners prompts continued cooperation (73). It remains unclear, however, whether bonobos also show higher degrees of cooperation and tolerance under natural conditions, under which the structure and rewards of the task are not determined by humans. It is not known, for example, whether bonobos show higher levels of cooperation than chimpanzees when hunting, or whether they share their kills more equitably. Similarly, it is not apparent whether bonobos ever engage in any behavior that is as cooperative and potentially costly as chimpanzees' patrolling behavior (61), or if they do, whether they are more likely than chimpanzees to share risks equitably.

Taken together, results suggest that cooperation in animals may be sustained by qualitatively different mechanisms than it is in humans. Indeed, experiments explicitly designed to compare the behavior of children and chimpanzees indicate that humans may be uniquely motivated to engage others' attention, share their intentions, emotions, and knowledge, and impose sanctions on noncooperators (57, 74, 75).

Measuring Contingent Cooperation

For several reasons, it has proved difficult to investigate contingent cooperation under natural conditions. First, in the absence of experiments, it is almost impossible to determine whether a given altruistic act is causally dependent upon a specific prior interaction. Second, many altruistic acts occur in different currencies—such as grooming and alliance support—whose relative values are difficult to calibrate. Moreover, even altruistic acts that occur in the same currency may not carry equal value for each participant. In species that form dominance hierarchies, a low-ranking individual may value alliance support from a more dominant partner more highly than vice versa. As a result, he may provide substantially more support to the dominant partner than he receives in return, yet still regard the relationship as reciprocal. Given these empirically intractable problems, almost any relationship can be termed reciprocal. Finally, the degree to which interactions are regarded as reciprocal often seems to be a function of the time scale under consideration. As already mentioned, grooming exchanges within single bouts are often unbalanced and asymmetrical. Nonetheless, over longer time periods, partners with close social bonds exhibit a high degree of reciprocity in grooming.

Correlations between grooming and alliance support have been documented in a variety of primates (76). In a meta-analysis involving 14 primate species, Schino (77) found a weak but highly significant correlation between grooming and alliances among long-term partners over extended periods, but little evidence that alliance support is motivated by a specific recent grooming bout. Indeed, in one study of captive Japanese macaques (*Macaca fuscata*), kin were never observed to support each other in the 30 min after grooming, even when they had the opportunity to do so (78). Similarly, although female hyenas form the majority of their alliances with close kin, there is no evidence that this support is reciprocal or based on the memory of a specific recent interaction (79).

Among male chimpanzees, individuals who groom most often are also those who form alliances and share meat at the highest rates. Cooperation thus involves the exchange of services in different currencies, with males reciprocating grooming for support, support for meat, and so on. Although exchanges are often asymmetrical within dyads over short time periods, they become more evenly balanced over longer periods of time and are not simply a byproduct of association frequency or genetic relatedness (80).

Possibly the most costly cooperative behavior shown by male chimpanzees occurs during boundary patrols, when the males in one community make incursions into the territories of their neighbors (61). These incursions are potentially risky, because a small party is vulnerable to attack if it encounters a larger party; incursions, therefore, are obligately cooperative. Although it remains unclear whether patrols are planned, they appear to involve some degree of shared intentionality. Little is known about the mechanisms that motivate chimpanzees to initiate and participate in these highly cooperative and risky ventures. It is not known, for example, whether chimpanzees take into consideration memory of another individual's behavior during previous patrols when deciding whether or not to join him in a patrol. Whether cooperation in this context is more, or less, contingent upon memory of previous events remains unclear.

Although chimpanzees' interactions with preferred partners become reciprocal over extended periods of time, tests on captive subjects have provided little evidence for contingency-based reciprocity. For example, in one experiment chimpanzees were given a choice of cooperating with either an individual who had previously helped them or one that had not (67). Although there was some evidence that subjects increased their cooperation with the more helpful partner, this effect was relatively weak, and

subjects did not consistently avoid noncooperators. In another experiment deliberately designed to test whether cooperation was contingency-based, Brosnan et al. (81) found no evidence that chimpanzees were more likely to provide food to a partner if that partner had previously provided food to them. Melis et al. (63) suggest that chimpanzees may be capable of contingent reciprocity, but that long-term partner preferences that develop over repeated interactions may override the decisions that chimpanzees make on the basis of immediate exchanges and rewards.

