

Nonhuman Species' Reactions to Inequity and their Implications for Fairness

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It is well known that humans respond negatively to inequity, but until recently little has been known about such responses in animals. Previous observational research in animals has shown hints that animals do respond to inequity. Chimpanzees respond with temper tantrums if they do not get what they desire, social canids refuse to play with individuals who violate social rules, and ravens show third party intervention against norm violations. Recent experimental work with nonhuman primates has given us a more detailed understanding. Capuchin monkeys and chimpanzees both respond negatively to distributional inequity. Moreover, chimpanzees show significant variation in response depending upon the social group they inhabit, with those from a short-term group or a relatively asocial living situation showing a much greater response to inequity than those from a long-term stable group. This mirrors human variation in responses to inequity, which are based upon the quality of the relationship. In this paper, I attempt to define "fairness" in a way that is useful for nonhuman studies and clarify what aspects are being examined in animal societies. I then place the animal work in the context of the studies on humans, especially as related to research in social psychology and economics. I conclude that studying the inequity response in animals is useful for a number of reasons, including the opportunity to gain insight into how this response functions in less complex organisms and social systems and clarification of our understanding of the evolution of this behavior.

KEY WORDS: fairness; inequity response; inequity aversion; nonhuman primate; nonhuman species.

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“THAT’S NOT FAIR!”

Most of us are accustomed to hearing this phrase, but what does it really mean? Does the idea of “unfairness” mean that the situation is not equal, is not equitable, or does not meet some other predetermined standard of “fair”? (Think here of the discrepancy between a fair salary for a well-performing baseball player and that of a favorite teacher—it may be debatable who is a greater asset to society, but no one in modern America would expect them to receive anything close to equal salaries.) This topic is of great interest to individuals ranging from students of the law weighing the justice of a decision to an average person mulling some outcome in their lives. A great deal of research has been devoted to what people perceive as fair in social psychology and in economics, with the social psychologists attempting to determine the psychological underpinnings and repercussions of this emotional response and the economists beginning to redraw the classical rationality assumption of economics with a more accurate approach that includes emotional responses. With all of this information regarding the sense of fairness in humans, it is surprising that only recently have scientists begun to take a look at other species.

If a sense of fairness seems ubiquitous in humans, it is not at all certain in nonhuman species (hereafter animals). In fact, there has been little speculation on the capability and even less empirical research; the first test explicitly examining how a nonhuman responds when treated unfairly was published only recently (Brosnan and de Waal, 2003a). One reason for this is the difficulty of determining subjective opinions in a nonverbal species. However, it is logical that if humans have developed a sense of fairness because it is beneficial in their interactions, this trait may have arisen in the primate (or another nonhuman) lineage and thus be present in other species as well (Brosnan and de Waal, 2004b). For instance, in humans, it has been proposed that individuals who have a sense of fairness are more likely to be successful in cooperative interactions (Fehr and Schmidt, 1999). There are a plethora of animal species that cooperate (Dugatkin, 1997), and any of these could have potentially developed a sense of fairness as well. How this trait varies between different animal species, and between humans and nonhumans, can give us insight into different situations in which the sense of fairness is advantageous, and perhaps insight into the evolution of cooperation and fairness in humans. Understanding the different stages of the evolutionary development of the sense of fairness allows us to understand more about why this behavior was important (ultimate causes) and how it works in the individual itself (proximate mechanisms). Despite the difficulties, carefully controlled studies, each geared towards some specifically defined element of the sense of fairness, can help us uncover this phenomenon in nonhuman species.

There are hints that other animals do compare their rewards to those of others. For instance, some animal species live in relatively tolerant societies, in which everyone receives some 'piece of the pie' (de Waal, 1996). Although not everyone receives the same sized piece, such a system may lead individuals to expect some level of equity between themselves and others. Individuals who do not get what they think they should receive may react, for instance, by having 'temper tantrums', in which the animal expresses serious discontent, typically directed at an offending individual.

Although there is good anecdotal or inferential evidence for reactions to inequitable distributions, in observational studies it is difficult or impossible to get at the underlying causation of the behaviors. Furthermore, the sense of fairness is proposed to be based on social emotions, like envy, greed, or moral indignation (Frank, 1988, 2001; Sanfey *et al.*, 2003), and it is challenging to uncover animals' emotions. This, too, makes studying fairness in animals a great deal more difficult. However, carefully controlled observational studies and experimental work can get around many of these problems, as has been well demonstrated by the rise in animal studies on other topics related to emotions, such as empathy, forgiveness, anxiety, and gratitude (Aureli and Smuncy, 2000; Bekoff, 2000; Bonnie and de Waal, 2004; de Waal and van Roosmalen, 1979; Flack and de Waal, 2000). As with these other topics, studying the sense of fairness in nonhuman animals allows us insight into how the behavior functions in a less complex system as well as some speculation on the origins of the behavior.

A SENSE OF FAIRNESS IN ANIMALS?

Imagine the following situation. Nancy loves cucumbers, and will always eat them if given an opportunity. However, one day she sees Winnie getting a grape (which they both like better than cucumbers) and then she is only given a cucumber! Nancy immediately throws the cucumber on the ground and turns away. Does this sound like anyone you know? Substitute chocolate for vegetables and the answer is probably yes. However, Nancy and Winnie are both capuchin monkeys showing a species normal response to distributional inequity (Brosnan and de Waal, 2003a).

Capuchin monkeys are not the only ones who react to inequity, either. Chimpanzees throw temper tantrums if their expectations are violated (Fig. 1). Social canids (e.g. wolves, coyotes, and domestic dogs) have a set of social rules regarding how rough play among juveniles can be, and if these rules are violated, the offending individual is excluded from play sessions. These are only a few examples in a relatively new field of study, but even from these it seems that animals do react when they feel that they have been treated inequitably.



Fig. 1. A chimpanzee, not getting the food it desired, throws a temper tantrum directed at the food possessor. Photograph courtesy of Frans B. M. de Waal.

Before embarking on a discussion of animals' sense of fairness, however, it is necessary to first define what is meant by "fairness" and how this can be approached in animals, then give a brief summary of what we may expect to find out about fairness in animals based upon both our knowledge of fairness in humans (garnered primarily from psychology and economics) and our knowledge of how animal societies are structured. Following this, I will discuss the evidence, both observational and experimental, for fairness in animals. I conclude with a delineation of the important questions to address regarding the sense of fairness in animals.

WHAT DO HUMANS THINK IS FAIR?

Humans appear to have a well-developed sense of fairness, responding poorly when they are treated unfairly, giving more than the minimum required in experimental games (Henrich *et al.*, 2001) and frequently

punishing in situations in which another individual behaves noncooperatively (Fehr and Rockenbach, 2003; Kahneman *et al.*, 1986; Zizzo and Oswald, 2001). To varying degrees, these inequity averse responses are seen across a wide variety of cultures and vary significantly depending upon the quality of the relationship between the individuals involved (Clark and Grote, 2003). They have recently been linked to emotional, as well as rational, processes (Frank, 1988, 2001; Sanfey *et al.*, 2003). There is some disagreement as to whether these responses are the result of “misfires,” that is, behaviors applied in an incorrect context (Johnson *et al.*, 2003), or have evolved to increase an individual’s relative fitness over the long term (Fehr and Gächter, 2003; Fehr and Henrich, 2003).

