



CHAPTER

19

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Responses to Inequity in Non-human Primates

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INTRODUCTION

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Humans are very sensitive to inequity. We respond badly when we are treated unfairly, we give more than the minimum amount required in experimental games, and we frequently punish in situations in which another individual behaves non-cooperatively (Kahneman *et al.*, 1986; Zizzo and Oswald, 2001; Fehr and Rockenbach, 2003). These inequity averse responses are seen across a wide variety of cultures (Henrich *et al.*, 2001), 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, both at the level of behavior and at the level of neural activity (Frank, 1988; Sanfey *et al.*, 2003).

About a decade ago, it was proposed that negative reactions to inequity might be beneficial as a mechanism for stabilizing cooperation in human societies (Fehr and Schmidt, 1999). Since then this approach has been applied in human research, and is beginning to be applied in non-human studies as well. This chapter provides a brief background on inequity aversion theory and research in humans, and then discusses the relevant research in non-human primates. It closes by comparing the two responses and discussing the implications that the non-human data have for the evolution of the inequity response.



INEQUITY AVERSION

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Although traditionally economics has used the simplifying assumption that humans are rational, maximizing their absolute gains in a directed way, in the latter half of the twentieth century the work done on experimental games (among other things) began to make it clear that this was not always the case. Either the games weren't tapping in to human economic choice behavior very well, or humans weren't always all that rational with regard to the maximization of their monetary wealth. Some economists began to develop new theories to explain these deviations from expected behavior in a wide variety of economic games. These theories typically incorporated other variables (often social preferences) in humans' calculations of utility.

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Among these is a class of models incorporating dislike of inequity into the human utility function, a concept already well-known from research in psychology (Walster *et al.*, 1978). The two primary models, Fehr and Schmidt's (1999) Inequity Aversion (IA) model and Bolton and Ockenfels's (2000) Theory of Equity, Reciprocity, and Competition (ERC) are based on this principle (see Box 19.1 for more details). The models predict that individuals dislike inequity, and therefore players get utility from minimizing the difference in payoffs between themselves and others (i.e.

equalizing their relative gains). Fehr and Schmidt's model explicitly included parameters for disadvantageous inequity aversion (the α parameter), inequity which is detrimental to the self, and advantageous inequity aversion (the β parameter), which is inequity advantageous to the self. Together these explain why, for instance, responders in the ultimatum game (see Box 19.2 for details on selected economic games) frequently turn down positive, but relatively much smaller, offers, and why proposers in the dictator game ever give anything at all. Aversion to inequity (or an egalitarian motive) has also been argued to explain behavior in random income games (in these games, each player is initially allocated a random amount of money which differs from the allocation of other players), in which individuals will pay to reduce wealthier individuals' incomes or supplement poorer individuals' incomes, even though distribution is random and no intention (positive or negative) was involved (Dawes *et al.*, 2007).

Another thing that these models have in common is the hypothesis that an aversion to inequity can stabilize cooperation. Individually, a sense of inequity is a useful rule of thumb for determining which other players or group members make the best cooperation partners (i.e., cooperate with individuals who share the payoffs). Within a group, acting to rectify inequity can advertise one's commitment to equity and

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BOX 19.1

THE FEHR-SCHMIDT MODEL OF INEQUITY AVERSION

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Fehr and Schmidt's model of inequity aversion assumes that individuals are interested not only in their own but also in others' gains. Hence, their model divides inequity into "disadvantageous" inequity, or that which harms the actor, and "advantageous" inequity, or that which harms another. Fehr and Schmidt's (1999) model differs from a similar model, the Equality, Reciprocity, and Competition (ERC) model (Bolton and Ockenfels, 2000) in its focus on absolute (rather than relative) differences in payoffs and its focus on comparisons among players (rather than summations of payoffs; Camerer, 2003). In most comparisons, the Fehr/Schmidt Inequity Aversion model appears to explain behavior better than does the ERC model.

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Mathematically, for the players i and k , player i 's utility function for the social allocation $X = \{x_1, x_2, \dots, x_n\}$ can be described as:

$$U_i(X) = x_i - \alpha / (n - 1) \sum \max(x_k - x_i, 0) - \beta / (n - 1) \sum \max(x_i - x_k, 0)$$
, where $k \neq i$ for the purposes of the summation. In this formulation, α represents "envy," or disadvantageous inequity aversion, and β represents "guilt," or advantageous inequity aversion. We can also assume that $0 = \beta_i < 1$ and $\beta_i = \alpha_i$, or that disadvantageous inequity aversion is stronger than advantageous inequity aversion. For the ultimatum game (see Box 19.2), for example, if player i is the responder, she should reject any offer less than $\alpha_i / (1 + 2\alpha_i)$, and the proposer (player k) should make offers dependent upon her β_k , or guilt. For more details, see Fehr and Schmidt, 1999, and Camerer, 2003.

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BOX 19.2

GAMES IN EXPERIMENTAL ECONOMICS

Experimental economics utilizes a number of “games” which can be used to elucidate subjects’ decision-making strategies and social preferences in controlled situations. For more details on these games, or additional games, see Chapter 5 of this volume, or Camerer 2003.

The Ultimatum Game

Invented by Werner Güth (Güth *et al.*, 1982), the ultimatum game (UG) is a bargaining game. The first player, or proposer, is given a sum of money and told to divide it between herself and a partner (typically anonymous), with the knowledge that the second player, or responder, can either accept the division and both will be rewarded as the proposer indicated, or can refuse the division, in which case neither player receives any money.

Although the most “rational” action is for the proposer to offer the least amount possible and for the responder to accept it (which is a gain for the responder), the game rarely goes this way in practice. The median offer by the proposer in most studies is 50% (the average is about 40%), and responders frequently refuse offers of less than this. This has been interpreted as individuals having a “taste” for fairness (see Box 19.1). Many social or situational factors will affect player’s responses in this game.

A recent study has found that chimpanzees act in the “rational” way – that is, responders will accept any offer (Jensen *et al.*, 2007). However, rationality also assumes that responders will only accept positive offers, and in this study chimpanzee responders accepted the payoff distribution 56% of the time when they got nothing at all, indicating that some or all of them failed to understand the contingencies of the game.

UG Variation: The Dictator Game

The dictator game (DG) is a variation on the UG which evaluates the fairness goals of the proposer. The DG is not really a game, as the proposer makes a unilateral decision about how to divide the money and the responder makes no decision and cannot affect the outcome. Not surprisingly, proposer divisions are much more lopsided in the DG than in the UG, with much less of the pot offered to the responder.

UG Variation: The Impunity Game

The impunity game (IG) is another variation on the UG in which the responder has only limited recourse. After the proposer makes a division, the responder can reject, but her rejection affects only her – and not the proposer’s – payoff.

Thus, the rational response is for proposers to offer the least amount possible and for responders to accept it, as in the DG (Bolton and Zwick, 1995).

However, responders often refuse their winnings, both when the proposer will know the responder’s actions and when the proposer is ignorant (i.e., the proposer believes them to be playing a DG; Yamagishi, 2007). While this is unexpected from a perspective of rationality, as this response leads to increased (rather than decreased) inequity, it may indicate that people’s responses serve not only to equalize outcomes but also to send a signal to both their partners and themselves. Such signals could constitute commitment devices (Frank, 1988) which inform others of the player’s refusal to participate in outcomes which do not have fair outcomes, increasing the player’s long-term gains in cooperative interactions. Similar responses are seen in non-human primates (Brosnan and de Waal, 2003, Brosnan *et al.*, 2005).

The Prisoner’s Dilemma Game

The prisoner’s dilemma game, a model of decision-making when interests do not intersect, allows two individuals to each make a decision to work together (cooperate) or not (defect). The payoff matrix is as follows (player 1 is indicated in bold, player 2 in italics):

| | Cooperate | Defect |
|------------------|----------------------------------|--------------------------------------|
| <i>Cooperate</i> | <i>Reward, Reward</i> | <i>Sucker, Temptation</i> |
| <i>Defect</i> | <i>Temptation, Sucker</i> | <i>Punishment, Punishment</i> |

Where Reward is the reward for mutual cooperation, Punishment is the payoff for mutual defection, Temptation is the payoff for defecting, and Sucker is the “Sucker’s payoff” for cooperating.

