

REVIEW SUMMARY

SOCIAL EVOLUTION

Evolution of responses to (un)fairness

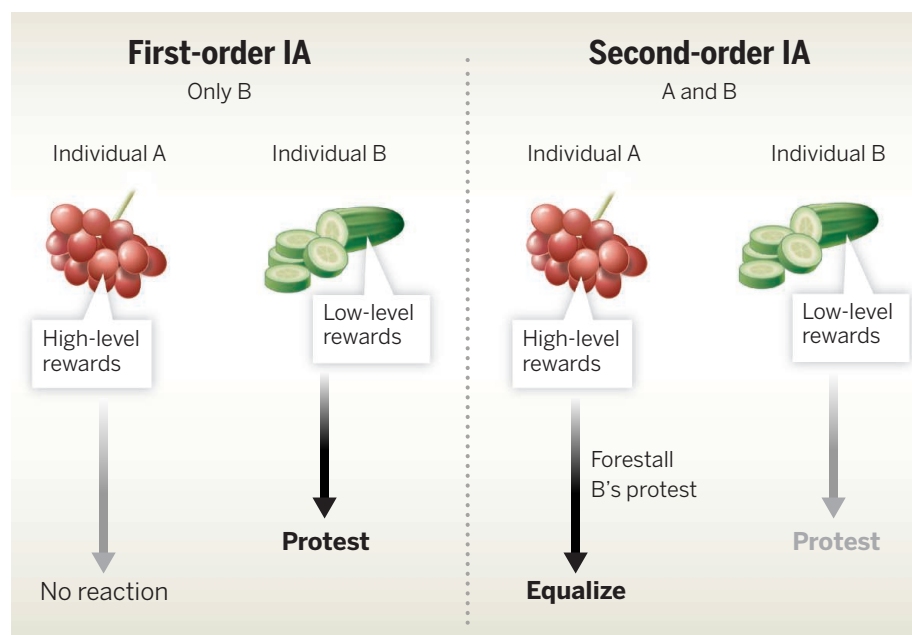
Sarah F. Brosnan^{1*} and Frans B. M. de Waal²

BACKGROUND: The human sense of fairness presents an evolutionary puzzle because it appears to run counter to the short-term interests of at least some parties. We not only react negatively to getting less than a partner but sometimes also to getting more, which seems illogical. Following an ideal of impartiality, we seek appropriate outcomes for everyone within the community, not just a few individuals, and, in particular, not just ourselves. Why do we react this way? Are we the only species to do so? Here, we consider the evidence with regard to nonhuman primates and other animals to illuminate the evolution of the sense of fairness. Because social ideals escape measurement, we focus on behavioral responses to equal versus unequal reward division. Moreover, a true sense of fairness includes taking account of receiving both less than a partner and more than a partner. Therefore, we consider the evidence for both of these in other species and how this informs our understanding of the evolution of fairness in humans.

ADVANCES: There is widespread evidence for sensitivity to receiving less than a partner, or “first-order inequity aversion” (IA), in species that cooperate outside mating bonds and kinship. In these studies, animals are paired with a social partner who receives a preferred reward for completing a task. Subjects may respond by refusing to participate or refusing to accept the food reward, and such reactions are compared with those following control tests in which both subjects receive the same reward for the same effort.

Increased responses when the partner receives a preferred reward are indicative of a sensitivity to inequity.

Thus far, passive and active protest against unfavorable outcomes has been documented in monkeys, apes, dogs, and birds. It is thought that these species compare their outcomes with those of others so as to judge the merit of their partnerships. They may turn away from partners that appropriate more than their



A diagram of the relationship between first-order IA and second-order IA. Individual A received high-level rewards, and individual B received low-level rewards. Individuals who recognize when they receive less than another may react against this situation—for instance, by finding a new cooperative partner. As reliance on cooperation increases, individuals also benefit from recognizing when they receive more, as this allows them to forestall first-order IA reactions in their partners and thereby maintain a successful cooperative relationship. This is the foundation of the full-blown human sense of fairness.

fair share of the yields of cooperation.

A complete sense of fairness also includes second-order IA, however, which seeks to equalize outcomes even at a short-term cost to the self. This requires individuals to give up an immediate benefit to stabilize a long-term valuable cooperative relationship. Second-order IA reactions have thus far been found only in humans and apes. We hypothesize that second-order IA requires anticipation of first-order IA in the partner and its negative impact on the relationship. To forestall these consequences, and ensure continued cooperation, outcomes are equalized between partners.

OUTLOOK: Thus, humans and other species seem to share basic reactions to inequity, which serves to sustain cooperation. We postulate that the basic emotional reactions and calculations underlying our

sense of fairness are rooted in our primate background and offer a model that places these reactions in the context of cooperative relationships.