Different disciplines have different labels for the study of this phenomenon. In behavioral economics, it is often referred to as inequity aversion, and the bulk of research relates to how humans respond to situations involving division of cash (e.g. Camerer, 2003). In the early social psychology literature, such research was carried out under the rubric of equity theory, and researchers were interested not only in how individuals restored equity, but also in the mechanisms which individuals use to do so, including compensation and, in lieu of direct equity restoration, psychological leveling mechanisms (Walster *et al.*, 1978). Finally, current research in social psychology addresses the issue in relation to procedural justice, organizational justice, and distributive justice (for a recent review, see *Personality and Social Psychology Review*, Vol. 7, No. 4—a special issue guest-edited by Linda J. Skitka and Faye J. Crosby).

An important distinction is made in inequity research in humans between situations which provide more benefit to the self and those which provide more benefit to another. The first concept is alternately termed ‘disadvantageous inequity aversion’ (IA) by experimental economists and ‘undercompensation’ by social psychologists and refers to situations in which the actor receives less than another individual (Fehr and Schmidt, 1999; Walster *et al.*, 1978). The second concept is relevant to a broader range of situations. Termed ‘advantageous inequity aversion’ (IA) or ‘overcompensation’, this refers to situations in which the actor receives more, or sees a third party receive more, than another individual. This can result either because the actor himself receives more (is overcompensated) and the partner receives less, or because the actor observes an inequitable interaction between two other individuals. In both situations, reactions to inequitable distributions can include sanctioning or punishment, psychological justification (e.g. degradation of the undercompensated individual) or rewarding of the undercompensated party by the actor.

There is some disagreement concerning the strength of the effects of advantageous IA in humans, in many respects reflecting the different disciplines in which the evidence is gathered. In economics, there is evidence

that people are more concerned with disadvantageous IA than with advantageous IA. This may reflect the discipline's focus on the exchange of money, rather than on psychological mechanisms. For instance, whereas people prefer equity to any sort of inequity, if inequity is present advantageous inequity is typically preferred to disadvantageous inequity (Loewenstein *et al.*, 1989). Furthermore, in an experiment in which subjects had to choose between two distributions (giving cash to self and another), if they were given an option between complete knowledge of both distributions or knowledge of only their own payoffs, subjects typically chose to ignore information that could have led to a fairer outcome at some cost to the self (Dana *et al.*, 2003).

Psychology research, on the other hand, indicates that advantageous IA can be quite important. People tend to respond negatively to both disadvantageous *and* advantageous inequity. Furthermore, when they are unable to restore actual equity, people often respond with psychological leveling mechanisms rather than material compensation. These mechanisms justify to the self why they deserved a superior reward and, hence, level the playing field (Walster *et al.*, 1978). In experiments where individuals can either allocate hypothetical funds or judge existing hypothetical allocations, allocators typically made equal allocations, even when they could have used information given to justify overbenefitting themselves. Interestingly, although judges tended to perceive these hypothetical allocations, which overbenefitted themselves, as almost as inequitable as those that benefited their partners, in one situation there was a strong bias favoring the in-group, indicating that there are situations in which people believe that equity is not the most desirable outcome (Diekmann *et al.*, 1997). Finally, behavior may be altered by a feeling of overbenefitting; for instance, children who perceive they were favored as children experience altered relationships with both parents and siblings (Boll *et al.*, 2005).

In psychological research on social justice, there are also distinctions made between procedural justice and distributive justice (e.g. Lind and Tyler, 1988). These distinctions provide a valuable framework for dissecting the factors involved in people's decisions. However, research in nonhumans has not yet reached the stage where we can address these different categories. Thus, I will not mention this distinction further in this article, but I hope that the time will come soon when they may be applied to nonhuman research as well.

Envy versus Greed

Reactions to inequity are obviously based upon expectations; this has been known with respect to nonhumans for almost 80 years (Tinklepaugh,

1928). Early studies with primates showed that they had expectations based upon what they had previously experienced and became upset if those expectations were violated. Tinklepaugh showed that individual monkeys will react negatively if they receive a reward that is less desirable than what they have been led to expect. He allowed macaques to observe him hiding an attractive food reward under a bucket. The next day he lifted the bucket and gave them the reward. On occasion, he would replace the good reward with a piece of lettuce without their knowledge. In these situations, when the bucket was lifted the monkeys reacted negatively, presumably because of the discrepancy between what they expected and what they actually received. These macaques' reactions were clearly based on violations of their expectations, but it is not necessarily a violation of equity because those expectations were based on what they had received in the past, rather than on what another individual had received. Perhaps their response is best described as feeling disappointed.

In observational studies involving chimpanzees, reactions similar to these have occurred in social situations. Individuals occasionally throw "temper tantrums" in situations in which their expectations for an outcome are apparently not met. Such reactions consist of screaming, chasing the individual responsible for the problem, beating of fists, etc., and generally appear similar to that of a young child. These tantrums typically arise in situations in which an individual expects some outcome that apparently does not occur. A good example is weaning conflict, although such reactions are seen in adults as well and have been interpreted as evidence for a crude moral sense in apes. Such reactions are assumed to be related to violations of expectations, which may arise when a situation is not equitable. However, with an observational study, it is difficult to quantify the cause of the perceived inequity and the tantrum is only a rough behavioral cue to the individual's state of mind (de Waal, 1996). Thus, although these are tantalizing clues that certainly point towards the possibility of an inequity response in these species, it is necessary to fortify these observations with experimental data.

Finally, to be truly based upon fairness concerns, the reaction cannot be based on a reward that is present but not actually given to another individual. To give an example, a child may desire ice cream as a snack rather than an apple because she knows that there is ice cream in the freezer, but it is not envy unless someone else is given the ice cream rather than an apple. This distinction is particularly important in experimental work on the sense of fairness, when researchers must distinguish between greed—wanting something that is a possibility—and envy—wanting what another individual possesses. Although at this point we cannot truly ascribe envy to a nonhuman, because we do not know

their motivations, we can study expectations based on what another individual receives.

The Evolution of the Inequity Response

There are several areas in which a strong reaction to inequity is proposed to be beneficial. First, it has been proposed that in the social arena, an aversion to inequity may promote beneficial cooperative interactions, because individuals who recognize that they are consistently getting less than a partner can look for another partner with whom to more successfully cooperate (Fehr and Schmidt, 1999). This should provide a more profitable environment for interaction for all cooperators.

Second, and related to this, having strong reactions to inequity may be one of Frank's proposed commitment devices (Frank, 1988, 2001). Such commitment devices are strong, emotional responses that are not under conscious control that cause people to respond in predictable ways to situations that might be against their best interest. Such devices may cause individuals to make "irrational" choices in the short-term, committing themselves to a path (such as revenge or romantic love) that leads to more propitious situations in the long term by convincing others of their high level of dedication to the situation. Similarly, reacting to an inequitable situation may cause a short-term loss if the individual sacrifices a potential (and inequitable) gain (e.g. refuses to accept advantageous inequity). However, this may have future benefits as it may discourage others from acting inequitably towards them in the future, or it may encourage other equitably minded individuals to seek them out for interactions. Thus, responding to inequity may act as a sort of insurance policy for ensuring future beneficial cooperative interactions. Aversion to inequity could serve a similar role in nonhumans, who show high levels of cooperation and evidence of emotional responses.

If the inequity response has evolved because it increases fitness, which I believe to be the case, this response probably did not arrive *de novo* (Brosnan and de Waal, 2004b). The links between current behavior and the long-term payoffs of rejecting inferior (yet positive) rewards seem too tenuous to have given rise directly to the sort of complex inequity responses we see in humans. I believe that the inequity response arose through a series of steps that at each point increased the individual's relative fitness. Assuming that this evolved before the hominid lineage split from the rest of the primates, these evolutionary precursors to inequity aversion are likely to be seen in other species, particularly nonhuman primates. By outlining the elements that are presumably required, we can look for inequity related behaviors in

other species, learn something about the preconditions for the behavior, and perhaps extrapolate information concerning the evolution of the behavior.