In the standard game, $Temptation > Reward > Punishment > Sucker's\ payoff$. Thus, in a non-repeated (one-shot) game, the optimum strategy is to defect no matter which decision one’s partner makes, as the payoffs are higher ($T > R, P > S$). However, in a repeated (or iterated) game, the best payoff comes from cooperation, because in the long run both players maximize their payoffs with mutual cooperation, rather than mutual defection ($R > P$). This, of course, assumes two players who will not continue to cooperate in the absence of cooperation from a partner. In an iterated game, the best strategy is some variation on “tit-for-tat,” in which each player chooses the option her partner chose on the previous round (developed by Anatol Rapoport; see Axelrod, 1984, for more details).

to one's cooperative partners (Frank, 1988), and can reduce the frustration of the less well-endowed individuals. If, in fact, inequity aversion is a mechanism for stabilizing cooperation, it is reasonable to assume that such behavior may exist in other cooperative species, including our non-human primate relatives.

p0190 Aversion to inequity implies, of course, a reaction to both over- and under-compensation, although these are likely not treated the same by most people. While it is often found that people prefer equity to any sort of inequity, advantageous inequity is typically preferred to disadvantageous inequity (Loewenstein *et al.*, 1989). Moreover, sometimes inequity, such as that favoring an *in-group* (one's own group), is even preferred (Diekmann *et al.*, 1997; Bernhard *et al.*, 2006). Furthermore, people tend to rectify inequity through psychological balancing mechanisms – justifying why they deserve a greater share – rather than material compensation (Walster *et al.*, 1978), and will usually choose to ignore information which could lead to a more fair outcome at a cost to the self (Dana *et al.*, 2003). Thus, it appears, humans are interested in fairness as an ideal, but self-interest still comes first in most situations.

p0200 Inequity aversion may not be the only explanation for these behaviors. A second set of models, the reciprocity models, are invoked to explain similar behavior patterns as do the inequity aversion models. These models incorporate intentions, and assume that much behavior can be explained by individuals' attempts to reward those who help them and punish those who hurt them (Rabin, 2001). Thus, responses are not based solely on individuals' interest in equity or fairness, but on their desire to rectify wrongs and reward good behavior. Punishment, in this view, is a form of reciprocity which may have evolved to stabilize cooperation (Fehr and Gächter, 2002; Boyd *et al.*, 2003).

p0210 Although in many cases predictions are similar, reciprocity and inequity-aversion models can be compared. In computerized situations, in which play against a computer (which lacks intentions) is compared with play against another person, people playing a computer are much less likely to reject low ultimatum game offers than in situations in which they play another human (Blount, 1995). This indicates an element of reciprocity in their actions. However, people will also take money away from others when income distributions are chosen at random (i.e., no intention can be attributed), indicating that equity concerns can outweigh reciprocity (or punishment) concerns (Dawes *et al.*, 2007). Thus, both inequity aversion and reciprocity appear to play a role in human decision-making.

p0220 There is an enormous literature on these games, indicating that many other factors are at work. For instance,

there is quite a bit of variation in how different cultures play the ultimatum game, although a broad survey of non-industrial cultures shows that no cultures play as if they were the *Homo economicus* parody, interested only in maximizing their own gains without paying attention to others' gains (Henrich *et al.*, 2001). Even in the culture in which proposers offered the least, the Machiguenga (a traditional, non-market society in the Amazonian rainforest), offers were well above the minimum. Individual variation plays a role as well. For instance, individuals who are in the lowest third of the population for self-esteem rarely respond to procedural inequity, indicating that personality or social factors affect individual responses (Wiesenfeld *et al.*, 2008). A recent study indicates that responder behavior in the ultimatum game is highly heritable (Wallace *et al.*, 2007), evidence which supports the presence of a genetic mechanism through which these reactions can be passed on. It is likely that personality, genes, and culture interact to create the range of responses that any one individual is likely to display.

Framing effects are important as well. For instance, offers drop – and these lower offers are accepted – if the role of the proposer is earned (in this case, through a high score on a quiz) rather than assigned randomly by the experimenter (Hoffman *et al.*, 1994). Social punishment drives offers in the other direction; proposers who know that their responders will be writing them a note after the division tend to offer higher amounts (Xiao and Houser, 2005). Interestingly, the responders actually accept lower amounts in these cases, but send back particularly vitriolic messages.

Although discussions of economic decision-making tend to invoke images of conscious cognition, an emotional component may be involved. Robert Frank argues that showing a strong negative response to inequity, perhaps especially if it is irrational (in the sense of costing more than the benefit gained from rectifying the inequity), may be a powerful commitment device which increases the fairness of one's treatment. Such a negative response may carry a short-term cost, but this is more than recouped by the long-term gains of being treated fairly in the future (Frank, 1988). Recent experimental evidence supports this view. Players in the impunity game (an ultimatum game in which responders can only reject their allotment; responders cannot affect the proposer's outcome; see Box 19.2) do refuse their rewards, even though this increases both absolute and relative inequity (Yamagishi, 2007). Perhaps a part of people's reactions is to show others, and themselves, that they will not accept such treatment.

Recently, brain-imaging has been added to the arsenal of study tools for understanding humans' behavior

in economic decision-making games. These studies corroborate this idea that emotional involvement is critical. Functional MRI, a technique for measuring the amount of oxygen in a given part of the brain (which correlates with activity) in real time, allows researchers to investigate what parts of the brain are activated during different decision-making tasks. These scans indicate activity in both conscious processing centers and areas of the brain correlated with emotion and impulse control during many of these decision-making games (see, for example, Sanfey *et al.*, 2003).

p0260 For instance, in a prisoner's dilemma game (see Box 19.2), during unfair responses activation is seen in both the anterior insula, associated with emotional processing, and the dorsolateral prefrontal cortex (DLPFC), associated more with cognition (Sanfey *et al.*, 2003). Increased activation of the anterior insula is seen when individuals reject unfair offers, perhaps indicating a higher degree of emotional involvement. Correlating with earlier behavioral data (Blount, 1995), brain activation is different for people playing the game against another human as against a computer.

p0270 A more recent study found that interrupting the right DLPFC (but not the left) with repetitive transcranial magnetic stimulation (TMS) increases the rate of acceptance of low offers. This suggests that the DLPFC is critical in over-riding the self-interested impulse to accept

all positive offers (Knoch *et al.*, 2006). Interestingly, in this case, behavior was the same in a computerized version of the task as in the human partner condition, indicating that the refusal of low offers may be based on reciprocity rather than inequity aversion.

WHY NON-HUMAN PRIMATES ARE RELEVANT TO INEQUITY

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Humans are primates, sharing a taxonomic Order (Order *Primates*) with all other primates and a Family (Family *Hominidae*) with the other great apes (see Figure 19.1). Of these, we are most closely related to chimpanzees and bonobos, both members of our sister Genus, *Pan*. Generally, primates are divided into Prosimians, which are the most phylogenetically ancient of the primates; the New World monkeys (or Platyrrhines), which diverged from the line that led to humans approximately 40 million years ago (and include the capuchin monkey, which is discussed further below); the Old World monkeys (or Catarrhines), which diverged approximately 20 million years ago; and the great apes, of which humans are a member, along with chimpanzees, bonobos, gorillas, and orangutans.

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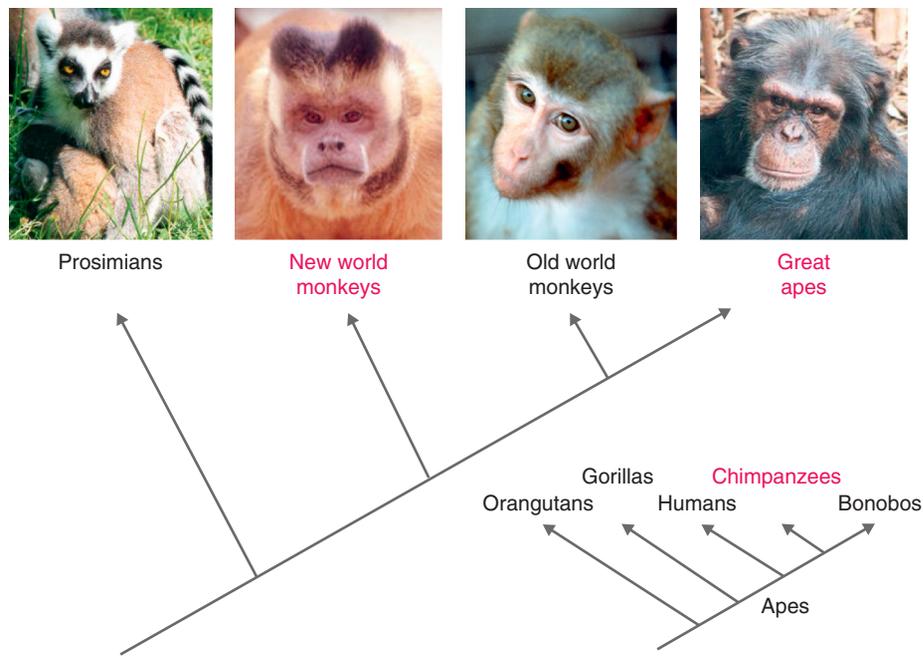


FIGURE 19.1 A taxonomic tree of the primate lineage, with species used in these studies indicated in red. Pictures indicate representative species of the four major taxonomic divisions of the Order Primates: Prosimians (a ring-tailed lemur female and her offspring), New World monkeys (an adult male capuchin monkey, one of the individuals used in these studies), Old World monkeys (an adult female rhesus macaque), and the Great Apes (an adult male chimpanzee, another individual used in these studies). An inset shows the relationships between the five members of the family Hominidae (the great apes). Photograph of the rhesus macaque by F. de Waal; all others by the author.

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p0290 Studying non-human primates, our closest evolutionary relatives, tells us a great deal about how we behave. A technique known as *behavioral phylogeny* allows comparisons to be made between different species to extrapolate the likelihood of common descent for any behavior (Boehm, 1999). Species with different degrees of relatedness (such as an Old World monkey species and a New World monkey species) are evaluated for a behavior, following which an attempt is made to reconstruct when the behavior arose and how it developed over evolutionary time. Studying species which are more closely related yields more information – thus the utility of studying primates, and perhaps particularly great apes, when concerned with human behaviors.

p0300 Moreover, studying primates offers some advantages over studying humans. Within a group of primates, we typically know their full social history and, particularly in captivity, have more knowledge of (and control over) their lifetime experiences. Non-human species are also unencumbered with complex cultural institutions, such as churches, schools, and governments, so their responses are likely to indicate what primates have evolved to do (although primates do have impressive social learning abilities which undoubtedly affect their behavior; de Waal, 2001). By studying non-human primates' behavior, we learn the basis of human behavior and can begin to tease apart what is evolved and what is the result of our extensive culture. Finally, non-human primate social systems are simpler than human systems, if only because the number of other possible interactors is limited. This means that it is more likely that we can begin to understand all of the factors affecting their behavior.

p0310 The species discussed in this chapter are the chimpanzee, *Pan troglodytes*, and the brown, or tufted, capuchin monkey, *Cebus apella*. These species are ideal for comparison with humans in social and cognitive behavior. Both species have much larger brains and neocortices for their body size than is expected, based on the average brain-to-body ratio for both mammals and primates (Rilling and Insel, 1999). This implies a premium on intelligence, which, in social animals, is often assumed to arise due to the necessity of navigating a complex social environment in group-living species (Byrne and Whiten, 1988). Moreover, both of these species share several behaviors – food-sharing, reciprocity, and cooperation – that are somewhat unusual in primates, yet common in humans. Importantly, these behaviors may also be relevant to recognition of and response to inequity. Observations of natural behaviors in chimpanzees led to the early conclusion that a sense of justice might exist in their society (de Waal, 1991). For instance, chimpanzees will assist others who are victims of attempted theft (Figure 19.2).