Future research should more explicitly investigate the key variables underlying IA, such as the degree of dependence on cooperation, anticipation of the way resource division affects relationships, and the freedom to choose among and change partners. A cross-species investigation with a standardized paradigm, including both first- and second-order IA, may further illuminate the factors involved and help verify or falsify the model proposed. ■

¹Departments of Psychology and Philosophy, Neuroscience Institute and Language Research Center, Georgia State University, Atlanta, GA, USA. ²Living Links, Yerkes National Primate Research Center and Psychology Department, Emory University, Atlanta, GA, USA.

*Corresponding author. E-mail: sarah.brosnan@gmail.com
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REVIEW

SOCIAL EVOLUTION

Evolution of responses to (un)fairness

Sarah F. Brosnan^{1*} and Frans B. M. de Waal²

The human sense of fairness is an evolutionary puzzle. To study this, we can look to other species, in which this can be translated empirically into responses to reward distribution. Passive and active protest against receiving less than a partner for the same task is widespread in species that cooperate outside kinship and mating bonds. There is less evidence that nonhuman species seek to equalize outcomes to their own detriment, yet the latter has been documented in our closest relatives, the apes. This reaction probably reflects an attempt to forestall partner dissatisfaction with obtained outcomes and its negative impact on future cooperation. We hypothesize that it is the evolution of this response that allowed the development of a complete sense of fairness in humans, which aims not at equality for its own sake but for the sake of continued cooperation.

Cooperation could not have evolved without mechanisms to ensure the sharing of payoffs. For an individual to cooperate with an unrelated partner to achieve goals that it cannot achieve alone or to exchange favors over time requires an ability to compare payoffs with investments. Given the ample evidence for mutualistic cooperation and reciprocal altruism (1, 2) in humans as well as other species (hereafter, animals), we therefore expect well-developed capacities for payoff evaluation in species that flexibly cooperate with individually known partners. We also expect negative reactions to excessive payoff imbalances, because such imbalances undermine cooperation among nonrelatives, which requires proportionality between effort and gain so that gains among parties jointly contributing to a given enterprise are shared.

Along with the human sense of fairness and justice, responses to inequity have enjoyed a long history of scholarship in philosophy, law, economics, and psychology. Yet the evolution of these responses and possible parallels in other species have only recently come into focus. Even though “contrast effects,” which describe how animals respond to unanticipated individual reward outcomes, have been known for nearly a century (3), the first study to measure reactions to interindividual outcome contrasts was published only in 2003 (4). In this study, brown capuchin monkeys (*Cebus apella*) became agitated and refused to perform a task for which a companion received superior rewards [see (5) for a video]. The monkeys’ protest was not due to the mere sight of unavailable superior rewards, because they showed it only if these rewards actually went to their partner. If superior rewards were merely visible, they were mostly ignored (4, 6). Since this early study, inequity responses have

been explored in a number of species and found to be most pronounced in animals that cooperate outside of the bonds of mating and kinship.

We propose that sensitivity to (in)equity offers several evolutionary benefits. First, animals need to recognize when they receive less than a partner, because this tells them that the benefits of cooperation may be in danger. By protesting against this situation, they show a response known as inequity aversion (IA). Evidence indicates that this behavior is widespread in cooperative species under many circumstances. As the reliance on cooperation increases, individuals also benefit from sensitivity to receiving more than another, which risks undermining cooperative partnerships. This behavior is likely taxonomically restricted, because it requires prediction of the partner’s reaction to getting less and its effect on the relationship. It also requires restraint to refrain from an immediately advantageous outcome. The pressure for increased cooperation combined with advanced cognitive abilities and emotional control allowed humans to evolve a complete sense of fairness. Here, we review the literature on IA in humans and other animals within an evolutionary framework of cooperation, social reciprocity, and conflict resolution. Our main conclusion is that the sense of fairness did not evolve for the sake of fairness per se but in order to reap the benefits of continued cooperation.

Responses to inequity

IA has been defined as a negative reaction to unequal outcomes (7). It is further subdivided into “disadvantageous IA,” or reactions to inequity to the detriment of the actor, and “advantageous IA,” also known as overcompensation, or reactions to inequity that benefits the actor (7). Responses to the first kind of IA offer a clear advantage if they help increase one’s own share. Not surprisingly, human studies indicate that disadvantageous IA emerges earlier (8) and is more pronounced than advantageous IA (9). Young children may even pay a cost to maintain their advantage (10), although advantageous IA may

have a more explicitly social focus (11). Disadvantageous IA is also the most common type in animals (see below). However, responses to overcompensation are also expected, as they, too, provide a long-term benefit (12). We have called disadvantageous IA “first-order inequity aversion” to indicate that it is the primary reaction, using “second-order inequity aversion” for the less common and less pronounced advantageous IA (Fig. 1) (13).