Disadvantageous inequity aversion refers to the willingness to sacrifice potential gain to block another individual from receiving a superior reward (Fehr and Schmidt, 1999), yet its evolutionary precursors may be much simpler. A first step is the recognition that other individuals obtain rewards that are different from one's own. Such an ability is also necessary for social learning, which has been documented in a number of species, including chimpanzees (Whiten, 1998; Whiten *et al.*, 1996) and capuchin monkeys (Brosnan and de Waal, 2004c). At the second level, the maligned individual reacts to this discrepancy, which requires that the individual feel strongly enough about the discrepancy to alter their behavior. At the third level is the willingness to sacrifice in order to punish a lucky individual. Following the evolution of disadvantageous inequity aversion, we speculate that advantageous inequity aversion may develop. It seems unlikely that one would notice or react to inequitable circumstances harming another individual before noticing one's own negative outcomes. Thus, there was likely little to no selective pressure for advantageous inequity aversion prior to the evolution of a reaction when one is underbenefitted. Such advantageous IA leads to the development of a proto-moral system in which individuals attempt to rectify discrepancies relative to others.

Of course, just because human and nonhuman animals have a trait in common does not necessarily mean that there is phylogenetic continuity. Similarity can be caused by common descent (homology) or by independent evolutionary events (analogy). For example, wasps, bluebirds, and Mexican free-tailed bats all have wings, but this is not due to common evolutionary descent but the independent evolution of wings at least three times during the evolution of animals. However, like physical traits, behavioral traits can be compared using a technique called behavioral phylogeny to ascertain the relative likelihood of common descent (Boehm, 1999; Preuschoft and van Hooff, 1995; Wrangham and Peterson, 1996). Such a technique will be very useful as more information is learned about the inequity response in a variety of different species, and may help us determine situations in which inequity responses evolved versus those in which inequity is a byproduct of advanced cognition or sociality.

WHAT DO ANIMALS THINK IS FAIR?

The concept of fairness as it is often used in these disciplines must be re-envisioned somewhat to be useful when discussing nonhuman species. In social psychology, fairness or justice is based upon people's subjective understanding of the equity of the situation. Such subjective approaches are

impossible in nonhumans, as we cannot ask them to relate their feelings on the matter or administer a survey in an attempt to assess their understanding of the situation. Thus, we must rely on the information provided by their behavioral reactions to inequitable situations, which makes it much more difficult to uncover psychological mechanisms.

One aspect of fairness that can be applied to humans and nonhumans alike is self-sacrifice in which individuals choose sub-optimal outcomes for themselves in order to maintain the conventions or norms societally considered to be “fair”. Scientists can assess nonhuman animals in this realm through behavioral observations of their reactions to different situations.

At this point, we know very little about nonhumans’ reactions to inequitable or unequal situations. Thus, prior to discussions of fairness, we must first investigate the species’ reactions to personal equity and inequity and determine the species’ conventions relating to fairness. We also have not yet begun to address how individuals may come to violate fairness norms in these species in the first place. Thus, in order to be consistent throughout this review I will use the term “inequity response” when referring to animals, and suggest its use in the future to cover the entire broad group of responses to inequity. This emphasizes the fact that in many cases involving nonhumans it is a response, or behavior, to an inequitable situation that is being studied, and not necessarily fairness in the sense usually intended in the human social psychology literature.

The Effect of Hierarchies and Dominance on the Sense of Fairness

Due to the hierarchical nature of animal societies and the often extreme imbalances in power, distributive fairness in animals will almost certainly not be about equality. Instead, fairness will probably center on equity or lax equality, keeping the distributions between individuals even enough that all of the players are willing to continue their participation in the joint effort. In fact, using the term “fair”, with the human connotations of such things as morality, may not be justified in many species.

In all animal societies, most of the variation between individuals is probably due to the character of the relationship between dominants and subordinates (de Waal, 1991, 1996). Individuals who are dominant in the group get more. They may or may not provide more (for instance, having a large alpha male may help in conflicts between groups of the same species, which benefits all group members), but dominants will collect most of the benefits in terms of food, mates, social partners, and breeding success. Subordinates, on the other hand, can choose to stay in the group and accept their lesser share, to diminish their participation to the lowest acceptable

level (think here of the employee who does just enough to avoid being fired), or can leave the group and try their chances somewhere else.

However, no social animal is completely free to leave their group, so the ease with which the dominants can coerce subordinates will depend upon the ease with which subordinates can leave (Vehrencamp, 1983). This will be a trade-off for both parties. Subordinates who emigrate leave offspring and other family, as well as a chance to be the dominant breeder in the future (Kokko and Johnstone, 1999), and face a very high cost when entering another group, making them unlikely to leave the group without serious cause. This empowers the dominant to maintain the inequitable balance. However, all social animals, including dominants, rely on each other for food, social interaction, and protection from both predators and other conspecifics (Krebs and Davies, 1993), so a dominant who tips the distribution too far to the inequitable side may find himself or herself without group mates. Much of the variation in dominance hierarchies may be due to outside ecological pressures; despotic dominance hierarchies, in which the dominants have full coercive power, are much more likely in situations with high competition for food or serious outside pressure from other conspecific groups or predators (van Schaik, 1989). Such a trade-off of alternatives occurs in humans as well. For instance, in close relationships any individual who is less dependent upon the other becomes dominant in decision-making due to their greater ability to seek alternatives (Kelley, 1979).

Thus, equity in a group of animals may boil down to finding a balance in which dominants get the lion's share but make staying in the group attractive enough that their subordinates do not abandon them. Obviously, these parameters will shift from species to species and group to group, dependent upon the factors just discussed. Conventions regarding fair distributions will depend a great deal upon an individual's species and his or her place within the hierarchy of the group.⁴

What Do We Expect to Find in Animals?

Obviously, then, we expect to find some level of inequity, but this should be tempered by the dynamics of the group. Given the difficulty in understanding all of the dynamics of a social group, in practice this will probably mean looking for different levels of the inequity response among different individuals or groups.

⁴The ideas presented in this subsection draw heavily on a presentation given by Oliver Goodenough at a conference on Law, Behavior, and the Brain hosted by the Gruter Institute for Law and Behavior in May, 2004 in Squaw Valley, California. I am grateful to Oliver for bringing this to my attention and for a long discussion that helped me formulate these ideas.

Much of the human research on fairness focuses on the reaction of individuals when they are treated inequitably, and this is the most obvious way to study animals as well. In fact, research has already begun in this area (Brosnan and de Waal, 2003a; Brosnan *et al.*, 2005; de Waal, 1991). Our goal is most easily accomplished in an experimental situation, but it can also be accomplished by observations of the group if it is known which behaviors reliably indicate distress and which situations might result in truly inequitable situations. In many cases, the reactions are easily quantified (refusal to participate, refusal to interact with the offending individual, protest, etc). Potentially, we can look at how individuals respond when they observe another individual being treated unfairly. Such reactions may take the form of long-term interactions, with favors given later in the day or consolation that offers psychological, if not material, support. Finally, we can examine how animals respond when they are given the chance to rectify inequity by assisting another with either favors or material donations. This is most easily quantified in experimental situations, as in an experiment examining choices about reward distribution.

There may also be significant variation in responses due to social group identification or relationship quality. In humans, there is considerable variation among different cultural groups in how their members respond to unfair situations (Henrich *et al.*, 2001; Lind and Earley, 1992). Furthermore, there is a great deal of variation based upon individual relationships. Individuals in positive or neutral relationships tend to be much more oriented towards equity than those in negative relationships (Loewenstein *et al.*, 1989), and individuals in close relationships are much more likely to possess a communal orientation than are those in less close relationships, who show a contingent response (Clark and Grote, 2003). This may be due to either a difference in perception or a difference in the span of the time frame used for assessment of equity.