FIGURE 19.2 Emily recruits support from the alpha male against the beta male, who has just attempted to take her food. Behaviors such as these indicate that chimpanzees may expect a certain level of equity in their daily lives. Photograph by the author.



FIGURE 19.3 A juvenile male eats from food in the possession of the alpha male while an adult female chimpanzee watches. Such close proximity may result in the female receiving food as well. Photograph by the author.

Food-sharing is rare outside of the mother/infant context in primates (Feistner and McGrew, 1989); however, both capuchins and chimpanzees commonly share food among adults and unrelated individuals (see Figure 19.3 for an example of begging and food-sharing among unrelated chimpanzees). In experiments with captive populations, capuchin monkeys not only food-share (de Waal, 1997a), but also tend to do so reciprocally (de Waal, 2000), more often sharing with those who shared with them. Food-sharing

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may also be a repayment for a service, as capuchins are more likely to share food with a partner who recently helped them in a cooperative task than with a partner who was inessential (de Waal and Berger, 2000). Finally, wild capuchin monkeys share food after successful hunts (Perry and Rose, 1994).

p0330 Chimpanzees also share food in reciprocal contexts (de Waal, 1989). For instance, chimpanzees are much more likely to share food with individuals who groomed them earlier in the day, and this tendency is much stronger for social partners who do not typically groom (de Waal, 1997b). This implies a scarcity effect, with more repayment due to an unusual behavior. Moreover, reciprocity works both ways; chimpanzees are also more likely to refuse to share with an individual who has not groomed them.

p0340 Chimpanzees also share food in the wild, typically sharing meat after a monkey hunt. This sharing may "buy" the sharer support, mating opportunities, or other social services from the recipient (Nishida, 1992; Rose, 1997; Mitani and Watts, 2001; but see Gilby, 2006 for an alternate view). One recent study indicates that male chimpanzees may also share difficult-to-obtain cultivated fruits with females, perhaps with future mating opportunities in mind (Hockings *et al.*, 2007). These two contexts indicate that food-sharing may be more valuable when the food is a costly commodity than when it is one that can be obtained easily and individually. Outside of the food context, chimpanzees also share services (grooming, support) reciprocally (Mitani, 2006; Duffy *et al.*, 2007).

p0350 Cooperation, closely linked to reciprocity and food-sharing, is also common in both species. For instance, a series of studies has been done on capuchin monkeys in which they must work together to pull in a heavily counterweighted tray in order to obtain food rewards. Capuchins are very good at intuitive cooperative tasks (Brosnan and de Waal, 2002), and seem to take their partner's behavior into account. Capuchins' performance is much lower when they cannot see their partner (Mendres and de Waal, 2000). They also appear to know that their partner is required to complete the task; monkeys paired with a partner who can leave the testing set-up at will pull predominantly when their partner is present in the testing area, and thus is also available to pull (Mendres and de Waal, 2000). Finally, capuchins are very sensitive to the distribution of rewards in a cooperative task. If rewards are sometimes clumped (monopolizable) and sometimes dispersed (spread apart, preventing monopolization), from the first exposure to the task, monkeys pull much less for clumped rewards (de Waal and Davis, 2002). This sensitivity to payoff indicates that they are aware of their partner both as a

cooperator for pulling in the tray and as a competitor in dividing the bounty. Chimpanzees, too, successfully utilize a bar-pull apparatus to obtain food rewards (Crawford, 1937). As with capuchins, chimpanzees are sensitive to the social context, cooperating more frequently with socially tolerant partners (Melis *et al.*, 2006a) and, when given the choice, recruiting tolerant partners (Melis *et al.*, 2006b).

In the wild, both capuchin monkeys and chimpanzees hunt vertebrate prey, which requires a cooperative effort (Rose, 1997). Moreover, some groups of chimpanzees show remarkable coordination of hunting behavior, typically taking the same roles in the hunt over time (Boesch, 1994). Capuchins also cooperatively defend themselves against predators (Perry *et al.*, 2003).

In all of these cases of cooperation, reciprocity, and food-sharing, individuals tend to share or cooperate based on what the other contributed. This indicates that the primates are concerned not only with their payoffs, but also with the effort involved in the other's action. Perhaps for any cooperative species, an accurate assessment of both effort (costs) and payoff (benefits) is required to ascertain when to cooperate (van Wolkenten *et al.*, 2007). Thus, these other cooperative primate species may be very good models for investigating the evolutionary origins of the response to inequity and fairness in humans.

REACTIONS TO INEQUITY IN NON-HUMAN PRIMATES

The Evolution of Inequity Aversion

It is unlikely that a behavior as complex as inequity aversion arose *de novo*. Instead, it probably evolved through a series of stages that were each beneficial to performers in their own right, ultimately resulting in the sort of complex understanding of inequity and fairness that we see in humans (Brosnan, 2006a, 2006b). Thus, while other species may or may not show behaviors that are identical to humans', these behaviors are likely to be steps in the same evolutionary process. Obviously, we expect to see more similarities in species that are more closely related to humans (such as chimpanzees) than more distantly related ones.

Previously, I have proposed four distinct steps in the evolution of the inequity response as we see it in humans (Brosnan and de Waal, 2004a; Brosnan, 2006b). The first is an ability to notice when rewards differ between individuals. While this seems obvious

from a human perspective, it is not at all certain in other species. This requires individuals to pay attention to another outside of a context in which that other individual is directly affecting them (i.e., not during a fight, a sexual encounter, etc). Moreover, it requires fairly advanced cognition to compare one's own rewards with those of another. However, it is likely that this ability arose in a different context than inequity. Many species socially learn, meaning that they acquire information or techniques from watching other individuals' actions or outcomes. This is an efficient way of acquiring information that changes frequently. Any species that learns socially must pay attention to other individual's rewards. Many species are known to socially learn, including chimpanzees and capuchin monkeys (Whiten, 1998; Brosnan and de Waal, 2004b). Thus, they possess the capability to compare their rewards to those of others.

p0400 A second step is to react negatively to discrepancies in the rewards between one's self and another. Essentially, this requires individuals not only to notice the outcomes of another (the first step), but also to react negatively to this difference. In fact, this alone may provide a fitness benefit, if this negative response to inequity causes individuals to seek new partners who might be more equitable. For instance, both capuchins and chimpanzees hunt cooperatively, then share the prey after the kill (Rose, 1997). If one individual in a partnership consistently receives little or no meat after the hunt, hunting with a new partner who shares more generously would increase the first individual's meat consumption (and evolutionary fitness, or reproductive potential). Individuals need not intentionally seek out better sharers, nor do they need to understand their motives for switching partners, for this to enhance the actor's evolutionary fitness. The positive outcome will yield a fitness benefit to any individual who is inclined to "shop around" for a better partner.

p0410 The third step is to take deliberate action to rectify inequity towards the self, which humans do (see "Inequity aversion" above). This is the most complex of the levels of inequity. It requires an understanding of how one's actions will alter the outcome of the partner, and some ability to inhibit, to give up the immediate reward. Non-human primates can inhibit their behavior, even in the face of an immediate reward (Beran, 2002; Evans and Westergaard, 2006), and show basic understanding of how their actions will be perceived by others (Hare *et al.*, 2000).

p0420 The fourth and final step in the evolution of inequity responses is a response against overcompensation (Walster *et al.*, 1978), or advantageous inequity aversion (Fehr and Schmidt, 1999). In this case,

individuals are uncomfortable when another individual receives less than they themselves do. This can be true both when the advantaged party is the self and when it is a third party (Andreoni *et al.*, 2002). Rectification usually takes the form of psychological leveling mechanisms (e.g. derogation, justification for receipt of the superior reward) or, more practically, material compensation.

Note that all four of these stages need to be developed in order to consider the response a sense of "fairness" or justice in the way that we mean it in humans (Brosnan, 2006a, 2006b). Particularly if a reaction to overcompensation is missing, the response is a one-sided response that is focused purely on the self. Generally, among humans there is an appeal to an "objective" level of fairness or justice by which actions are to be judged. (Of course, objectivity is still in the eye of the beholder.) Since it is difficult or impossible to determine a non-human's ideals, in these studies we examine purely behavior, not motivation, with the goal of determining situations in which the primates show evidence of one of these stages and, ultimately, a potential evolutionary trajectory from comparisons between these species.

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Reactions to Disadvantageous Inequity

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Eighty years ago, a comparative psychologist named Otto Tinklepaugh examined macaques' responses to violation of expectation (Tinklepaugh, 1928). Monkeys were shown a food, which was then hidden. Later, the researcher uncovered it and gave it to the monkey. Sometimes, he switched the food with a less desirable one without the monkey's knowledge. In these cases, the monkeys responded by becoming upset and refusing the less valuable foods. This demonstrated that these monkeys had expectations about what they should have received.