The connection between IA and fairness is not straightforward. The hallmark of the human sense of fairness is the idea of impartiality; that is, human fairness or justice is based on the idea of appropriate outcomes applied to everyone within the community, not just a few individuals, and, in particular, not just oneself. Thus, outcomes are judged against a standard, or an ideal. There is variation in this ideal across cultures or situations, but there is consistency within a given context. This complete sense of fairness likely requires abstraction at the community level as well as language (to establish a consistent set of ideals), both of which capacities may be restricted to our species (14). Community concern is not wholly absent in other primates, however, and neither is impartiality, such as when policing males break up fights (15).

Inasmuch as social ideals escape measurement, a sense of fairness is impossible to prove or disprove in animals. Reactions to inequity, on the other hand, are open to empirical investigation by creating situations in which one individual receives more or less than another. These reactions typically manifest as a rejection of a received reward or an unwillingness to participate in the interaction (Fig. 2A). In most experiments, subjects must complete a simple task to receive a reward (Table 1). To control for the social aspect of the interaction, these experiments often combine with ones on contrast effects that measure how subjects respond to a lesser reward after having just received a better reward (contrast) or another lesser one (control). It has been found that the mere visibility of better rewards is not the issue, because primates reliably perform tasks for lesser rewards regardless of whether or not better ones are immediately in front of them (6, 16). Experiments on IA have shown that there is substantial variation among species in this response, even within the primates; some species respond more strongly to contrast effects (17), others more strongly to disadvantageous inequity (4, 16); some respond to both (18), and some seem indifferent to either condition (19, 20).

There are also important individual differences in response that hint at the situations in which inequity responses provide an advantage. For instance, merely feeding unequal foods fails to generate the same reaction; hence, an effortful task is essential (6, 16, 20) (Table 1), even though the nature of the task may be irrelevant (20). A second methodological issue emerges when we consider all reported studies regardless of species. Animals tested with an effortful task respond to inequity almost exclusively when seated closely side-by-side, compared with tests in which

¹Departments of Psychology and Philosophy, Neuroscience Institute and Language Research Center, Georgia State University, Atlanta, GA, USA. ²Living Links, Yerkes National Primate Research Center and Psychology Department, Emory University, Atlanta, GA, USA.

*Corresponding author. E-mail: sarah.brosnan@gmail.com

they sat far apart or across from each other, in which few IA responses were observed (Table 1). This suggests that physical proximity may be integral to IA outcomes, possibly because of the relationship between proximity and cooperation and the way proximity facilitates information gathering about the partner (21). Finally, individual differences have been found in some species, notably chimpanzees, who show substantial variation even within the same experiment (16, 22, 23). Responses also seem influenced by dominance rank, sex, and relationship quality. This is the case in humans as well, where factors such as relationship quality (24), personality (25), and the scale of competition (26) influence responses

to unfair outcomes. Additional work to determine the influence of these and other factors on animal IA responses will provide additional nuance in our understanding of the evolution of IA (Table 1).

First-order IA has been documented in controlled experiments in capuchin monkeys [(4, 6, 27–29), but see also (30)], macaques (18, 31), chimpanzees [(16, 22), but see also (32, 23)], dogs (33–35), and crows (36), and it has been implied in rodents (37). These animals refuse lesser rewards if a partner receives better ones and/or stop performing after multiple exposures to such outcomes. At first sight, this response is counterintuitive, as it reduces absolute outcome (the subject passes

up a less-preferred, but still beneficial, reward) while increasing inequity (the partner still receives the preferred reward versus the other receiving nothing). If the goal of IA is to minimize current inequity (7), these animals show the wrong response.

New lines of evidence, however, have led to a reassessment of this evaluation. First, humans, too, respond in this way. The workhorse of inequity studies has been the ultimatum game (UG), in which one individual, the proposer, must decide how to divide a set sum of money. The second individual, the responder, then must decide whether to accept this division—in which case both individuals receive the money as allocated—or refuse it, in which case neither party receives anything (38). Decades of research demonstrate that, while there is variation among cultures (39), human proposers tend to make higher offers than the minimum required and responders tend to reject offers that are skewed (40), showing that humans, too, meet the first criterion, turning down net positive outcomes.

In most situations of unfairness, we have no recourse, however. How do humans respond when a refusal punishes only themselves? The impunity game (IG) is a related game for which a refusal by the responder still allows the proposer their allocated sum, whereas the responder receives nothing. This situation is similar to most inequity tasks applied to animals, in which subjects have the option to refuse but their refusal does not alter the other's outcome (41). Recent studies show refusals at about half the levels seen in the UG (42), bringing the human reaction close to that of animals refusing poorer rewards even if doing so decreases absolute gains and increases inequity.