In fact, this is not so different from animal societies. Many animal species show evidence of “cultural” variation or socially transmitted traditions that differ between groups (Fragaszy and Perry, 2003). Chimpanzees show variation in several dozen different behaviors ranging from tool use strategies (e.g. ant/termite dipping or nut cracking) to social interactions (e.g. the use of a “leaf clipping” display or hand-clasp grooming) (de Waal and Seres, 1997; Lefebvre, 1995; McGrew, 1992; McGrew and Tutin, 1978; Nishida, 1980; van Schaik *et al.*, 2003; Whiten *et al.*, 1999; Wrangham *et al.*, 1994). However, chimpanzees are not alone in this; another great apes species, the orangutan, shows cultural variation in tool use (*Pongo pygmaeus*; van Schaik *et al.*, 2003), and various macaque species show cultural variation in both foraging and play behaviors (*Macaca* sp.; Huffman, 1996; Wheatley, 1988). These examples mainly include material culture, but other species show cultural variation in group character and social behaviors.

Baboons show cultural transmission of group standards of behavior (*Papio anubis*; Sapolsky and Share, 2004), and capuchin monkeys show cultural variation in feeding behavior and social traditions (*Cebus capucinus*; Panger *et al.*, 2002; Perry *et al.*, 2003a; Perry and Manson, 2003; Perry *et al.*, 2003b). Furthermore, the nonhuman primates are not alone in showing culture; such behavior has been proposed in species ranging from rats to cetaceans (e.g. Deecke *et al.*, 2000; Terkel, 1996).

Animals are also capable of showing contingent behavior and can take into account the social environment and how it will affect expected payoffs. For instance, several species adjust their food calling depending upon both the social environment and the quantity or divisibility of available food (Caine *et al.*, 1995; Chapman and Lefebvre, 1990; Elgar, 1986; Evans and Marler, 1994; Hauser *et al.*, 1993; van Krunkelsven *et al.*, 1996). In one study, it was found that individuals suppressed calls for a small, unshareable amount of food but did not for a larger amount of food (15 apples) that presumably could not have been consumed before the food possessor was discovered by the group (Brosnan and de Waal, 2003b). In another study, unrelated to food calling, capuchin monkeys adjusted their willingness to participate in a cooperative task dependent upon the food distribution. If the food was distributed such that each individual could easily obtain their food upon participating, cooperation occurred frequently. However, if the position of the food was adjusted such that one individual could easily dominate both food rewards, cooperation failed to occur from the first trial, indicating that the subordinate monkeys did not need experience to recognize that this situation was unlikely to be rewarding (de Waal and Davis, 2002). There is a high likelihood that, as with humans, animals will show variation between groups and across relationship types.

Animals may have a different assessment of value depending upon other factors unrelated to the current interaction. Individuals behaviors may be affected by their gender, their rank, whether they are pregnant or lactating, whether they have recently eaten, been groomed, or mated, as well as their personal preferences for various commodities (Seyfarth and Cheney, 1988). Such variation makes observational research (in humans and nonhumans) challenging, and requires a careful tuning of rewards and efforts in experimental research.

Along these lines, in many animal species the level of despotism present in the dominance hierarchy will make a significant impact on distributions. A subordinate individual in a relatively tolerant species (e.g., a chimpanzee), can throw a temper tantrum in front of a dominant with little expectation of retribution, but a subordinate member of a relatively despotic species (e.g., a rhesus macaque) has no recourse against a more dominant individual (de Waal, 1991). Because of this difference, individuals in tolerant societies may

have some expectation of equity in day-to-day transactions, while those in less tolerant societies may never view equity as a possibility (de Waal, 1996).

One promising (if challenging) area of animal research pertains to the link between social emotions and the sense of fairness. Obviously, animals cannot be asked what their feelings are (as humans can), so we rely on observation of behaviors correlated with different presumed emotional states. Recent advances in neural imaging and physiological evaluation measures may make it easier to correlate human and animal emotions using brain activation as a proxy. Although this, too, is fraught with peril (human and animal brains are different in form, and perhaps function as well), it may be a good way to rigorously investigate emotions in nonhumans. Both imaging data and behavioral sequences can be related to complex behaviors such as the inequity response, reconciliation, gratitude, and even morality. Historically, all of these subjects have been limited to human research, but they are currently experiencing a surge of interest in animals as well.

Finally, as mentioned previously, behavior related to fairness is more likely in cooperative species. Taken as a whole, these approaches will allow us to explore the sense of fairness in animals with the same rigor as in research on humans. As we will discuss next, some steps have already been taken in this direction.

RESPONSES TO INEQUITY IN ANIMALS

Most people who have spent significant periods of time with animals seem to assume that animals respond to being treated inequitably. I have had horse trainers tell me that horses who see another individual receive a superior reward will fail to work for a lesser reward (even if the task has been established as eliciting a lower reward). Dog owners note that their pets react if one gets a treat and the other does not. However, all of this is anecdotal evidence and lacks the rigor of carefully conducted experimental research. Although there has been excellent research on rare behaviors using the compilation of anecdotes (see Byrne and Whiten, 1988 for a good example of this approach), and anecdotes are often a good starting point for a research question, it is always better to provide consistent, empirically gathered data to support scientific hypotheses whenever possible to better demonstrate the causes and consequences of a behavior and to eliminate alternative possibilities.

Initial research investigating responses to inequity or unfairness was based on observational studies. These studies revealed natural examples of situations in which animals seem to be responding to inequitable treatment.

“Fair Play” in Social Canids

One of the first researchers to explicitly investigate the effects of fairness considerations on animal societies was Marc Bekoff, in his work on social canids (Bekoff, 2004). Bekoff studies social play and has found in both wolves and domestic dogs that individuals who do not engage in fair play seem to be at a disadvantage. In play behavior shown by young canids, individuals who are much stronger or older typically self-handicap during play and excessive aggression is not tolerated. This behavior apparently represents a group norm. Bekoff found that individuals who failed to exhibit such leveling behavior were excluded from play sessions. Their playmates failed to solicit rough individuals for play sessions and even left when they joined play groups. As a result, individuals who violate group norms do not interact nearly as much with other pups their age. Play seems to be important for these social animals as an opportunity to learn how to cooperate and negotiate social agreements in a situation in which mistakes or transgressions will be forgiven (Bekoff, 2004).

More startling is evidence that there is a direct fitness consequence to this behavior. Bekoff has found that when coyotes mature, individuals who are ostracized from play sessions are much more likely to leave the pack than those who are included. Furthermore, the mortality rate for individuals who stay in the pack is 20%, while mortality is 55% for those who leave the pack—more than double that of their stay-at-home counterparts. Thus, there is apparently a direct fitness link between playing fairly and early survival, rendering this behavior highly susceptible to alteration through natural selection. To my knowledge, this is the first good evidence of a direct fitness effect of violating social norms or standards.

A model of the evolution of fairness during the development of play behavior further shows that playing fairly may be an evolutionarily stable strategy (ESS) (Dugatkin and Bekoff, 2003). Given two developmental stages and the chance to either play fairly or unfairly at each stage (four different options), all four options could co-exist as long as none was an ESS, but during model simulations only playing fairly at *both* stages of development ever emerged as an ESS. Given this, Dugatkin and Bekoff suggest that fair play should always be more common in species with multiple developmental stages of fairness.