Curiously, similar experiments conducted with other species have provided more positive evidence for contingent cooperation in the context of food exchange. For example, capuchin monkeys are more likely to share food with a partner who has previously shared food with them (82). Similarly, in experiments in which rats were trained to pull a stick to deliver food to another rat in an adjoining cage, subjects were more likely to help a partner who had previously helped them than one who had previously not helped them (83).

Several investigations conducted under more natural conditions have also provided some indications of contingent cooperation. Unfortunately, however, interpretation has been complicated by the lack of follow-up experiments to correct for potential confounds. For example, in the well known study of vampire bats (*Desmodus rotundus*) (84), most reciprocal exchanges of blood occurred among close kin. In addition, although some individuals regularly exchanged blood with unrelated partners, it was not clear whether any specific act of regurgitation was contingent upon a specific recent donation.

An investigation of mobbing behavior in pied flycatchers (*Ficedula hypoleuca*) provides more convincing evidence for contingent cooperation (85). In this experiment, subjects had the opportunity to help one of two neighbors mob an owl. One of these neighbors had recently helped the subjects to mob an owl at their own nest box, whereas the other had been prevented from doing so by the experimenters. Subjects were significantly more likely to help previous supporters than apparent defectors, suggesting that cooperative behavior was contingent upon memory of the neighbors' behavior.

There is also some evidence that monkeys may sometimes rely on memory of recent interactions when choosing to join another in an alliance, even though most alliances are based on long-term partner preferences. In one experiment conducted with captive long-tailed macaques (*Macaca fascicularis*), females were found to be more willing to support a lower-ranking female in an aggressive dispute after being groomed by that female than in the absence of grooming (86). In another experiment, female baboons were played the recruitment call of a lower-ranking female at least 10 min after either grooming with her or threatening her. Hearing the recruitment call of a recent grooming partner caused subjects to move in the direction of the loudspeaker and approach their former partner, but only when the two were not close relatives (87). Importantly, females' responses were not influenced by any type of recent interaction, because subjects responded to their former partner's recruitment call only after grooming, and not after aggression. Similarly, their responses were not prompted only by the motivation to resume a friendly interaction, because prior grooming alone did not elicit approach. Instead, subjects were most likely to approach their grooming partner when they had also heard her recruitment call. Thus, females' willingness to attend to the recruitment calls of other individuals appeared to be prompted at least in part by memory of a specific friendly interaction.

In sum, several factors may interact to motivate contingent cooperation in animals under natural conditions: the strength of the partners' social relationship, the nature of their recent interactions, and the opportunity to reengage in some form of cooperative behavior. Animals appear to possess many of the cognitive abilities thought to be essential for the emergence of contingent cooperation, if in rudimentary form. Nonetheless, such

cooperation appears to be less common than the noncontingent cooperation that develops among kin and long-term partners.

Detection of Noncooperators

If cooperation depends in part on the memory of previous behavior, why do animals not avoid or punish freeloaders? In captivity, chimpanzees continue to work with noncooperators despite receiving inequitable returns (63, 64). In addition, although they retaliate against an individual who steals food from them, they do not attempt to punish those who obtain disproportionate rewards, nor are they motivated to damage the welfare of others simply for its own sake (i.e., spite) (64, 65, 88).

Under natural conditions, too, freeloaders appear to be tolerated. For example, among feral dogs (*Canis lupus familiaris*), participation in intergroup contests declines with increasing group size, and high-ranking individuals are more likely to avoid being at the front of the pack (89). However, there is no evidence that defectors are punished. Individual lionesses (*Panthera leo*) also vary predictably in their participation in territorial conflicts. In playback experiments that simulated the approach of an aggressive intruder, some females consistently advanced toward the source of the calls, whereas others consistently lagged behind, avoiding the potential cost of a conflict (90). Advancers appeared to be aware of the laggards' behavior, because they often looked back at them; nonetheless, they did not subsequently avoid or punish them. Similarly, male chimpanzees do not participate equally in boundary patrols (80). Some individuals are allowed to reap the benefits of territorial integrity without incurring any costs.