The game context cannot include all possible outcomes that exist in natural social interactions, however. In the standard inequity task, refusals only hurt the actor, whereas in a natural social context, protest against inequity may lead to the actor either receiving a larger share or seeking out a better partner to work with. Despite the

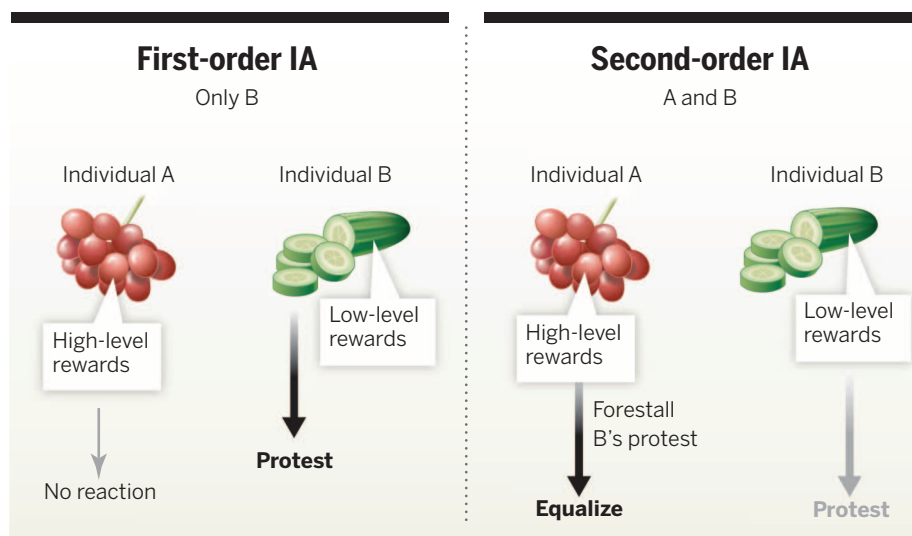
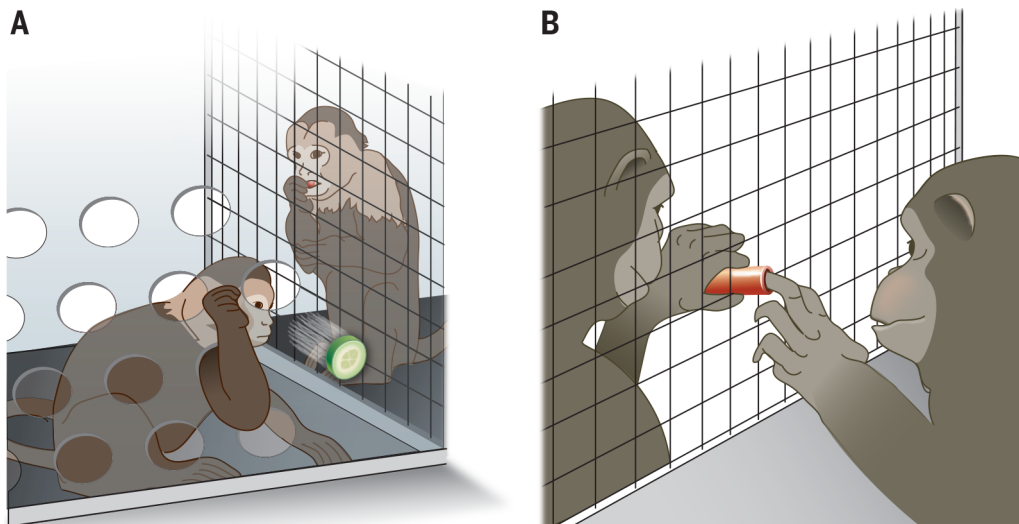


Fig. 1. A diagram of the relationship between first-order IA and second-order IA. Individual A received high-level rewards, and individual B received low-level rewards. Individuals who recognize when they receive less than another may react against this situation so as to maintain beneficial outcomes of cooperation, for instance, by finding a new cooperative partner. As reliance on cooperation increases, individuals also benefit from recognizing when they receive more, as this allows them to forestall first-order IA reactions in their partners and thereby maintain a successful cooperative relationship. Second-order IA requires advanced cognition and emotional control and thus far has only been seen in chimpanzees and humans. This is the foundation of the full-blown human sense of fairness.

Fig. 2. Subjects' responses in the standard inequity task and the UG.

(A) Capuchin monkeys during the original "monkeys reject unequal pay" experiment (4). The monkey on the left is rejecting the lesser reward, a cucumber slice, after viewing the partner receive a more preferred grape for the same amount of work. See video (5). (B) Chimpanzees during the UG (81). The chimpanzee who has just made the token choice (right) hands the token to her partner, who needs to accept and hand it over to the experimenter in order for both of them to receive the rewards corresponding with the token choice.



short-term costs, rejection of inequity may produce long-term gains by signaling to the partner that a relationship is about to end or by leading the actor to exit the relationship and replace it with a better one.