Although this example does not touch on material inequity, which has been the main focus of this review, such an example of behavioral inequity is very useful. First, it extends the scope of the investigation from inequity of material goods to inequitable behaviors, showing yet another area in which the human inequity response may have evolved. Secondly, this provides an exciting glimpse at the way inequity considerations could directly influence

the survival and reproduction of an individual, making it an immediate target of natural selection.

Morality in a Nonhuman?

The above examples of social canids may even represent something akin to morality in animals. Bekoff suggests that in learning the art of social negotiation, conflict resolution, compromise, and cooperation, young canids (and other species) can learn the basics of the social norms that will govern their adult lives in the pack (Bekoff, 2001). Such norms may be the building blocks or the evolutionary precursors of social morality. Thus, social equity and morality may be tightly interconnected.

Working definitions of morality are few and far between, possibly because it is assumed that the concept of morality is already well-understood and possibly because it is such a difficult concept to define. However, morality has been broken down into four components, allowing for a more sophisticated conceptual and rigorous experimental approach. These include a sympathy-related capacity (e.g. attachment, cognitive empathy), a norm-related capacity (e.g. internalization of prescriptive social rules, social expectations), reciprocity (including moralistic aggression), and getting along with others (e.g. peacemaking, intentionality in relationship maintenance, negotiation) (de Waal, 1996; Flack and de Waal, 2000). These building blocks specify behaviors that are observable and measurable in animals, characteristics that are vital for any working definition of a concept as thorny as morality or inequality. Several animal species, including the social canids discussed above and a number of nonhuman primates, exhibit behaviors that seem to fit one or more of these categories (Flack and de Waal, 2000).

However, lest we fall into the trap of believing that complex social behavior is present only in mammals, it is useful to look at another highly social, highly intelligent animal, the raven. Research on birds, particularly ravens and other corvids, some species of crows, and parrots, have yielded reports of cognition and complex social behavior that seem at least equivalent to that of primates (Pepperberg, 2002; Weir *et al.*, 2002), and morality is no exception.

In a long-term study of ravens, Bernt Heinrich finds evidence of third party enforcement of social norms (Heinrich, 1999). Ravens have a social norm that a food possessor can maintain possession of their food regardless of which other ravens are present. Any individual who violates this by attempting to grab a piece will be attacked by another raven that is both unrelated to the food possessor and does not stand to lose any food of their own (e.g. there is no self-serving intent). Thus, it appears that there is an expectation of equitable behavior (in the sense of following social norms) that

is of so much importance to ravens that they will attack the offending party *even though* the aggressor was not wronged. Thus, aggression is used to enforce not only the equitable treatment of one's self, but of others as well.

INEQUITY AVERSION IN NONHUMAN PRIMATES

We have already discussed several examples of the inequity response in nonhuman primates, all gleaned from extensive observation over the years. However, while observational methods can tell us a great deal, observation alone can only show correlation, never causation. Thus, although we may learn that behaviors are related, we cannot know how they influence each other without conducting controlled experiments. Furthermore, as discussed earlier, different individuals may have different preferences that can influence their decisions and bias observational results. In an experimental situation it is possible to rank different individuals' preferences and to control every aspect of the experimental procedure to accurately determine which stimulus is causing a behavior.

In my own work, I have examined inequity aversion in two different primate species, capuchin monkeys (*Cebus apella*) and chimpanzees (*Pan troglodytes*) (Brosnan and Waal, 2003a; Brosnan *et al.*, 2005). These species were chosen because they demonstrate many of the characteristics that seem to be prerequisites for inequity aversion. Both primate species are highly tolerant, so that individuals can expect to maintain possession of items or receive some share of resources, even if they are subordinate. Of course, this relative level of tolerance does not mean that rank is nonexistent or that subordinates frequently protest against dominants, but it does mean that subordinates can protest without fear of retribution. This creates a baseline level of expectation of equity that makes individuals more likely to react to inequitable situations, and hence makes it more likely that reactions to inequity would evolve (de Waal, 1996). These species are also highly cooperative and, as inequity aversion is proposed to promote human cooperation, it seemed logical to first look at two cooperative species (Boesch, 1994; Brosnan and Waal, 2002; de Waal and Berger, 2000; de Waal and Brosnan, 2006; de Waal and Davis, 2002; Mendres and de Waal, 2000).

Furthermore, the fact that both species are closely related to each other—and to humans—allows a comparative evolutionary approach that, although not conclusive, may shed light on the evolutionary trajectory of this trait. Chimpanzees in particular are very closely related to us and are often studied to elucidate the behavior of our early ancestors on the assumption that behaviors shared by apes and humans may indicate that such behavior was present in our last common ancestor (Boehm, 1999; Tomasello, 1999; Wrangham and Peterson, 1996).

This experiment was intended to elucidate only one aspect of a disadvantageous inequity aversion, that is, whether the primates reacted when another individual received a superior reward, and one aspect of advantageous inequity aversion, that is, whether individuals reacted when they were overbenefitted.

Nonhuman Primate Subjects

The subjects included 10 brown capuchin monkeys from two social groups at the Yerkes National Primate Research Center, in Atlanta, Georgia, USA. These included three adult males, two subadult males, and five adult females. None of the males showed any tendency towards reaction so all of the results reported are for the five adult females. All but one of the adult females were pregnant and/or carrying a dependent offspring at some point during testing. The groups in which the subjects lived were housed in two large, indoor/outdoor enclosures. For testing, unrelated (e.g. individuals who are not related through their female lineage) same-sex pairs were separated into a testing chamber. The test chamber was divided by a mesh partition into two equal-sized ($36 \times 60 \times 60$ cm) compartments, such that subjects had visual, vocal, and limited tactile access to a conspecific in the other compartment, but could not physically interfere with the other's interactions with the experimenter. For testing, subjects were enclosed in one compartment while the other compartment either contained the model monkey or was empty. The test chamber was backed by an opaque panel so that in the test chamber, subjects had vocal, but no visual or tactile, contact with their group. This allowed us to interact with subjects in a controlled manner with minimal distractions. Dependent offspring were always allowed into the test chamber with their mothers.

Chimpanzee subjects were adult chimpanzees from the Yerkes National Primate Research Center, Atlanta, GA USA. Four individuals, from the Yerkes Main Center, lived continuously as pairs, housed in indoor-outdoor runs which had a "window" of mesh between neighboring runs that allows the chimpanzees visual and vocal contact with other pair-housed groups. These pairs (1MM, 1FF) were tested in the outdoor section of their runs. Sixteen individuals came from two different social groups at the Yerkes Field Station. These individuals lived in large outdoor corals with interior runs. Each social group consisted of 18–22 chimpanzees (only a subset of adults from each group was tested) with a normal demographic distribution. Individuals entered or left the group only through birth, illness, or death. One group (G-2) had been housed together for more than 30 years (i.e. long-term social group, 8F, 2M), and all subjects but one were born and reared within the group; the exceptional subject was present

at the group formation and was the alpha female at the time of testing. The other social group (G-12) had been put together a mere 8 years before the study (Seres *et al.*, 2001) (i.e. short-term social group, 4F, 2M). Thus, no subject had been born in the group and most individuals had been introduced as adults. For testing, unrelated (e.g. individuals who are not related through their female lineage) same-sex pairs were isolated from the rest of their group in indoor cages of their home enclosure. All subjects were adults, and the age distribution between subjects in different groups was similar.

Experimental Testing Procedure

The procedure used in this test was an exchange paradigm that had previously been used in other testing situations for several years with the capuchins and for 6–10 months with the pair-housed chimpanzees and the long-term social group and for 3 months with the short-term social group (Brosnan and de Waal, 2004a, 2005). However, while familiar with exchange, no subject had had any experience with a situation in which they were rewarded differently from a partner prior to this experiment and no pre-training on reactions to inequity was done prior to the results reported here.