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What Tinklepaugh did not do was investigate how they responded to a partner getting a better reward. Would the monkeys then form expectations based on what their partner received, and respond negatively if they got a less good reward than their partner? Our group has now performed this experiment. Our studies have investigated whether primates would be willing to complete an exchange interaction (return a token and accept a food reward) if their partners got a better food for the same "price," an exchange (see Figure 19.4 for a sketch of the test set-up). We tested capuchin monkeys and chimpanzees in pairs, with members of their social groups as their partners. In each case, one member of the pair, the partner, received a good reward (in this case a grape)

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FIGURE 19.4 An adult female capuchin monkey completes an exchange with the experimenter, returning a token for which she will receive a food reward. An adult male from her social group looks on. Sketch by G. Bragg and F. de Waal (after a video still).

for completing an exchange with the experimenter, while the subject received a reward which was less valuable, but nonetheless typically desired (a piece of cucumber), for the same work – the exchange. These results were compared to a control in which both individuals exchanged to receive a cucumber, as well as several other conditions discussed below. We measured subjects' willingness to complete the exchange interaction and their willingness to consume the cucumber once they had received it. It turned out that subjects responded in each way about half of the time, so for the following analyses, unless otherwise noted, these categories are pooled and willingness to complete the interaction (return the token AND consume the food) is reported. In both species, subjects completed virtually all exchanges when both individuals got cucumber (the equitable situation), but failed to complete the interaction in as many as 80% of trials in which their partner got the (better) grape (Figure 19.5; Brosnan and de Waal, 2003; Brosnan, Schiff, and de

Waal, 2005). Thus, both the ape and the monkey appear to be responding negatively to receiving less.

However, a few possibilities must be eliminated p0460 before this can be considered a reaction to inequity. For instance, it may just be "greed," or a desire for a better food that is available, rather than "envy," or a desire for a better food that another individual currently possesses (Brosnan and de Waal, 2004a; Wynne, 2004). To take this in to account we did an additional control, in which subjects were shown a grape, following which they exchanged and received only a cucumber piece. With the capuchins, this was done in two different ways. In the first, the subject was isolated, rather than being tested as a member of a pair, and grapes were placed in the partner's side of the testing chamber prior to each exchange. In this way, subjects saw the grapes pile up while they continued to receive only cucumber (Brosnan and de Waal, 2003). Subjects discriminated between this and the situation in which a partner received the grape, becoming more likely to accept the cucumber over time when no other monkey received a grape (Figure 19.6a). However, in this situation subjects were tested alone, while in all other conditions subjects were tested with a social partner. Although it seems minor, for a gregarious species such a change in the social environment may have large effects. Thus, we used a second method with the capuchins, as well as with the chimpanzees, in which subjects remained with their partner and each was shown a grape immediately before their exchange. Again, individuals were exposed to grapes in this testing situation, but no other subject received one. As when subjects were tested alone, subjects in both species discriminated between this and the situation in which a partner received the grape, becoming more likely to accept the cucumber over time when no other individual received a grape (see chimpanzee data and capuchin data in Figures 19.6b and 19.6c, respectively; Brosnan *et al.*, 2005; van Wolkenten *et al.*, 2007). This indicates that the partner receiving a grape is much more important than the presence of grapes alone.

A second possibility is that the subjects were p0470 responding negatively to the contrast between what they got in the current session and what they had received in previous sessions – a phenomenon sometimes called the frustration effect. Perhaps a monkey receiving a cucumber, but remembering the receipt of a grape in the last session, is responding negatively to the contrast with their previous experience, rather than the contrast with their partner's current experience. A study finding evidence for the frustration effect under these conditions, however, left out both the exchange task and a comparison between frustration and inequity, making it unclear what the critical

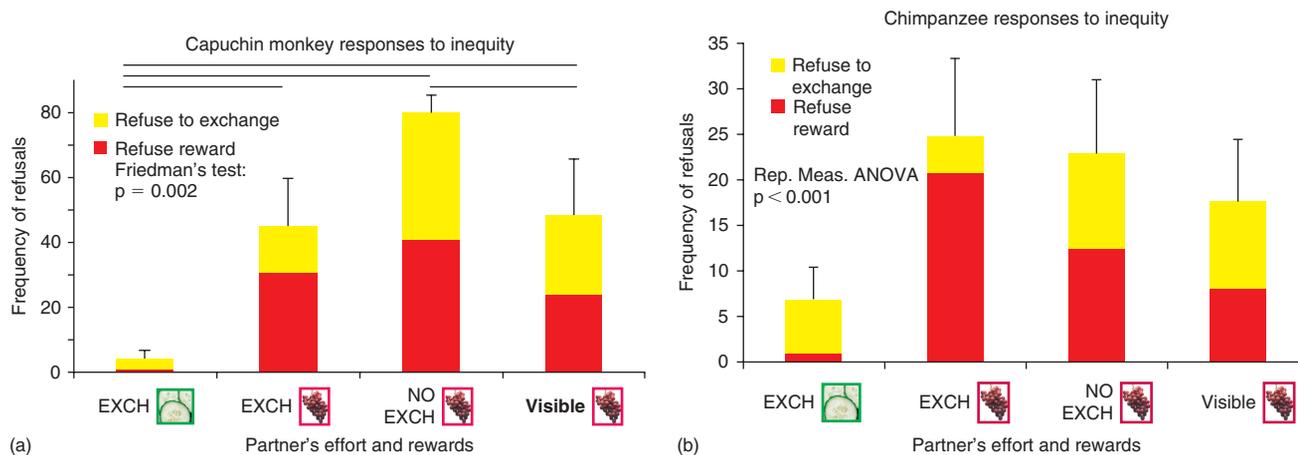


FIGURE 19.5 The distribution of refusals in the original conditions. The subject always exchanged for a cucumber, while the partner's rewards and effort required varied (indicated on the x-axis; cucumber or grape for reward, exchange or no exchange for effort). In the "Visible grape" condition, grapes were visible but no primate received one. Paler bars indicate refusal to return the token; darker bars indicate refusal to accept the reward. Standard error bars are for the total measure (refusal to return the token and refusal to accept the reward combined). Subjects were much more likely to refuse to participate when the partner received a better reward, either for the same or for less effort. Significant differences from *post hoc* tests are indicated by horizontal lines over bars. (a) Data for capuchin monkeys. Reprinted from Brosnan and de Waal (2003). (b) Data for chimpanzees. Reprinted from Brosnan *et al.* (2005).

factor is in the monkeys' responses (Brosnan and de Waal, 2006; Roma *et al.*, 2006).

We recently completed a much larger study, replicating our original work with more conditions (discussed below) and more subjects. This allowed us to investigate how subjects' rewards in previous sessions affected their current responses. If frustration is a factor, then subjects should be more inclined to refuse to participate in sessions immediately following those in which they received grapes. However, we found no evidence that previous experience had any effect on their response; subjects were no more likely to refuse to participate if they had received a grape (frustration) versus a cucumber (no frustration) on the previous test. Thus, if frustration does play a role, it is swamped by the response to inequity (Figure 19.7; van Wolkenten *et al.*, 2007).

Context is also critical in responses to inequity. Several studies have looked for inequity using a task in which foods are simply handed to the subjects, without any sort of task. One study found an increase in the rate of food consumption when the subject got a less desirable food than their partner received (Bräuer *et al.*, 2006), but in none of these studies did subjects respond to inequity by refusing to participate (Dindo and de Waal, 2006; Dubreuil *et al.*, 2006). However, one of these studies utilized the same subjects who responded to inequity in three other studies involving a task (both of the exchange tasks discussed above and a study discussed below in "Reactions to an 'unfair' partner"). Thus, the lack of response to inequity in situations without a task is not a general

lack of response to inequity, but instead appears to be specific to situations involving a specific task or effort (Dindo and de Waal, 2006).

If responses to inequity arose in the context of cooperative effort, responses to inequity would not be expected in situations with no required effort. When effort is involved, payoff equity becomes much more critical. To place this in an ecological context, a monkey who learns to forage in a certain tree after seeing another individual obtain better food there (the equivalent of being handed a reward) is exhibiting social learning, not inequity. The fact that one found a better cache of food should not alter their relationship. However, if the same two monkeys hunt cooperatively, and one individual takes a much larger portion of the ensuing kill, then the disadvantaged partner does need to evaluate their relationship and possibly find a new hunting partner who shares the prey (payoff) more equitably. Joint efforts must be rewarded jointly, or the cooperative effort will fall apart.