First-order IA and cooperation

The evolution of cooperation requires that its benefits reach all contributing parties in roughly similar amounts. Natural selection works on every individual's relative advantage compared with others; hence, gaining an absolute benefit is insufficient. If individuals were satisfied with any absolute benefit, they might still face negative fitness consequences if they were doing less

well than competing others. It makes sense, therefore, to compare one's gains with those of others (43). Additionally, individuals must base decisions to cooperate on the entire history of interaction with a particular partner, not just any single interaction. Reciprocity requires a long-term evaluation of effort versus payoff balance.

The above perspective applies only to species with extensive cooperation outside of kinship relationships. The absence of flexible partner choice in the hymenoptera, for example, eliminates the need to compare efforts with payoffs. Our closest relatives, bonobos and chimpanzees, on the other hand, frequently cooperate with nonkin. Chimpanzees hunt together (44), form

political coalitions and other reciprocal relations (45), collectively defend territories (46) and mates (47), and actively share food [e.g., (48)]. DNA collected in the field shows that most long-term male-male partnerships lack kinship ties (49). Bonobos show the same pattern. Females frequently share food and maintain a cooperative network that allows them to dominate males despite the fact that females are the migratory sex, hence largely unrelated within each community (50). In captive settings, bonobos even share food with outsiders (51).

Experimental studies of cooperation in primates began in 1936 with an experiment on cooperatively pulling chimpanzees (52). Since then,

Table 1. Publications since 2003 on IA in a variety of nonhuman species.

The studies are divided into those using an effortful task and those that merely fed unequal foods. Tasks include exchange, in which the subject returns a token to the experimenter and subsequently receives a food reward; pulling, in which subjects must pull in a tray to bring themselves and/or others food rewards; target, in which the subject must hold on to a token for a specified period of time to receive a food reward; and none, in which the subject (and/or partner)

receives food for "free," without completing a task. The "shake paw" and "sit on command" tasks were specific to domestic dogs (because they are in their behavioral repertoire already). The UG requires a proposer to choose one of two reward divisions, which then must be accepted by the responder, who can either accept the proposal, in which case both subjects get the food as proposed, or reject it, in which case neither subject gets anything. The table also notes the nature of the task and whether individuals were sitting near each other or not.

Species	Task	Side-by-side and near	Evidence of		Contrast effect	Other effects
			1st-order IA	2nd-order IA		
Food rewards for task						
Chimpanzees	Exchange (22)	Yes	Yes	–	No	Social tie
	Exchange (16)	Yes	Yes	Yes	Yes	Rank, sex, task
	Exchange (92)	Yes	Yes	–	No	Sex
	Exchange (23)	No	No	–	–	
	UG (79)	No	–	No	–	
	UG (80)	No	No	No	–	
	UG (81)	Yes	–	Yes	–	
Bonobo	Exchange (23)	No	Maybe	–	–	
	UG (80)	No	No	No	–	
Orangutan	Exchange (23)	No	No	–	–	
	Exchange (19)	Yes	No	No	No	
Long-tailed macaque	Pulling (31)	Yes	Yes			Rank, social tie
Rhesus macaque	Target (18)	Yes	Yes	No	Yes	Ontogeny
Capuchin monkey	Exchange (4)	Yes	Yes	–	No	
	Exchange (6)	Yes	Yes	–	No	Task, effort
	Pulling (27)	Yes	Yes	–	No	
	Pulling (28)	No	Yes	Yes	–	Rank, visual access
	Exchange (30)	Yes	No	–	No	
Squirrel monkey	Exchange (93)	No	No	–	–	
	Exchange (17)	Yes	No	No	Yes	Sex, task
	Target (20)	Yes	No	No	Yes	Sex
Owl monkey	Target (20)	Yes	No	No	No	
Common marmoset	Target (20)	Yes	No	No	No	
Tamarin	Exchange (74)	Yes	No	No	Yes	Task
Domestic dog	Shake paw (33)	Yes	Yes	–	No	
	Various (34)	Yes	Yes	–	–	
	Sit on command (35)	Yes	Yes/No	No	–	Age, ownership history, training history
Crow	Exchange (36)	Yes	Yes	–	–	Effort
Raven	Exchange (36)	Yes	Yes	–	–	Effort
Feeding without task						
Chimpanzee	None (32)	No	No	–	No	Rank
Bonobo	None (32)	No	No	–	No	
Gorilla	None (32)	No	No	–	No	
Capuchin monkey	None (94)	Yes	No	–	Yes	
	None (95)	Yes	No	–	–	
	None [(93), study 2]	Yes	No	–	–	

mutualistic cooperation has been demonstrated experimentally in most of the great apes, many monkey species, and also in nonprimates, including elephants, hyenas, and birds (53). Thus, we might expect that members of these species are sensitive to their own outcomes relative to those of a social partner. This would be in line with early work on IA in economics, which linked responses to inequity and cooperation (7). Individuals who perceive unequal outcomes may use this information to cease cooperation and find a new partner. If outcomes are sufficiently unequal, by chance alone cooperating with other partners will likely result in better outcomes (43). Research in other species supports a connection with cooperation in three different ways: (i) responses to inequity in the context of cooperation, (ii) phylogenetic comparisons, and (iii) responses in species facing partner-choice restrictions.