For exchange, subjects were given a token (a small granite rock for capuchins and a 20 cm long, 3.7 cm diameter white PVC pipe for chimpanzees) which they had to return to the experimenter to receive a food reward. Food rewards were placed in bowls or buckets in front of the subjects, who could easily see what was in the buckets. However, neither the subject nor the partner was shown what reward they would receive for any given exchange until they had successfully returned the token.

Food rewards were chosen on the basis of independent dichotomous-choice food preference tests (Brosnan and de Waal, 2004a) to determine which of a pair of food items the chimpanzees preferred. Ultimately, grapes were used as the high value food item for all individuals of both species. Cucumber pieces were used for the low value food for all except for the pair-housed chimpanzees, for which celery pieces were used instead.

Each test session consisted of a series of 50 alternating trials, with trials alternating between the partner and the subject such that each individual received 25 trials per session and the partner always exchanged immediately prior to the subject. Trials were separated only by the amount of time it took the exchanger to get ready for the next trial (approximately 10 s). Individuals were paired with a partner who remained the same throughout testing.

Experimental Paradigms

Each subject underwent four tests. The Equity Test (ET) was a baseline test in which both the subject and the partner exchanged for a low-value reward (cucumber or celery). For the Inequity Test (IT), which determined their response to an unequal reward distribution, the partner initially exchanged a token for a high value reward (grape) followed by the subject exchanging a token for a low value reward. There were also several controls. First was the Effort Control Test (EC), which allowed us to separate the amount of effort from the value of the rewards. In this, the partner was initially handed a high value reward without having to exchange any tokens for it (e.g. it was a gift), following which the subject had to exchange a token to receive the low value reward. Finally, and perhaps most important, was the Food Control Test (FC), which examined how subjects reacted when a higher-value food was available but no other individual received it. This test separates what might colloquially be called “envy” (wanting what another has) from “greed” (see above section for more detail). In this test, the higher value reward was shown to the subject, but not given to a conspecific, following which the subject had to exchange a token for a low-value reward.

For each individual, we measured the frequency of refusals to exchange and the latency to exchange. Refusals to exchange were divided into two categories, not returning the token and refusing the reward. Because subjects were not shown what reward they would receive prior to exchange, both responses represented an unusual reaction to the testing situation. These responses included passive refusals (refusing to return the token or accept the reward) as well as active ones (throwing the token or reward out of the cage). To be conservative, an exchange was only considered a refusal to accept the reward if it never came into the vicinity of the subject’s mouth. Latency to exchange was the amount of time it took for individuals to return the token to the experimenter’s hand from the time they received it from the experimenter. This was measured for all successfully completed exchanges, including those in which the individual failed to consume the food reward.

Capuchin and Chimpanzee Reactions to Inequity

Compared to their reactions when both received the same reward, both capuchin monkeys and chimpanzees were much less likely to be willing to complete the work, a simple exchange, or accept the reward, when their partner got the better deal (see Fig. 2; *Cebus* $F(3, 16) = 25.78, p < 0.001$; *Pan* $F(24, 55) = 3.87, p < 0.0001$; Brosnan and de Waal, 2003a; Brosnan *et al.*, 2005). Moreover, among capuchin monkeys, if the partner didn’t have to do the work to get the better reward, but was handed it for “free,” the

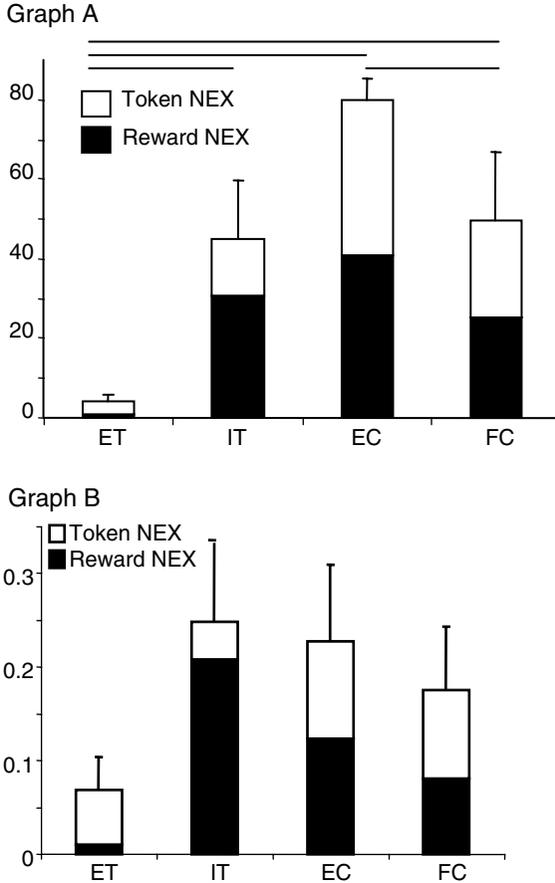


Fig. 2. Mean \pm SEM of failures to exchange for the capuchin monkeys (Graph A) and chimpanzees (Graph B) across the four test types. The black bars represent the proportion of nonexchanges due to refusal to accept the reward (Reward NEX), and the white bars represent the proportion of nonexchanges due to refusal to return the token (Token NEX). ET, Equality Test, IT, Inequality Test, EC, Effort Control, FC, Food Control. Capuchin data reprinted from *Nature* 425, 297–299, chimpanzee data from *Proceedings of the Royal Society of London, series B* 272 (1560), 253–258.

subjects were even more likely to quit participating, indicating that they do pay attention to the effort as well as the value of the reward. Interestingly, the same was not true of chimpanzees, which showed no increased reaction for these no-effort trials. There are several possible explanations for this. First of all, it is possible that chimpanzees simply do not attend to effort required to obtain a reward. However, it seems unlikely that capuchins do attend to effort and chimpanzees do not, particularly as both species attend to reward differences. The more likely possibility is that the amount of effort

required to exchange the token was less significant for the chimpanzees and so they showed no response. For a capuchin monkey, returning the token typically required both hands and a full-body movement. The chimpanzees, on the other hand, could return the token by moving only a single arm and did not have to move from their position. Thus, a future test requiring a greater amount of effort on the part of the chimpanzees is required to determine whether chimpanzees attend to effort.

The results of the critical fourth control, in which a higher value food was visible but no other individual could receive it, indicated that while subjects clearly show some response to the presence of a higher value food, their reactions are also driven by social comparison. Chimpanzees, but not capuchins, showed an overall lower level of response in this EC test than in the IT, implying that they do notice and react differently when a partner does not receive the better reward. However, in both species, the most striking difference was in the level of reaction over the course of the 25-trial session. As compared to sessions in which their partner got the better reward (IT and EC), subjects' reaction to the presence of this high-valued food decreased significantly over the course of the session, indicating that although higher value food items are clearly preferred, they do not elicit quite such dismay if no other primate receives them (Fig. 3; *Cebus* and *Pan* $p < 0.001$). In tests in which their partner received the higher value food, the capuchin's frequency of refusal to participate increased over time, while the chimpanzee's frequency of refusal to participate remained uniformly high.

Effects of Gender and Rank on Responses

There was no effect of rank on reactions in either species. We expected to find that more dominant individuals were much more upset by being treated inequitably than their more subordinate counterparts because even in these relatively tolerant species the dominants are accustomed to receiving more. One possible explanation for this is that the subjects perceived that the inequity was brought on not by their partner but by the human experimenter. In support of this, any negative behavioral reactions (e.g. threats) were directed at the experimenter, not at the partner, and there was no retaliation following the experiment (e.g. the dominant attacking the subordinate).