Of course, if effort is required, it is possible that differences in effort may generate differences in response. In the second exchange study (van Wolkenten *et al.*, 2007), we included conditions in which subjects had to exchange only a single time and others in which subjects had to exchange three times ("high effort" condition) to get the reward. Capuchin monkeys are sensitive to effort, responding less frequently and more slowly when they must expend more effort to obtain a reward. This is also modulated by reward value. When working for good rewards (grapes), monkeys are somewhat indifferent to the amount of effort required,

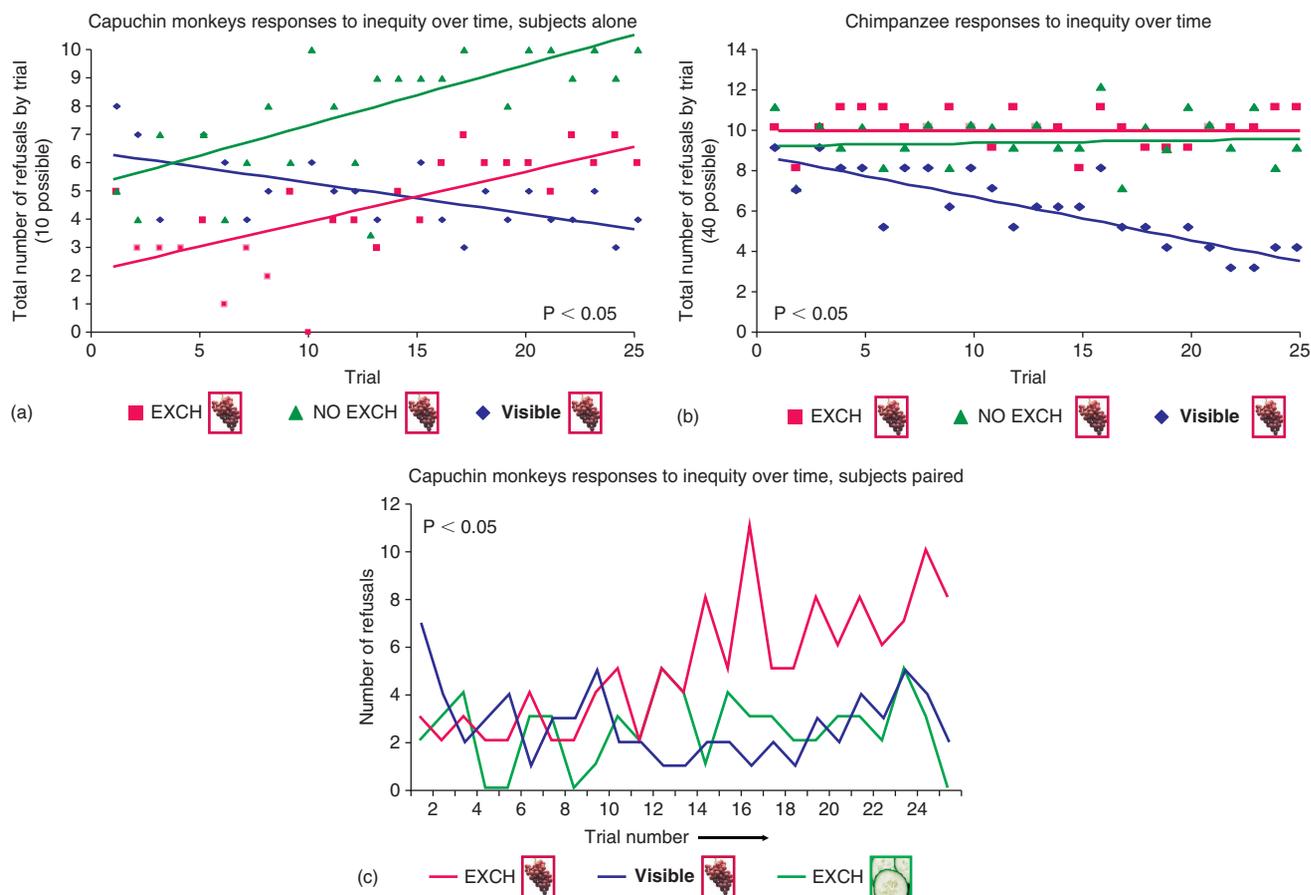


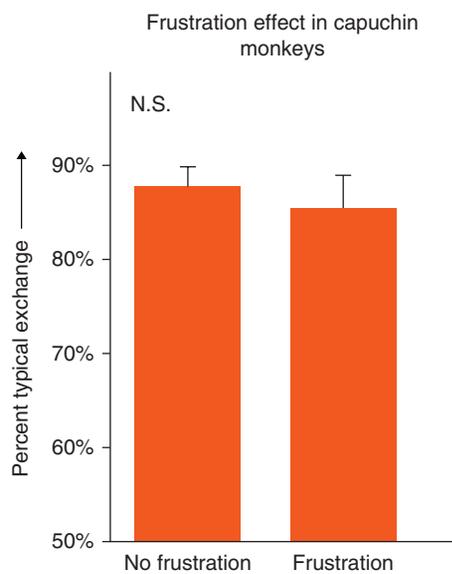
FIGURE 19.6 The total number of refusals to exchange by trial in the three test conditions (explained in Figure 19.5). Subjects' willingness to complete the interactions changed over time dependent upon whether grapes were only visible (Visible grape condition) or were given to a partner (Exchange grape, No exchange grape). Figure 19.6c lacks the No exchange grape condition, but includes the control equity condition in which both individuals receive cucumbers for comparison. This indicates that the refusals depicted in Figure 19.4 are due not to the mere presence of grapes, but to the fact that another individual received them. (a) Data for capuchin monkeys tested alone. Reprinted from Brosnan (2006b). (b) Data for chimpanzees tested in pairs. Reprinted from Brosnan *et al.* (2005). (c) Data for capuchin monkeys tested in pairs. Reprinted from van Wolkenten *et al.* (2007).

completing the task equally often in situations requiring both low and high effort. However, when reward value is low (cucumbers), monkeys are very sensitive to effort, completing many fewer trials when the effort required is high (van Wolkenten *et al.*, 2007). Note that this means that capuchins are only willing to forego a reward if it is not particularly valuable. Thus, capuchins are sensitive to the price of "disdaining" a reward.

However, the above simply means that the monkeys are sensitive to their own level of effort, and not necessarily to the effort of their partner in comparison to their own. While earlier studies indicated the importance of effort (Brosnan and de Waal, 2003), later studies have cast doubt on this (Fontenot *et al.*, 2007). Thus, we also compared the situation in which the both individuals had to work (exchange) for the same foods, but the effort – or number of exchanges – required differed. In this case, subjects did not refuse

more frequently when their partner worked less hard (exchanged only once), indicating that variations based on effort may be due to one's own assessment of effort, rather than comparisons with the partner's effort. However, this involved only small differences in effort (one exchange versus three), so potentially larger differences in effort, or a different context, could elicit a different response. Given that inequity may have arisen in a cooperative context, a cooperative task may be the most appropriate context for continued investigation (see "Reactions to an 'unfair' partner" below for such a task).

One final factor that may play a role is the relationship between the individual in question and his or her social partner. In the case of capuchin monkeys, the identity of the social partner did not appear to affect their responses. However, chimpanzees from a long-term stable social group were much less likely



f0070 **FIGURE 19.7** The frequency of subjects' refusals to exchange for cucumber dependent upon whether the subject received grape (frustration) or cucumber (no frustration) in the previous session. Subjects were no more likely to refuse to exchange in the frustration condition, indicating that their response is not simply a contrast between the current cucumber and previously available rewards. Reprinted from van Wolkenten *et al.* (2007).

to respond negatively when their partner, from that social group, received a better reward, than were those from a group which had been formed much more recently (Figure 19.8; Brosnan *et al.*, 2005). Although time together and the strength of their relationships are confounded here, this is critical evidence that some aspect of social environment affects the inequity response. This is true in humans as well. Humans in close, communal relationships show much less response to inequity than do those in more distant, or more contingent, relationships (Clark and Grote, 2003). Perhaps the chimpanzees which had lived together literally since birth simply had better relationships than those introduced as adults, and do not respond to inequity. In fact, one other study, which found that chimpanzee responders in an analog to a limited form ultimatum game typically accepted all rewards, also used subjects from a stable social group (Jensen *et al.*, 2007). The social context of inequity is a critical element, and one which is currently being examined in more detail.

p0540 In the economic understanding of inequity aversion, a negative reaction to inequity should alter payoffs in a way that maximizes equity (Henrich, 2004). Thus, a key difference between how the primates responded and the predictions of the inequity aversion models is that refusing the cucumber in this situation is economically irrational. If subjects are

inequity averse, they should never react in a way that increases both absolute and relative inequity (this is irrational), yet this is exactly what the primates are doing. Subjects did not change their immediate outcome, their long-term outcome, or their partner's outcome when they refused to accept the lesser reward. Thus, their behavior is difficult to explain using existing models. Of course, even humans may respond in this "irrational" way, as, for instance, in the impunity game (see Box 19.2 and Yamagishi, 2007; however, see also Bolton and Zwick, 1995, for the opposite finding).

Why might people and primates respond in this way? This response cannot be explained by either inequity aversion or reciprocity. First, it is possible that in the primates' normal interactions, their responses, *would* alter payoffs. In the experiment, subjects were trapped for 25 trials, whereas in the wild, subjects could cease interaction with an inequitable partner and go to find a more equitable one. Second, in a cooperative task (in which individuals work together for joint rewards), if one individual stops cooperating, neither individual can achieve the payoff, essentially rendering the payoff equal (that is, nothing; see "Reactions to an 'unfair' partner," below). Finally, this response may be, in both humans and non-human primates, an emotional response that functions as a commitment device (Yamagishi, 2007). Subjects may respond "in spite of themselves" in the experimental task, even though there is nothing to be gained in this specific context. The hypothesis that this response is driven by emotion in non-humans as well as humans is one that deserves much more investigation.

Reactions to Advantageous Inequity

A critical component of "fairness" includes responding to situations which are disadvantageous to another individual. In the preceding studies, individuals disliked being treated inequitably as compared to their partners, but none of the subjects responded differently if they were the advantaged partner. Capuchin monkeys frequently allowed their partner to take their cucumber pieces (passive sharing), but no monkey ever allowed a partner to take his or her grape (Brosnan and de Waal, 2003). Among chimpanzees, in less than 1% of cases (5 of 2000) did an individual who received grape allow the cucumber-receiving partner to have the grape (Brosnan *et al.*, 2005). This rate of sharing is much lower has been seen by these same individuals in other studies (de Waal, 1997b).