There may be several reasons for animals' apparent tolerance of freeloaders. First, in at least some cases, participants may derive inclusive fitness benefits through freeloaders' survival and reproduction. Freeloaders might also cooperate in other currencies, such as hunting. It is also possible that some individuals benefit more than others from the maintenance of the territory's integrity. This explanation may account for the greater participation of dominant individuals in some other primate species, like vervet monkeys (91) and ring-tailed lemurs (*Lemur catta*) (92). Finally, however, animals may lack the cognitive capacity to foster or infer deceptive intent, or to impose sanctions on perceived cheaters. If true, animals may well not be capable of achieving the sort of extreme cooperation manifested by humans toward non-relatives and even complete strangers, which is sustained not only by sanctions against inequity, deception, and spite, but also by concerns about reputation and prestige (1, 57, 88).

This last objection, however, only denies the possibility for human-like contingent cooperation in animals; it does not rule it out entirely. The detection of cheaters does not in principle require the ability to impute complex mental states like deception to others. It could arise through relatively simple associative processes, by which animals learn to avoid individuals whose presence is associated with a negative experience. Such associations may underlie contingent cooperation in flycatchers, for example.

Indeed, mental state attribution may be irrelevant to contingent cooperation in animals. Schino and Aureli (93) have argued that the focus on cognitive constraints in discussions of contingent cooperation confuses proximate and ultimate explanations for behavior. Altruistic behaviors may be favored by natural selection because of the subsequent benefits they confer, but what motivates animals to behave altruistically are the previous benefits they have received. In this view, the accumulation of multiple, cooperative exchanges over time causes animals to form partner-specific emotional bonds that prompt future altruistic behavior. Thus, reciprocity may be maintained by a kind of partner-specific "emotional bookkeeping" (93) that permits long-term tracking of

multiple partners and facilitates cooperation in different behavioral currencies. The resulting bonds that develop between preferred partners may motivate future positive interactions without the need for explicit tabulation of favors given and returned, or calculations of anticipated benefits (94). For unrelated females who interact at low rates, a single grooming bout may temporarily elevate a female's positive emotions toward her partner sufficiently above baseline to influence her immediate interactions with her. In contrast, grooming and support among females with close bonds (who are also usually kin) should be less subject to immediate contingencies and less influenced by single interactions. Many of these proximate mechanisms may also motivate social interactions in humans. It seems unlikely, for example, that the formation of close bonds among humans is driven by expectations that such bonds will enhance health and longevity.

Finally, it is important to emphasize that, although the absence of punishment in animals may derive partly from cognitive constraints, a strict accounting of services given and received is likely maladaptive in groups in which individuals establish close bonds and interact regularly with familiar partners in a variety of contexts. In fact, although the cognitive constraints that supposedly limit contingent cooperation in animals is often contrasted with humans' sensitivity to inequitable exchanges, human friendships are rarely contingency-based. Numerous studies have shown that people seldom keep tabs of costs and benefits in interactions with regular partners (95). Although people become resentful and dissatisfied when exchanges within a friendship are consistently unbalanced, tallying of favors given and received are typically reserved for infrequent associates. There is even some question about the extent to which extreme prosociality reflects an entirely innate human psychological trait. Recent cross-cultural studies have suggested that cultural norms that promote fairness and the punishment of violators may be more common in large-scale industrialized societies—in which people often interact with strangers—than in smaller, less market-based, communities, in which individuals interact primarily with familiar partners, and where mechanisms associated with kin selection and long-term reciprocity may be more relevant to social relations (96).

These observations emphasize again the importance of distinguishing between proximate and ultimate explanations when considering cooperation in animals. Whether animals have the cognitive capacity to engage in contingent cooperation is one question; whether it is always adaptive for them to do is another. It may well be that the relative rarity of contingent cooperation in animals stems less from the inability to keep track of recent interactions (and even, perhaps, to anticipate future ones) than from the willingness to tolerate short-term inequities with regular partners.

Finally, most studies of mental state attribution in animals to date have been conducted on captive animals, using paradigms and rewards determined by human experimenters. It is to be hoped that future investigations will attempt to address these questions under more natural conditions, on the animals' own terms. Until such experiments are conducted, we can only speculate about the selective forces that might favor the evolution of a theory of mind, and its function in social interactions.

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