Among chimpanzees, there was no evidence of a sex difference in response. Males and females were equally likely to react to inequitable treatment. However, among capuchins, only females showed any response to inequity (recall that the reported results are for females only). While we do not know the cause of this difference, it is similar to a sex difference found in

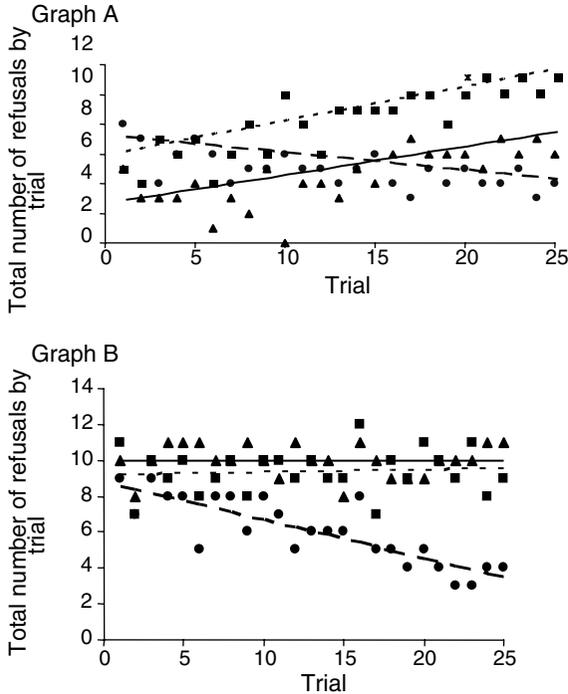


Fig. 3. Sum of the failures to exchange for each subject across sessions within a test type. Graph A represents capuchin monkeys and Graph B chimpanzees. Lines represent the linear regression of the data. Only those tests in which a higher-value reward was utilized are included (IT, EC, FC). Filled squares represent the Equality Test, filled triangles represent the Effort Control Test, and filled circles represent the Food Control Test. Chimpanzee data reprinted from *Proceedings of the Royal Society of London, series B* 272 (1560), 253–258.

previous exchange studies (Brosnan and de Waal, 2004a) and reciprocity work (de Waal, 1997b; di Bitetti, 1997) in this species of capuchin.

Several independent lines of evidence indicate that female brown capuchin monkeys are more reciprocal than males in both food sharing (de Waal, 1997a) and allogrooming (di Bitetti, 1997). In field situations, females allogroom more reciprocally than do males (di Bitetti, 1997). In experimental situations, capuchin males share indiscriminately with almost all partners, regardless of return benefits, whereas capuchin females share on a reciprocal basis, meaning that there is a contingency between give and take (de Waal, 1997a). It has been hypothesized that this different attitude to sharing and exchange may have evolved owing to different reproductive strategies and societal pressures on males and females. Alpha males among brown capuchins are typically the only breeding male in a group for a period of up to 7 years while females remain in the same group their entire lives.

Thus, males may most increase their fitness by sharing indiscriminately with females and juveniles in the group, as they are most likely the fathers of current and future juveniles. On the other hand, females are reproductively vested only in themselves and their offspring and can most increase their fitness by restricting sharing to their own offspring and close female allies with whom they have developed a reciprocal relationship (de Waal, 1997a). Perhaps this asymmetry leads to males who pay little or no attention to inequity within their group, insofar as the benefit is always bestowed upon offspring or the mother of potential future offspring. On the other hand, in females, whose reproductive interests involve female kin or close associates, the asymmetry present in this test may lead them to pay strong attention to equity.

Advantageous Inequity Aversion

Neither species showed advantageous inequity aversion. In the case of the capuchins, no partner ever shared their grape with a subject who was receiving cucumber (Brosnan and de Waal, 2003a). In fact, in several situations in which the subject rejected the cucumber slice, the partner would finish their grape and then reach through the mesh to take the subject's cucumber and eat it as well! Apparently to monkeys, cucumbers taste better if you have already had a grape.

Among the chimpanzees, in the IT and EC tests, in which the partner received the superior reward but the subject receives the lower-value reward, not one of the 20 partners ever refused to exchange the token. There were four instances of potential sharing of the grape among 2000 interactions in which one individual received a grape and the other a cucumber, representing at best a sharing rate of 0.002% (Brosnan *et al.*, 2005), which is much lower than spontaneous sharing within a group of chimpanzees (de Waal, 1989). In several of these cases, however, it appeared that the partner accidentally dropped the grape (the anatomy of chimpanzee's hands makes grasping such a small object difficult) and then allowed the partner to collect it. In no instance was there active sharing, in which the advantaged partner handed the disadvantaged subject their grape. Finally, the partner's latency to exchange was no different if the subject received a lesser-value reward than if the subject received the same reward (comparing partner latency to exchange in the ET versus IT: $t = -1.44$, $df = 19$, $p = 0.17$), indicating that this inequitable situation did not change their behavior.

While it is noteworthy that there was never any action by the partner to equalize their relatively advantaged state, whether or not this lack of reaction when an individual is overbenefitted reflects a lack of societal norms for equity (and hence a lack of fairness in the human sense) is still debatable.

From this experiment there is no evidence of the lucky individual making an effort to rectify the situation or any sort of psychological distress, which might have been evidenced through changes in the speed of the interaction. However, this test was not designed to explicitly test for advantageous inequity aversion, and thus may have missed it. A better test would involve a comparison of behaviors between situations in which only one receives a large endowment of some easily shareable food followed versus one in which both receive large endowments of the food.

Social Effects on the Inequity Response

There was one other large difference between the chimpanzees and the capuchin monkeys (Brosnan *et al.*, 2005). In both species, individuals from multiple groups were tested (see *Nonhuman Primate Subjects*). The capuchins came from two different social groups, but the level of response did not differ among individuals from different groups. However, the chimpanzees showed large differences among the three groups ($F_{2,13} = 4.84, p = 0.0269$). The four pair-housed subjects and six subjects from a social group that had been created 8 years previously (when the individuals were already adults) showed a strong response to inequity, similar to that of the capuchins. However, there was a vastly different response from 10 subjects in another social group that had been housed together for greater than 30 years and in which all but one of the subjects were born into the group. These individuals who had grown up together showed virtually no response to inequity, with individuals consistently accepting the inequitable distribution (Fig. 4). Given that the other groups all reacted to inequity, it seems unlikely that this group does not notice when the situation is to their disadvantage. Instead, it seems that they do not react to this negative situation.

Intriguingly, these individuals who almost always complete the exchange interaction also take about half the amount of time to complete the interaction than the chimpanzees who frequently refuse to exchange ($t = 7.36, df = 4, p = 0.005$). This is true in all cases including the equity test, indicating that the speed of interaction is not related to the distribution of food rewards. From this test, however, we cannot determine causation, yet it is intriguing that those individuals who take more time, and thus may have time to evaluate the situation, are more likely to react to inequity.