Reward distribution in cooperation experiments

Capuchin monkeys have been widely tested on the classical barpull paradigm in which two individuals work together (52). They produce mutual food rewards and appear to grasp the need for a partner (54). However, when individuals cooperate for unequal rewards, their behavior becomes more contingent upon their partner's, reflecting sensitivity to reward distribution. These monkeys show "payment for labor" in that they share more easily with partners who have helped them obtain food than with partners who did not. Conversely, partners quit helping if rewards are not shared (55). This sensitivity to payoffs is not limited to situations in which rewards are preassigned by the experimenter. It extends to those in which the monkeys themselves decide the reward division. Monkeys are less likely to pull for clumped rewards that their partner can monopolize than for distributed rewards that are easily divided. They make this distinction on the very first trial, indicating that it is not a conditioning effect, and the distinction varies with the level of tolerance between both partners (56).

Moreover, although these monkeys cooperate to the same degree for distributed rewards that are either equal or unequal, partnerships that alternated each individual's access to a preferred reward when rewards were unequal were almost three times as likely to cooperate successfully (57). The reluctance to cooperate with a monopolizing partner suggests that it is not inequity per se but the way partner attitude combines with inequity that impedes cooperation. This is reminiscent of children's focus on partiality over inequity (58) and moreover has implications for human cooperation, whereby individuals are not likely to forget the past and cooperate just because the payoff structure is now in their favor. In these experiments, monkeys did not respond with refusal to an isolated instance of inequity but required multiple instances before cooperation broke down (different thresholds for ceasing cooperation may be one cause of the individual variation in these responses). Even if rewards even out over time, in any given interaction one

individual will usually do better than another. The monkeys appeared to integrate outcomes over multiple trials, allowing for cooperation in a wide range of situations.

Chimpanzees, too, are sensitive to reward distribution. They cooperate more successfully with a partner who, in other contexts, shares more tolerantly (59). Given a choice between potential partners, they prefer partners with whom they have a tolerant relationship (60). When goals conflict, such as when two individuals have the option to cooperate for equal (5 versus 5 rewards) or unequal (10 versus 1) payoffs, chimpanzees still manage to obtain food on the majority of trials. Even though dominant individuals prefer the possibility of 10 rewards, on almost half the trials the pair negotiate to work for the equal division (61). On the other hand, given a choice, chimpanzees prefer to work alone rather than collaborate (62) and, unlike capuchin monkeys (55), may not share more with a helper than a non-helper (63). The latter result needs further testing, however, given indications that wild chimpanzees that contributed to a group hunt are given preferential access to the resulting meat (44).





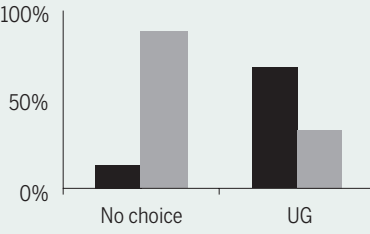
Phylogeny: Cooperative versus noncooperative species

Another way to explore the interplay between cooperation and inequity is to look across species. Pronounced first-order IA has been observed

in chimpanzees and brown capuchin monkeys (4, 6, 16, 22, 27, 28), two species that are highly cooperative—for example, they hunt in groups for prey that is hard to capture by a single hunter (48, 64). Moreover, chimpanzees seem attentive to their partner's rewards, even if they are inferior to their own (16), and both species behave prosocially in at least some experimental tests [(65–67), but see (68, 69)], thus having the potential for second-order IA. Beyond these two primates, recent evidence indicates that bonobos (23) and several macaque species (*Macaca* spp.) (18, 31) also respond negatively to getting a reward inferior to that of a partner. These primates, too, are highly cooperative. There are observations of group hunting in bonobos (70) and, although macaques do not show such behavior, they have an extensive alliance network among both kin and nonkin (71).

On the other hand, primates less likely to cooperate with nonkin, including orangutans (*Pongo* spp.) (19, 23) and squirrel monkeys (*Saimiri* spp.) (17, 20), have thus far failed to show IA. Neither taxonomic relations among the primates nor brain size, relative brain size, or social organization predict the known distribution of IA as well, it appears, as does the tendency to cooperate with individuals who are neither kin nor mates (41). Beyond the primates, IA has also been documented in domestic dogs (*Canis lupus familiaris*) (33, 34), a species derived

Table 2. Studies on a variety of animals thus far have indicated five domains that help explain the variation in IA.