However, these studies are not ideal for investigating how individuals respond to advantageous inequity. The food pieces are small and (by design)

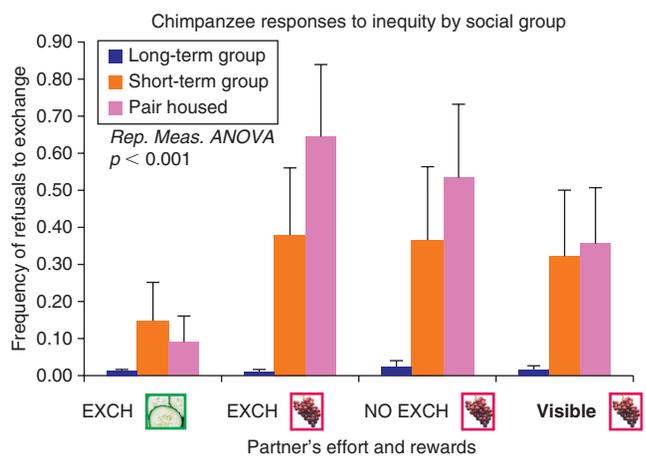


FIGURE 19.8 This figure further breaks down the data presented in Figure 19.5b, indicating that responses varied greatly dependent upon the social group. Chimpanzees from a long-term social group were much less likely to respond to inequity than those from shorter-term or pair-house situations, indicating that subjects' relationships or other social factors influence the response to inequity. Reprinted from Brosnan *et al.* (2005).

difficult to share. Thus, rectifying inequity requires the advantaged individual to give up the entire grape – essentially rendering them disadvantaged. We recently examined the willingness of chimpanzees to give food to a partner (see Chapter 18 for more details on methods and results). Subjects could choose from two options, one of which brought food to them and one of which which brought food to both them and a partner (prosocial option). Rewards were identical, and subjects received the same reward no matter what they chose. We compared subjects' responses when paired with another individual to their responses when alone, to avoid the possibility that subjects chose the "prosocial," or two-food, option due to the presence of additional food.

In fact, subjects were indifferent to their partner's outcomes. None of the 18 subjects from two different facilities ever showed a significant tendency to reward partners more when there was a partner present than when next to an empty cage; nor was there an effect overall (Silk *et al.*, 2005). Another similar study with a third group of chimpanzees found the same results (Jensen *et al.*, 2006). However, it is possible that the subjects were simply so excited by the prospect of receiving food that they made a choice for themselves without attending to the option of rewarding a partner.

Thus, we completed a separate study (the study order was counterbalanced between facilities) with the same subjects in which chimpanzees could make *two* choices, in any order, one of which rewarded just them and one of which rewarded their partner. In this case, while the majority of subjects were again

indifferent, one female chose the prosocial option at a significantly higher rate when next to her partner than when next to an empty cage, and three other subjects from the same facility showed a tendency in this direction (out of 18 subjects). Moreover, on their initial session, the subjects in this facility chose the prosocial option more when a partner was present than absent (Vonk *et al.*, 2008; see also Chapter 18 of this volume).

Thus, while in these tests chimpanzees have been seen to be predominantly disinterested in their partner's rewards, there is a hint that they may have the capacity to make prosocial choices. In other situations, enculturated (i.e., human-reared) chimpanzees respond in a similarly helpful fashion to that of small children in a simple helping task (Warneken and Tomasello, 2006), and non-enculturated chimpanzees will assist both humans and other chimpanzees in other helping tasks (Warneken *et al.*, 2007). These helping behaviors, involving assistance rather than the donation of food, are more similar to the sorts of situations in which behaviors that appear empathetic have been reported previously (de Waal, 2006). Given the relative rarity of sharing of vegetable foods (as opposed to meat) in chimpanzees, it may not be surprising that behavior is different in experimental settings in which food is the reward versus those which involve only helping behavior. Social environment, too, may be critical, as cooperatively breeding marmosets do show prosocial behavior in food contexts (Burkart *et al.*, 2007).

It is likely that chimpanzees, at least, do show some prosocial behavior in some social contexts, although further research is needed to clarify what these contexts are (Brosnan, 2008; see also Chapter 18 of this volume). Whether this prosocial capacity is sufficiently well developed to manifest as a full sense of fairness in chimpanzees is still unknown. Certainly in the experimental exchange study, in which subjects responded negatively when they got less food than a partner, neither species showed altered behavior for the advantaged partner. Until further research is done, involving different contexts and different costs and benefits, it is best to avoid assuming that chimpanzees, or other primates, are concerned with overcompensation.

Reactions to an "Unfair" Partner

While previous work on distributional inequity focused on the distribution of rewards, more recent work on cooperation for unequal rewards shows that, in cooperative contexts, subjects may be more attuned to their partner's behavior than to the rewards themselves. Capuchins are very sensitive to both the social context and physical aspects of cooperation. In fact,

on their first exposure to a mutualistic task in which individuals must work together to pull in a tray which brings both food, subordinate monkeys will refuse to cooperate for shared rewards if those rewards are monopolizable (de Waal and Davis, 2002).

p0630 In the previous exchange experiments, the monkeys' unequal rewards were allocated by the experimenter. The partner did not affect the outcome, and neither individual could do anything to affect the other's reward. This is likely not the case in natural situations; thus, in the current experiment, the subjects controlled the allocation of rewards. This was done using a bar-pull task, which has been used extensively to test cooperation and altruism in capuchin monkeys (see "Why non-human primates are relevant to inequity," above). A tray is weighted such that no capuchin can pull it in alone, but, working together, two individuals can bring it in. On the tray are two rewards, one for each monkey. Sometimes these rewards were the same (equal condition) and sometimes they were different (unequal condition). Subjects were not separated for this task, so they had to work out for themselves which monkey would pull for which reward, meaning that the monkeys themselves controlled the payoff distribution, or allocation of rewards. Note that if either individual refused to participate, the bar-pull tray could not be pulled in and neither got "paid."

p0640 In this situation, the distribution of the rewards did not affect a pair's cooperative success. However, the behavior of the partner strongly affected their responses. In the unequal condition (different rewards), some monkeys dominated the better reward, never giving their partners a chance to obtain it. Other monkeys were more egalitarian, taking the better reward only about half of the time in this unequal condition (Figure 19.9a). Pairs in which both individuals shared in the better rewards were almost three times as successful at the cooperative task as compared to those pairs in which one member consistently claimed the better reward (Figure 19.9b). Interestingly, this was true in both the unequal *and* the equal conditions. Monkeys whose partners took the better reward in the unequal condition quit cooperating in all conditions, whether or not there was a possibility of receiving a less good reward. An analysis of rewards obtained shows that, due to the much higher rate of cooperation, the egalitarian strategy resulted in far more rewards for both monkeys (Brosnan *et al.*, 2006).

p0650 It appears that these monkeys are reacting against unfair partners, rather than attempting to maximize reward intake. Monkeys simply did not cooperate with individuals who dominated the better rewards, even when the payoffs would have been the same. From a reward maximization perspective, this makes

no sense, as subjects always got one of the rewards, so when rewards were equal, both individuals benefited equally. In fact, monkeys who failed to cooperate were no less likely to come over and observe the food rewards, so presumably they could have evaluated each trial independently. Perhaps they improve their long-term outcomes by avoiding individuals who typically do not behave equitably. This, too, hints at an emotional response against a partner.

Chimpanzees are likely to behave in a similar fashion, reacting against partners who do not treat them equitably. Although the same study has not been completed, work with cooperative tasks in chimpanzees shows that they are sensitive to partner behavior. Chimpanzees are much more likely to cooperate with individuals who tolerantly share food with them (Melis *et al.*, 2006a) and actively recruit tolerant partners (Melis *et al.*, 2006b) for cooperative enterprises. Future studies which further investigate monkeys' and apes' responses in cooperative tasks will clarify how sensitivity to context evolved, and whether it typically functions to increase payoffs over the long run.

Comparison of Human and Non-human Primate Responses to Inequity

Capuchin monkeys and chimpanzees both respond very negatively to receiving less benefit than a partner. This sort of reaction is similar to one we see in humans, as in the ultimatum game or the impunity game, in which people will turn down an absolute gain if the outcome is not equitable (Güth *et al.*, 1982), sometimes even when the response does not result in more equity between partners (Yamagishi, 2007). However, the reaction in non-human primates is not exactly the same as that seen in humans. The primary difference is that non-human primates do not respond to receiving more than their partner. Humans seem to treat "fairness" as a norm, while non-human primates appear more interested in their own outcomes. Of course, humans are not always interested in their fellow man's well-being, either, and do not always respond to overcompensation (see "Inequity aversion"). Future work with primates may uncover situations in which primates, too, are concerned about equity for others. Studying these situations would shed light on the contexts which elicit this response in humans.

