Chapter 11
Evolved Irrationality? Equity and the Origins of Human Economic Behavior

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Abstract While the economic approach to human decision-making characterizes our choices in terms of how we maximize utility, in many cases, such an approach fails to predict the decisions we actually make. Specifically, preference-biases such as loss-aversion and reference-dependence demonstrate that decision-makers make relative (rather than absolute) comparisons in judging the quality of their rewards. In the case of inequity aversion, decision-makers take into account not just their own earnings, but also the quality of another individual's reward. In this chapter, we discuss an evolutionary approach to uncovering the origins of these irrational economic strategies. To do this, we review recent experiments showing that nonhuman primates possess a variety of economic tendencies previously thought to be unique to humans. The existence of economic decision-making biases outside of our species implies that ancestral organisms may have possessed these same tendencies – suggesting that humans' biased economic decisions may actually have been adaptive in evolutionarily ancient environments, even though they might be characterized as irrational in contemporary economic settings.

11.1 *Homo economicus*: Model Subject or Tall Tale?

One of the major challenges facing humans from all cultural backgrounds is how to make good decisions. In the human species, decision-making seems remarkably complicated – judging the potential benefit of even simple choices, like walking to the theater to see a movie, can be incredibly tough. Is there a better movie playing

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somewhere else? Am I being charged a fair price for the ticket? Is the person in the next theater enjoying himself more than I am? And how does seeing the movie compare to something else I could be doing with my time, like re-reading my favorite novel? The answers to each of these questions will, undoubtedly, affect the value of my choice to go to the movies. In addition, even posing these kinds of questions enlists a vast array of sophisticated mental operations: taking others' perspectives, making comparisons to other similar situations, imagining the consequences of other hypothetical actions, and so on. Making even very simple decisions is therefore a tough cognitive task, not just for our own species but for other nonhuman creatures as well.

The question of how decision-makers should go about making their decisions is one that has plagued a number of academic fields for some time. One of the most heralded answers to this tough question comes from the field of classical economics. The economic approach thinks of the rational decision-maker as someone who maximizes his utility in any decision-making scenario. Economists begin by assuming that a decision-maker has certain stable preferences, and that he makes decisions that optimally satisfy these preferences. If a decision-maker did indeed make decisions based on factors that were consistent across many contexts and possessed preferences that were not heavily influenced by the way he processed information, then one would conveniently be able to interpret his behavior according to this utility-maximizing approach. A perfectly rational subject such as this – a *Homo economicus* – would therefore be expected to choose to go to the movies whenever this action would deliver more utility than the other options that *Homo economicus* would have to sacrifice in order to attend the film.

Notably, several important economic phenomena – such as pricing behavior in markets – are, in fact, neatly consistent with the *Homo economicus* utility-maximizing model.[1] Despite the potential advantages of a traditional economic approach in such cases, a similarly notable body of empirical research suggests that humans do not always behave like aspiring *Homo economici*. Many phenomena that are common in human decision-making – for example, giving anonymously to charity, helping a stranger cross the street, or switching your preferences based on context – do not necessarily make sense from the perspective of perfect utility maximization (see reviews in Kahneman et al. 1982; Camerer 1998). Indeed, when considering real human behavior, using *Homo economicus* as a normative standard leads to strong and often unrealistic assumptions about how

[1] It's not just humans that sometimes obey the maxims of utility-maximization. Indeed, researchers have previously identified economically-rational feeding strategies in a variety of organisms (for reviews, see Glimcher 2003; Krebs and Davies 1993). To take one famous example, great tits behave as though they are optimizing their foraging utility when they make decisions about remaining in (or leaving) a feeding patch (Cowie 1977).

people ought to act: for example, the assumption that decision-makers always selfishly maximize their own wealth level (which would presumably conflict with anonymously giving money away), or the assumption that preferences are stable regardless of how information is presented. Studies conducted by social psychologists, anthropologists, and economists suggest that, instead of behaving like *Homo economicus*, decision-makers' choices are constrained in predictable ways: we sacrifice self-interest to invest in fairness norms (see Kahneman et al. 1986) and punish wrongdoers (Henrich et al. 2004), and will change our decisions systematically based on the wording of different problems (Kahneman and Tversky, 2000). In short, humans do not actually behave like classical economists would predict, even when their own self-interest is at stake.