Comparison	IA is facilitated when subjects can easily perceive each other's pay for a task (i.e. sit side-by-side and in full view), which facilitates comparison.										
Phylogeny		Species with extensive cooperation among nonkin and nonmates show more pronounced IA.									
Cooperation	Individuals who equalize outcomes by sharing or alternating between high-level rewards cooperate more successfully.										
Partner choice		IA is most likely to evolve in situations with relatively unconstrained partner choice. This may influence coalition and alliance formation. In contrast, cooperative breeders, with constrained kin-based partner choice, show no IA.									
Cognition	Second-order IA (aversion to overcompensation) is a form of conflict resolution resting on anticipation of negative consequences in first-order IA. In the UG, chimpanzees anticipate partner's reactions and choose an equal token (black bar) more often than a selfish one (gray bar) when the partner has a choice (UG) than when it has not (No choice).	 <table border="1"> <caption>Data for Table 2 Cognition Bar Chart</caption> <thead> <tr> <th>Condition</th> <th>Equal Token (Black Bar)</th> <th>Selfish Token (Gray Bar)</th> </tr> </thead> <tbody> <tr> <td>No choice</td> <td>~15%</td> <td>~85%</td> </tr> <tr> <td>UG</td> <td>~75%</td> <td>~25%</td> </tr> </tbody> </table>	Condition	Equal Token (Black Bar)	Selfish Token (Gray Bar)	No choice	~15%	~85%	UG	~75%	~25%
Condition	Equal Token (Black Bar)	Selfish Token (Gray Bar)									
No choice	~15%	~85%									
UG	~75%	~25%									

from a long line of cooperative hunters (72). Like monkeys, dogs are sensitive only to whether their outcomes are wanting as compared with those of others (35). Corvids are cooperative birds (73), and some species have shown IA in experiments. They may be more sensitive to inequities in effort than in reward, however (36).

Future research is needed to determine the degree to which the hypothesis of coevolution of IA and cooperation (41) extends beyond these species. For instance, do other animals with frequent nonkin cooperation, such as elephants, cetaceans, and noncanine social carnivores, also respond negatively to situations of inequity? We also need more research on noncooperative species. For example, a comparison between domestic cats and dogs may be useful, where we would predict cats (solitary hunters) to be less sensitive to reward distribution than dogs.

Constrained partner choice

Not all cooperative animals can easily find new partners. For example, the *Callithrichidae* (marmosets and tamarins) are cooperative breeders, a social system in which both parents and adult offspring are essential for offspring care. For obvious reasons, the cost of partner switching is high. Of the two callithrichid species tested on IA, neither responded negatively to receiving a lesser reward than their social partner (20, 74). Even though not classified as cooperative breeders, owl monkeys (*Aotus spp.*), too, show pair-bonding and dual parental care and also fail to respond to inequity (20).

Even without cooperative breeding, in species with relationships developed over many years of play, grooming, mutual support, and other services, responses to inequity should wear off since replacement of long-term partners becomes too costly. There is indeed evidence that IA is less pronounced in well-established human friendships compared with relationships among acquaintances and colleagues (24), and the same has been reported for chimpanzees. A group of captive chimpanzees that grew up and lived together in the same space for more than 30 years showed far less IA than a similarly housed group of chimpanzees with a much shorter history (22).

Future research is needed to explore the degree to which both relationship quality and the costs of partner switching influence responses to inequity. One might predict, for instance, that if the evolution of IA requires cooperation under relatively unconstrained partner choice, hunting parties may be a prime example. Hunting parties change composition from one occasion to the next, whereas long-term friendships and pair-bonding may not be as conducive to pronounced IA. In the laboratory, we might anticipate that individuals show different responses in newly formed partnerships as compared with longer-term ones, particularly in the case of biparental care or cooperatively breeding species in which long-term relationships have produced offspring. For species for whom the costs of partner switching are too high, we may expect to see other partner-control mechanisms, such as punishment,

play a greater role (75). Understanding the situations in which partner choice influences inequity responses will be critical for understanding the formation of coalitions and alliances (76).

Second-order inequity aversion

Until recently, second-order IA was unreported for nonhuman animals. Its explanation is more complex than that of first-order IA, which simply requires that one individual responds to an unequal outcome to avoid being taken advantage of. For second-order IA, in contrast, the advantages are less obvious, because this reaction occurs when the actor enjoys an advantage. Apart from humans, evidence for second-order IA is thus far restricted to chimpanzees. The first sign came from a study in which the apes reacted negatively not only to a lesser reward but also when they received a better one. In other words, subjects responded to any inequity, not just the disadvantageous kind (16). Subsequently, chimpanzees were tested on the UG, considered the gold standard of the human sense of fairness (see “Responses to inequity” above). In most cultures, humans typically offer a 50/50 split (77, 78). In contrast, one UG study on chimpanzees found them to share the smallest possible amount with their partner [(79); see also (80)]. However, because the methodology of this experiment deviated substantially from the typical human UG, Proctor *et al.* (Fig. 2B) (81) applied a more intuitive UG for both apes and 3- to 5-year-old human children.