Even with this difference, however, similarities predominate. In both humans and non-human primates, the social partner's actions appear to be more important than the actual payoff. Capuchin monkeys will accept an unequal payoff in the short term if the long-term payoffs are similar. This reaction promotes

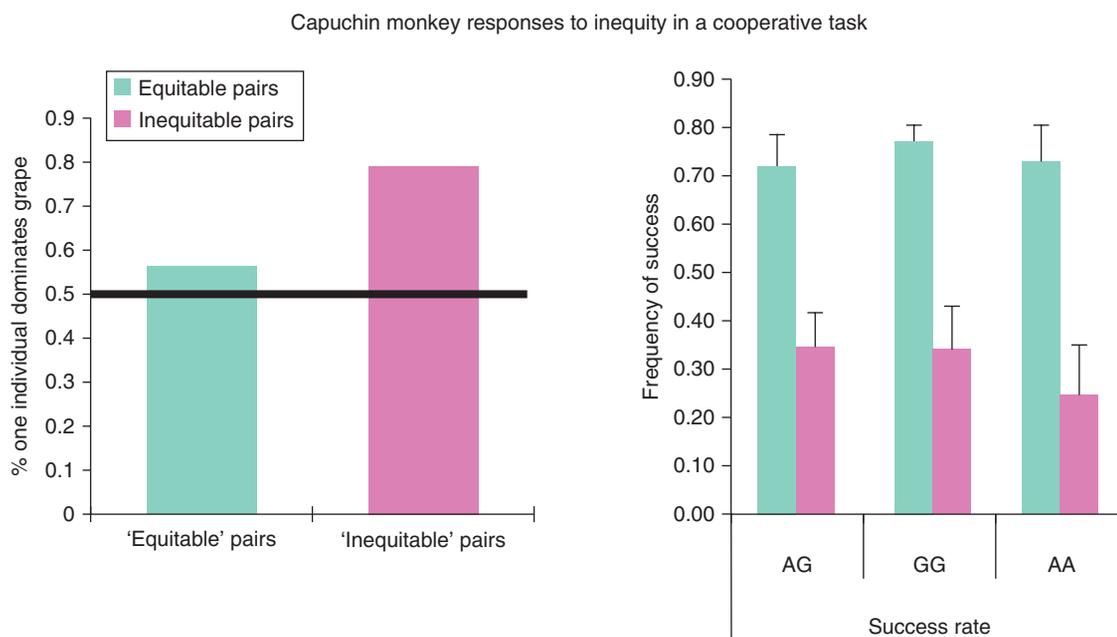


FIGURE 19.9 The frequency of successful cooperation for “equitable” and “inequitable” pairs in an unequally rewarded cooperation task. Some pairs (equitable) took turns receiving the higher-value reward, while in other pairs (inequitable) one individual claimed most of the better rewards. Equitable pairs were almost three times as likely to successfully cooperate in all conditions, including those with equitable rewards. AG = one subject gets apple, one subject gets grape; GG = both subjects get grape; AA = both subjects get apple. Reprinted from Brosnan *et al.* (2006).

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cooperation in situations in which immediate payoffs are not identical or one player makes a “mistake,” behaving non-cooperatively when he or she either intended to cooperate or did not understand the task. Individuals who view the interaction through a more long-term lens will ultimately maintain more cooperative opportunities.

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Social context is undoubtedly important for both humans and non-human primates. Humans and chimpanzees both appear more likely to tolerate inequity in close relationships. Both humans and non-human primates, too, are highly influenced by the partner’s behavior, perhaps more so than the reward distribution. Monkeys, for instance, overlook short-term inequity if the long-term payoffs are equitable. Such a focus on partner behavior and intentions, even over payoffs, may also support cooperation.

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Non-human primates show several hallmarks of an emotional reaction to inequity. For instance, primates respond to distributional inequity in ways that lower their payoff, and respond negatively to a partner who has treated them inequitably, even in situations in which rewards are equal. Given what we know about the human response from imaging studies, it seems likely that these reactions are processed in emotion centers of the brain in non-human primates as well. Future studies that are able to investigate brain

activity in awake primates interacting socially with other primates will help to clarify these questions.



Much work remains to be done before we fully understand the evolution of fairness. The experiments comparing monkeys, apes, and humans are not typically identical. This leaves open the possibility of secondary social or experimental factors influencing responses differently in the two species. For instance, non-human primate partners are always paired non-anonymously with a social partner from their group (they become too anxious to participate if paired with a stranger). In experimental economics games, on the other hand, people are typically tested with no cues as to their social partner’s identity, or see them only on a screen. However, even the threat of anonymous, written, impersonal negative social feedback increases offers (Xiao and Houser, 2005), implying that results might be quite different in games which include social interaction.

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CONCLUSIONS

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Like humans, primates respond negatively to inequity directed against themselves. As with humans, these responses are difficult to explain with a single

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model of inequity aversion or reciprocity. Reciprocity may explain why, in the cooperative bar-pull study, monkeys were willing to accept a lesser reward on some trials if overall payoffs were the same. Inequity aversion may explain why a capuchin would refuse to cooperate when a partner routinely claims the better reward in an unequal payoff situation. Yet, refusing a reward in the exchange tasks actually increases relative inequity, which violates the inequity aversion models. This behavior, which occurs in humans as well as capuchin monkeys and chimpanzees, is difficult to explain. Perhaps for all three species, refusal to participate can be explained not only by inequity aversion and reciprocity, but also as a commitment device. Clearly, more research is needed to understand the mechanism for rejection in non-human primates, and to better understand the evolution of the behavior.

p0730 Non-human primates provide a valuable model for studying human behavior, including reactions to inequity. Responses to inequity, for instance, likely evolved in a common ancestor to humans, apes, and monkeys (and are possibly more ancient than this); thus, understanding how such a response manifests and the factors which affect it in other species helps us to understand how the reaction evolved into what we see in humans.

s0150 Acknowledgments

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References

- Andreoni, J., Brown, P.M., and Vesterlund, L. (2002). What makes an allocation fair? Some experimental evidence. *Games Econ. Behav.* 40, 1–24.
- Axelrod, R. (1984). *The Evolution of Cooperation*. New York, NY: Basic Books.
- Beran, M.J. (2002). Maintenance of self-imposed delay of gratification by four chimpanzees (*Pan troglodytes*) and an orangutan (*Pongo pygmaeus*). *J. Gen. Psychol.* 129, 49–66.
- Bernhard, H., Fischbacher, U., and Fehr, E. (2006). Parochial altruism in humans. *Nature* 442, 912–915.
- Blount, S. (1995). When social outcomes aren't fair: the effect of causal attributions on preferences. *Org. Behav. Hum. Dec. Proc.* 63, 131–144.
- Boehm, C. (1999). *Hierarchy in the Forest: The Evolution of Egalitarian Behavior*. Cambridge, MA: Harvard University Press.
- Boesch, C. (1994). Cooperative hunting in wild chimpanzees. *Animal Behav.* 48, 653–667.
- Bolton, G.E. and Ockenfels, A. (2000). ERC: A theory of equity, reciprocity, and competition. *Am. Econ. Rev.* 90, 166–193.
- Bolton, G.E. and Zwick, R. (1995). Anonymity versus punishment in Ultimatum Game bargaining. *Games Econ. Behav.* 10, 95–121.
- Boyd, R., Gintis, H., Bowles, S., and Richerson, P.J. (2003). The evolution of altruistic punishment. *PNAS* 100, 3531–3535.
- Bräuer, J., Call, J., and Tomasello, M. (2006). Are apes really inequity averse? *Proc. R. Soc. Lond. B* 273, 3123–3128.
- Brosnan, S.F. (2006a). At a crossroads of disciplines. *Social Justice Res.* 19, 218–227.
- Brosnan, S.F. (2006b). Nonhuman species' reactions to inequity and their implications for fairness. *Social Justice Res.* 19, 153–185.
- Brosnan, S.F. (2008). Inequity and prosocial behavior in chimpanzees. In: E.V. Lonsdorf, S. Ross, and T. Matsuzawa (eds), *The Mind of the Chimpanzee*. Chicago, IL: University of Chicago Press, (in press).
- Brosnan, S.F. and de Waal, F.B.M. (2002). A proximate perspective on reciprocal altruism. *Hum. Nature* 13, 129–152.
- Brosnan, S.F. and de Waal, F.B.M. (2003). Monkeys reject unequal pay. *Nature* 425, 297–299.
- Brosnan, S.F. and de Waal, F.B.M. (2004a). Reply to Henrich and Wynne. *Nature* 428, 140.
- Brosnan, S.F. and de Waal, F.B.M. (2004b). Socially learned preferences for differentially rewarded tokens in the brown capuchin monkey, *Cebus apella*. *J. Comp. Psychol.* 118, 133–139.
- Brosnan, S.F. and de Waal, F.B.M. (2006). Partial support from a non-replication: comment on Roma, Silberberg, Ruggiero, and Suomi. *J. Comp. Psychol.* 120, 74–75.
- Brosnan, S.F., Schiff, H.C., and de Waal, F.B.M. (2005). Tolerance for inequity may increase with social closeness in chimpanzees. *Proc. R. Soc. Lond. B* 1560, 253–258.
- Brosnan, S.F., Freeman, C., and de Waal, F.B.M. (2006). Partner's behavior, not reward distribution, determines success in an unequal cooperative task in capuchin monkeys. *Am. J. Primatol.* 68, 713–724.
- Burkart, J., Fehr, E., Efferson, C., and van Schaik, C.P. (2007). Other-regarding preferences in a non-human primate: common marmosets provision food altruistically. *PNAS* 104, 19762–19766.
- Byrne, R.W. and Whiten, A. (1988). *Machiavellian Intelligence*. Oxford: Clarendon Press.
- Camerer, C. (2003). *Behavioral Game Theory: Experiments in Strategic Interaction*. Princeton, NJ: Princeton University Press.
- Clark, M.S. and Grote, N.K. (2003). Close relationships. In: T. Millon and M.J. Lerner (eds), *Handbook of Psychology: Personality and Social Psychology*, Vol. 5. New York, NY: John Wiley & Sons, pp. 447–461.
- Crawford, M. (1937). The cooperative solving of problems by young chimpanzees. *Comp. Psychol. Monogr.* 14, 1–88.
- Dana, J.D., Weber, R.A., and Kuang, J. (2003). Exploiting moral wriggle room: behavior inconsistent with a preference for fair outcomes. Carnegie Mellon Behavioral Decision Research Working Paper No. 349, <http://ssrn.com/abstract=400900>.
- Dawes, C.T., Fowler, J.H., Johnson, T. et al. (2007). Egalitarian motives in humans. *Nature* 446, 794–796.
- de Waal, F.B.M. (1989). Food sharing and reciprocal obligations among chimpanzees. *J. Hum. Evol.* 18, 433–459.
- de Waal, F.B.M. (1991). The chimpanzee's sense of social regularity and its relation to the human sense of justice. *Am. Behav. Scientist* 34, 335–349.
- de Waal, F.B.M. (1997a). Food transfers through mesh in brown capuchins. *J. Comp. Psychol.* 111, 370–378.
- de Waal, F.B.M. (1997b). The chimpanzee's service economy: food for grooming. *Evol. Hum. Behav.* 18, 375–386.
- de Waal, F.B.M. (2000). Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behav.* 60, 253–261.
- de Waal, F.B.M. (2001). *The Ape and the Sushi Master*. New York, NY: Basic Books.