These seemingly "irrational" human tendencies can be considered puzzling not just from a classical economic perspective, but also from an evolutionary one. Presumably, the decision-making behavior of modern humans has been shaped over time by natural selection: the economic strategies observed today are thus likely to have been shaped over generations of competition for scarce resources. Because rational decision-making behavior plausibly increases an organism's chance of survival, one would assume that our human ancestors might indeed have figured out ways to optimally maximize their expected payoffs, which would thus lead to maximizing the ultimate evolutionary currency – survival and reproductive success. In this way, our deviation from the optimal normative model of expected utility maximization poses not just an economic dilemma, but also an evolutionary one.

How then did humans develop such irrational strategies for making decisions? Some researchers have attempted to explain the origins of human irrationality through an adaptive (or, following Tinbergen's terminology, functional) approach that examines whether purportedly irrational strategies actually can work to increase survival and reproductive success (e.g., Gigerenzer et al. 1999; Gigerenzer and Selten 2001). Here, we approach the problem of human irrationality from a slightly different level of analysis. Specifically, we take a phylogenetic approach to these seemingly irrational behaviors, one that focuses on whether these tendencies exist not just in human decision-making but also in the decision-making of our close primate relatives. We argue that people violate the standard assumptions of rational choice because their economic decision-making reflects a set of mental processes that are actually evolutionarily quite ancient, even though they conflict with certain norms of economic rationality. In this sense, economic irrationalities may have originated in ancestrally related species, and may therefore emerge independently of human-specific cultural experiences.

In this chapter, we examine the evolutionary origins of several key features of our "irrational" economic behavior. We first review each of these phenomena in human economic behavior and then investigate the evolutionary origins of these phenomena by exploring whether similar features exist in the decision-making of closely related primates. We then examine what each of these phenomena means for the evolutionary origins of human economic behavior more generally.

11.2 The Irrationality of Human Preferences

One of the standard assumptions made by rational accounts of human decision-making is the idea that decision-makers should have preferences that are stable over time and consistent across contexts. Indeed, much of the field of economics rests on assumption that preferences are stable enough to be modeled and used to make formal predictions. Unfortunately, despite the usefulness of assumptions concerning the stability of our preferences, there is a growing body of empirical work demonstrating that humans do not obey these classic assumptions. Much of the early empirical evidence for these preference violations came from the groundbreaking work of Daniel Kahneman and Amos Tversky (e.g., Kahneman and Tversky 1979; Tversky and Kahneman 1981, 1986). Beginning in the 1970s, these researchers developed elegant empirical demonstrations of situations in which decision-makers reliably failed to make rational choices.

One of Kahneman and Tversky's most famous early observations was that people's choices seem to vary based on the context in which they are made. Such context-specificity in choice seems to violate a central assumption of rational choice, the invariance assumption, namely, that people should treat any presentation of the same information identically. Rather than always choosing the option with the highest expected payoff, people seem to make different decisions when problems are described in different ways. Take, for example, the two scenarios first presented by Kahneman and Tversky (1979):

Scenario 1: Gains
You have been given $1,000. You are now asked to choose between:
a. 50% chance to receive another $1,000 and 50% chance to receive nothing [16% of subjects choose this option]
b. Receiving $500 with certainty [84% of subjects choose this option]

Scenario 2: Losses
You have been given $2,000. You are now asked to choose between:
a. 50% chance to lose $1,000 and 50% chance to lose nothing [69% of subjects choose this option]
b. Losing $500 with certainty [31% of subjects choose this option]

Note first that the two scenarios are simply alternate formulations of the same final outcomes: each scenario involves a choice between either a risky final payoff of either $2,000 or $1,000 [A] or a sure final payoff of $1,500. People may vary in how much they'd like to gamble by taking choice A over choice B, but they should not have a different preference for risk-taking in Scenario 1 and Scenario 2, since the two scenarios actually present participants with the same two choices. But as shown above, people did show different preferences across the two scenarios. When the final payoffs were represented or "framed" in terms of a gain, as in Scenario 1, the majority of people chose to go for the safe option. In contrast, when the payoffs were framed as losses, most people chose the riskier option. Kahneman and

Tversky labeled this phenomena the "reflection effect": when given a safe and risky choice with the same average payoff, people paradoxically choose the risky gamble when the options are framed to emphasize losses, but not when the same choices are presented as gains These examples demonstrate the puzzling result that when subjects are given alternate formulations of the same set of choices, their preferences flip from being risk-averse to being risk-seeking.