Proposers were presented with a choice of two differently colored tokens that could be exchanged for food. The tokens represented equal versus unequal reward divisions, and the partner needed to agree and participate in the exchange (Fig. 2B), an element similar to the typical human UG. Token choices in this situation were compared with choices when the partner's agreement was not needed. Similar to humans in the UG, the chimpanzees more often split the rewards equally if they needed their partner than if they did not. Because children behaved similarly in this token-exchange game, the study suggests shared patterns of proactive decision-making in relation to fair outcomes in both species (81).

Even though neither the apes nor the children in this study actively refused offers, behavioral protest did occur. Subjects occasionally reacted to selfish offers by spitting water at the other or hitting the mesh partition (apes) or saying “you got more than me” (children). Acceptance of offers despite behavioral protest is typical of young children (82). Strategic choices in the UG may be tied to emotional control rather than to social preferences, knowledge of norms, or perspective-taking abilities. In one study, 85% of the younger children claimed to reject unfair offers, but only 12.5% of them actually did. Only after 7 years of age do children resist the temptation of rewards and begin to refuse low offers for strategic reasons (83).

Reasons to refuse unfair offers in the UG are obvious enough. Refusals punish the actor, which may lead to better outcomes in the future. The individual making the offer, on the other hand,

may anticipate negative reactions and strive for an equitable outcome to forestall them. This would amount to anticipatory conflict resolution, which may be the main rationale for second-order IA if those who divide the rewards try to eliminate reasons for frustration in their partners (Fig. 1). The better the anticipatory capacities of a species, the better it will be able to avoid first-order IA in others by showing second-order IA. Planning ahead has been demonstrated in apes in relation to tool use (84), as has anticipatory conflict resolution. Captive bonobos and chimpanzees show a grooming and play peak right before feeding time and engage in high levels of appeasing and sociosexual body contact upon food arrival (85, 86). These primates thus anticipate competition and actively seek to reduce it. Second-order IA in chimpanzees may serve the same goal. Given the need to anticipate the partner's reactions as well as forgo short-term positive outcomes to gain long-term ones, individuals must have some emotional control. Although there are no studies linking self-control and IA in other species, in human children self-control is a limiting factor. Perhaps not surprisingly, the species with strong IA responses also delay gratification in experimental tests [e.g., (87, 88)].

Finally, second-order IA may directly benefit an individual by enhancing its reputation, which may increase that individual's long-term access to beneficial relationships (12). Humans are much more likely to donate in a public goods game when they are recognizable (89) and cooperate more when they have the feeling of being watched (90), indicating that being nice only occurs when positive fitness gains are expected from a second-order IA reaction. To what degree this explanation may apply to species other than our own is as yet unclear, although there is evidence that apes pay attention to the generosity of others without necessarily having directly experienced it (91).

The evolution of fairness

Not only are signs of first-order IA evident in several cooperative species, in the form of a negative reaction to disadvantageous unequal outcomes, but also our closest relatives, the anthropoid apes, show evidence of second-order IA, an essential component of human fairness because it seeks to equalize outcomes. Thus, humans and other species seem to share basic reactions to inequity, which serve the need for sustained cooperation (Table 2). Humans' unprecedented brain enlargement allows for greater understanding of the benefits of self-control in the context of resource division. Additionally, the development of language enabled communication about third parties, which may have enhanced the role of reputation building. Despite these differences, many of the basic emotional reactions and calculations underlying our sense of fairness seem rooted in our primate background. We suggest that future research more explicitly investigate what we consider the key variables underlying IA, including dependence on cooperation, anticipation of the way resource division affects relationships, and

the freedom to choose and change partners, as well as the relative roles of first- and second-order IA. A cross-species investigation with a standardized paradigm may further illuminate the factors involved and help verify or falsify the model proposed.

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Evolution of responses to (un)fairness

Sarah F. Brosnan and Frans B. M. de Waal

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The evolutionary benefits of behaving fairly

Humans have a deep and innate sense of fairness. Humans, however, are not the only species to react to apparent inequities. Brosnan and de Waal propose that inequity aversion can be broken down into two levels. At the most basic level, individuals react to immediate unequal distribution of a reward for equal effort expended, whereas at the second, they show the ability to accept a current unequal distribution with the expectation that over time distribution will equalize. This second level facilitates cooperation over time and requires the cognitive abilities both to assess current distribution and envision future opportunities for equalization. As cognitive abilities advanced across the primate lineage, this more complex accounting of equal distribution and cooperation may have developed into the complete sense of fairness we see in humans today.

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