- de Waal, F.B.M. (2006). *Primates and Philosophers*. Princeton, NJ: Princeton University Press.
- de Waal, F.B.M. and Berger, M.L. (2000). Payment for labour in monkeys. *Nature* 404, 563.
- de Waal, F.B.M. and Davis, J.M. (2002). Capuchin cognitive ecology: cooperation based on projected returns. *Neuropsychologia* 1492, 1–8.
- Diekmann, K.A., Samuels, S.M., Ross, L., and Bazerman, M.H. (1997). Self-interest and fairness in problems of resource allocation: allocators versus recipients. *J. Pers. Social Psychol.* 72, 1061–1074.
- Dindo, M. and de Waal, F.B.M. (2006). Partner effects on food consumption in brown capuchin monkeys. *Am. J. Primatol.* 69, 1–6.
- Dubreuil, D., Gentile, M.S., and Visalberghi, E. (2006). Are capuchin monkeys (*Cebus apella*) inequity averse? *Proc. R. Soc. Lond. B* 273, 1223–1228.
- Duffy, K.G., Wrangham, R.W., and Silk, J.B. (2007). Male chimpanzees exchange political support for mating opportunities. *Curr. Biol.* 17, R586.
- Evans, T.A. and Westergaard, G.C. (2006). Self-control and tool use in tufted capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* 120, 163–166.
- Fehr, E. and Gächter, S. (2002). Altruistic punishment in humans. *Nature* 415, 137–140.
- Fehr, E. and Rockenbach, B. (2003). Detrimental effects of sanctions on human altruism. *Nature* 422, 137–140.
- Fehr, E. and Schmidt, K.M. (1999). A theory of fairness, competition, and cooperation. *Q. J. Economics* 114, 817–868.
- Feistner, A.T.C. and McGrew, W.C. (1989). Food-sharing in primates: a critical review. In: P.K. Seth and S. Seth (eds), *Perspectives in Primate Biology*, Vol. 3. New Delhi: Today and Tomorrow's Printers and Publishers, pp. 21–36.
- Fontenot, M.B., Watson, S.L., Roberts, K.A., and Miller, R.W. (2007). Effects of food preferences on token exchange and behavioural responses to inequality in tufted capuchin monkeys, *Cebus apella*. *Animal Behav.* 74, 487–496.
- Frank, R.H. (1988). *Passions Within Reason: The Strategic Role of the Emotions*. New York, NY: W.W. Norton & Co.
- Gilby, I.C. (2006). Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Animal Behav.* 71, 953–963.
- Güth, W., Schmittberger, R., and Schwartz, B. (1982). An experimental analysis of ultimatum bargaining. *J. Econ. Behav. Org.* 3, 367–388.
- Hare, B., Call, J., Agnetta, B., and Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behav.* 59, 771–785.
- Henrich, J. (2004). Inequity aversion in capuchins. *Nature* 428, 139.
- Henrich, J., Boyd, R., Bowles, S. et al. (2001). In search of *Homo Economicus*: behavioral experiments in 15 small-scale societies. *Am. Econ. Rev.* 91, 73–78.
- Hockings, K.J., Humle, T., Anderson, J.R. et al. (2007). Chimpanzees share forbidden fruit. *PLoS ONE* 2, e886, doi:10.1371/journal.pone.0000886.
- Hoffman, E., McCabe, K., Shachat, K., and Smith, V. (1994). Preferences, property rights and anonymity in bargaining games. *Games Econ. Behav.* 7, 346–380.
- Jensen, K., Hare, B., Call, J., and Tomasello, M. (2006). What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proc. R. Soc. Lond. B* 273, 1013–1021.
- Jensen, K., Call, J., and Tomasello, M. (2007). Chimpanzees are rational maximizers in an Ultimatum Game. *Science* 318, 107–109.
- Kahneman, D., Knetsch, J.L., and Thaler, R. (1986). Fairness as a constraint on profit seeking: entitlements in the market. *Am. Econ. Rev.* 76, 728–741.
- Knoch, D., Pascual-Leone, A., Meyer, K. et al. (2006). Diminishing reciprocal fairness by disrupting the right prefrontal cortex. *Science* 314, 829–832.
- Loewenstein, G.F., Thompson, L., and Bazerman, M.H. (1989). Social utility and decision making in interpersonal contexts. *J. Pers. Social Psychol.* 57, 426–441.
- Melis, A.P., Hare, B., and Tomasello, M. (2006a). Engineering cooperation in chimpanzees: tolerance constraints on cooperation. *Animal Behav.* 72, 275–286.
- Melis, A.P., Hare, B., and Tomasello, M. (2006b). Chimpanzees recruit the best collaborators. *Science* 311, 1297–1300.
- Mendres, K.A. and de Waal, F.B.M. (2000). Capuchins do cooperate: the advantage of an intuitive task. *Animal Behav.* 60, 523–529.
- Mitani, J.C. (2006). Reciprocal exchange in chimpanzees and other primates. In: P. Kapeller and C.P. van Schaik (eds), *Cooperation in Primates and Humans: Evolution and Mechanisms*. Berlin: Springer, pp. 111–113.
- Mitani, J.C. and Watts, D.P. (2001). Why do chimpanzees hunt and share meat? *Animal Behav.* 61, 915–924.
- Nishida, T., Hasegawa, T., Hayaki, H. et al. (1992). Meat-sharing as a coalition strategy by an alpha male chimpanzee? In: T. Nishida, W.C. McGrew, P. Marler et al. (eds), *Topics in Primatology: Human Origins*, Vol. 1. Tokyo: University of Tokyo Press, pp. 159–174.
- Perry, S. and Rose, L. (1994). Begging and transfer of coati meat by white-faced capuchin monkeys, *Cebus capucinus*. *Primates* 35, 409–415.
- Perry, S., Manson, J.H., Dower, G., and Wikbert, E. (2003). White-faced capuchins cooperate to rescue a groupmate from a Boa constrictor. *Folia Primatologica* 74, 109–111.
- Rabin, M. (2001). Incorporating fairness into game theory and economics. *Am. Econ. Rev.* 83, 1281–1301.
- Rilling, J.K. and Insel, T. (1999). The primate neocortex in comparative perspective using magnetic resonance imaging. *J. Hum. Evol.* 16, 191–233.
- Roma, P.G., Silberberg, A., Ruggiero, A.M., and Suomi, S.J. (2006). Capuchin monkeys, inequity aversion, and the frustration effect. *J. Comp. Psychol.* 120, 67–73.
- Rose, L.M. (1997). Vertebrate predation and food-sharing in *Cebus* and *Pan*. *Intl J. Primatol.* 18, 727–765.
- Sanfey, A.G., Rilling, J.K., Aronson, J.A. et al. (2003). The neural basis of economic decision-making in the Ultimatum game. *Science* 300, 1755–1758.
- Silk, J.B., Brosnan, S.F., Vonk, J. et al. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. *Nature* 437, 1357–1359.
- Tinklepaugh, O.L. (1928). An experimental study of representative factors in monkeys. *J. Comp. Psychol.* 8, 197–236.
- van Wolkenten, M., Brosnan, S.F., and de Waal, F.B.M. (2007). Inequity responses in monkeys are modified by effort. *Proc. Natl Acad. Sci.* 104, 18854–18859.
- Vonk, J., Brosnan, S.F., Silk, J.B. et al. (2008). Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Animal Behav.*
- Wallace, B., Cesarini, D., Lichtenstein, P., and Johannesson, M. (2007). Heritability of ultimatum game responder behavior. *Proc. Natl Acad. Sci.* 104, 15631–15634.
- Walster, H.E., Walster, G.W., and Berscheid, E. (1978). *Equity: Theory and Research*. Boston, MA: Allyn and Bacon.
- Warneken, F. and Tomasello, M. (2006). Altruistic helping in human infants and young chimpanzees. *Science* 311, 1301–1303.
- Warneken, F., Hare, B., Melis, A.P. et al. (2007). Spontaneous altruism by chimpanzees and young children. *PLoS Biol.* 5, e184.
- Whiten, A. (1998). Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* 112, 270–281.

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- Wiesenfeld, B.M., Swann, W.B., Jr, Brockner, J., and Bartel, C.A. (2008). Is more fairness always preferred? Self-esteem moderates reactions to procedural justice. *Acad. Management J.* 50, 1235–1253.
- Wynne, C.D.L. (2004). Fair refusal by capuchin monkeys. *Nature* 428, 140.
- Xiao, E. and Houser, D. (2005). Emotional expression in human punishment behavior. *Proc. Natl Acad. Sci.* 102, 7398–7401.
- Yamagishi, T. (2007). Reciprocity, strong reciprocity, and fairness. Paper presented at the Society for Experimental Social Psychology, Chicago, IL.
- Zizzo, D.J. and Oswald, A. (2001). Are people willing to pay to reduce other's incomes? *Annales d'Economie et de Statistique*, 63–64, 39–62.