This response to inequity also fits well with other data. Aside from their response to inequity, the long-term social group in our study shows high levels of reciprocity in food sharing and grooming, a behavior that is presumably associated with equity, (de Waal, 1997a), extensive reconciliation after fights (Preuschoft *et al.*, 2002), and a tendency to avoid confrontation (Hare *et al.*, 2000), while those in the short term group were still working out

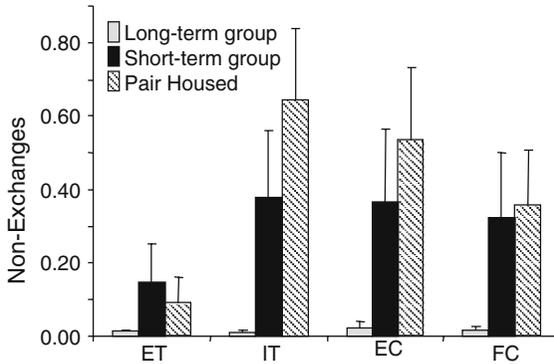


Fig. 4. Mean \pm SEM of failures to exchange for each of the three housing conditions across the four test types. Gray bars represent subjects from the long-term social group, which had been co-housed for more than 30 years, black bars represent subjects from the short-term social group, which had been co-housed for approximately 8 years, and diagonally hatched bars represent subjects who were pair housed. ET, Equality Test, IT, Inequality Test, EC, Effort Control, FC, Food Control. Reprinted from *Proceedings of the Royal Society of London, series B 272 (1560)*, 253–258.

issues 4 years after group formation (Seres *et al.*, 2001). Although one test is insufficient to understand all of the contingencies of how relationships affect responses to inequity, it is interesting that individuals who had grown up together and had social interactions implying harmony showed communal orientation to the IT while those from the less stable situations showed more contingent rules. Furthermore, it is known that chimpanzees will alter their behavior depending upon the current social situation (Brosnan and de Waal, 2003b), their housing situation (Aureli *et al.*, 1997; Baker *et al.*, 2000), or their social group (Whiten *et al.*, 1999). However, due to the scarcity of chimpanzees most behavioral testing utilizes individuals from only a single social group (or chimpanzees from pair- or single-housed situations). Bearing these results in mind, future behavioral studies need to take the chimpanzees' background and familiarity into account and test multiple groups whenever possible to avoid bias in the data set.

In humans, current theory proposes that individuals in close or positive relationships follow communal rules that do not pay overt attention to fairness, whereas those in less stable relationships utilize contingent rule-based behavior such as equity or inequality (Clark and Grote, 2003; Loewenstein *et al.*, 1989). Such committed relationships are also highly correlated with willingness to sacrifice (van Lange *et al.*, 1997). If our long-term group of chimpanzees has similarly close relationships, the inequity presented to them may be largely irrelevant within the context of their relationships. Further study of multiple social groups is certainly warranted,

both in primates and in other species, so that we get a full picture of animals' responses.

This ability to recognize when you are being treated inequitably is a response we might expect in humans as well. In fact, its presence in two nonhuman primates certainly implies that it could have a long evolutionary history, with the responses of the ape and monkey representing stages in the evolution of the complex responses to inequity exhibited by humans. Whether the nonhuman primates' decisions are, like humans, driven by emotion is unknown, although behaviors such as the throwing of tokens outside of the testing facility during testing (common among both species) implicate some level of emotional involvement. Hopefully, some day advances in imaging techniques, such as fMRI scans, that could be used with nonhuman primates in reasonably unrestrained situations will be available to shed some light on this question.

Research Questions for the Future

Experimental research on inequity responses in animals is in its infancy, yet it is a potentially fruitful subject. Further work may give us insight not only into the sense of fairness, but also into such traits as empathy, gratitude, and morality. However, more background work needs to be done before we can properly interpret these results in the context of the other behaviors. Below is a list of the research topics that I think will be important to address in the next few years.

First, more experimental research on a wider variety of species and taxa will allow a broader understanding of the phenomenon. It would be good to understand which species show an inequity response and what these species share in common in their social organization or ecology. Such information will help us understand the conditions under which inequity responses are beneficial and may provide further insight into questions of phylogenetic continuity. Given that inequity responses are intrinsically social, highly social species such as cetaceans, elephants, nonhuman primates, social carnivores, and corvids are obviously a good place to start, but it will also be important to examine other, less social species, particularly asocial species closely related to social species that show an inequity response. This will address questions of evolutionary descent and environmental effects on the behavior, as well as identifying situations that do not fit expectations, which can be quite informative.

Second, it is important to broaden the research paradigm. At this point, much of the research in nonhumans has been focused on simply demonstrating that animals respond to inequity. Given the relative infancy of such studies, this is to be expected. However, it will be interesting to see the limits

of the behavior, as well as how effective the response appears to be in rectifying inequity in both the long term and the short term. Furthermore, it should be possible to disentangle efforts, rewards, and norms violations in nonhumans just as it is in humans, perhaps leading to correlates with the human ideas of organizational justice, procedural justice, distributive justice, and so forth.

Third, much closer attention should be paid to the social context of the inequity response, and how the reactions vary based upon different social situations. This has important implications in humans, and is likely to be important in nonhumans as well. This is challenging for many animal researchers, particularly those who study large-bodied, long-lived organisms, insofar as experiments require large samples of individuals who preferably were born into and have lived long-term in demographically normal group situations, but it is worth the effort.

Fourth, as we gain more information about the criteria for and reactions surrounding inequity in animal species, mathematical models predicting individual's behavior will become even more important. A start has already been made in this direction (Dugatkin and Bekoff, 2003), but further modeling efforts will enhance our predictive ability and understanding of these phenomena.

Fifth, gaps between disciplines must be bridged in a more effective manner. Thus far, most work on inequity has taken place in psychology and economics, yet these disciplines are very different in their approaches, questions, and results, and communication has been sparse. Furthermore, other fields, such as behavioral biology, anthropology, and the law, have much to contribute. Combining these approaches would be mutually beneficial, and may help to expand our understanding of the phenomenon. The burgeoning study of inequity responses in animals offers a fresh chance at such interdisciplinary collaboration, which can only enhance the quality of the research.

Finally, we need to look for the psychological underpinnings of this behavior in animals. Unlike humans, animals cannot be debriefed, surveyed, or polled after an experiment to see what they were thinking and why they responded the way they did. With nonhumans, all assertions must be based solely on the animal's behavior. New technologies such as functional MRI, which have been such a boon to human psychology, including with respect to inequity responses (Sanfey *et al.*, 2003), may well assist in animal studies. Though brain structures clearly differ, such technology allows for at least a rough comparison between the species. Furthermore, when studying humans it would be of great utility to use behavioral measures in correlation with verbal debriefing. Not only will this make the literature more comparable, but it may enhance research in its own right by relying less heavily on personal testimony.

CONCLUSIONS

Animals from a variety of different taxa appear to have at least some sense of when a given situation is inequitable. Monkeys and apes respond when they get less of a reward than a partner, coyotes who do not learn to 'play fair' end up leaving the group, which is reminiscent of ostracism, a similar punishment for humans who are not sufficiently prosocial (Boehm, 1999), and ravens attack those who violate social norms (Bekoff, 2004; Brosnan and de Waal, 2003a; Brosnan *et al.*, 2005; Heinrich, 1999). But what does this really mean for humans? Can such information teach us about ourselves or about how we evolved?

The short answer to all of these questions is yes. There has been quite a bit of debate over whether prosocial behaviors in general are the result of natural selection or culture (Bierhoff, 2002). In other words, do people respond to inequity because they are somehow wired to do so or because they are trained by our complex cultural institutions to make such responses (Fehr and Gächter, 2003; Johnson *et al.*, 2003)? The presence of the roots of fairness in such a wide variety of taxa implies that at least some aspect of the response is evolved.

Furthermore, the high degree of variation found in human responses is apparently reflected in chimpanzees (Brosnan *et al.*, 2005). Because human responses, too, are strongly affected by relationships (Clark and Grote, 2003; Loewenstein *et al.*, 1989), it is very interesting to see such variation in another species. Further study on chimpanzees and other social species may tell us more about the conditions that lead to variability in responses in our own species, as well as elucidating the evolution of the behavior.

We can learn a great deal about ourselves by examining other species. In other species, we see a mirror of ourselves stripped of the complications of language and complex culture so we can learn more about our innate responses to inequity. Future advances in the study of inequity responses in nonhuman species will complement those in the human literature and create a more integrated view of justice-related behavior in all species.

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