The reflection effect nicely illustrates two central features of human economic choice that violate the assumptions of a *Homo economicus* model. The first feature is that human economic choice is based on *relative* rather than absolute payoffs. Kahneman and Tversky described this phenomenon in terms of what they called a "reference point" bias; people seem to evaluate different options in regards to a particular (usually arbitrary) *reference point* (e.g., one's current asset position in a particular experimental gamble, etc.). The second feature concerns the fact that people treat options differently depending on whether their choices lead to positive (gains) or negative (losses) outcomes relative to their reference point. As the scenarios above demonstrate, people tended to be risk-averse when dealing with outcomes that are gains relative to their reference point – they chose sure smaller gains over larger riskier gains – but became risk-seeking when dealing with losses – they preferred a risky chance not to have any loss over a sure small loss. Kahneman and Tversky famously described this phenomenon in terms loss aversion – people work harder to avoid losses than they do to seek out equally sized gains.[2] As Kahneman and Tversky (1979) observed in the above scenario, the disutility that decision-makers experience from losses tends to be greater than the utility they experience with identically sized gains. Such loss aversion makes relative changes in the negative direction far more salient than negative changes in the positive direction (see Kahneman and Tversky 2000 for review).

These two features of human economic choice – reference dependence and loss aversion – explain many real-world irrationalities in human economic decision-making. For example, investors are reluctant to sell real estate (Genesove and Mayer 2001) or stocks (Odean 1998) for less than their buying price, even when doing so would be profitable. Making choices based on reaching predetermined reference-levels also leads to poor business decisions in the real world. The behavioral economist Colin Camerer famously observed that reference dependence and loss aversion lead New York cab drivers to work less hard than they should when presented with more lucrative conditions (such as on rainy days when the supply of potential clients is higher) in part because they tend to work until they hit

[2] Kahneman and Tversky (1979, 1981) developed a formal descriptive account of choice behavior known as Prospect Theory to explain reference dependence and loss aversion. Prospect Theory posits that people represent choices in terms of their *value*. Values are described in relative terms and are measured as losses or gains relative to a specified (yet often arbitrary) reference point. Because of loss aversion, there is a kink in the value function at the reference point, such that receiving a gain of a certain size (e.g., gaining $100) is associated with an increase in value that is far smaller (i.e., about half as large) than the decrease in value associated with an identically sized loss (e.g., losing $100).

a certain reference payoff level; this leads cab drivers to mistakenly work longer days when the supply of clients is low and shorter days when the supply of clients is higher. Finally, reference dependence and loss aversion are thought to be responsible for an irrational phenomenon known as the endowment effect, a bias in which people overvalue objects they own. The endowment effect can lead to real-world problems in bartering and bilateral trade (see Thaler 1980). In one famous example, Kahneman et al. (1990) gave a group of participants one of two identically priced items – a coffee mug or a box of pens. They then allowed subjects to barter with each other for the alternative item. Few objects seem to trade hands in part because owners tended to demand a larger price to sell or trade their object than non-owners were willing to pay to buy it. Kahneman and colleagues interpreted this phenomenon in terms of loss aversion: owners think of bartering in terms of losing their owned object. Losses affect well-being more severely than equally sized gains, which can lead an owner to systematically over-estimate how much money he should demand when selling his possession. In fact, Kahneman and colleagues observed that owners sometimes demand nearly twice as much as buyers are willing to pay in order to give up an owned item.

In summary, humans decision-making appears to exhibit two phenomena that violate the tenets of rational utility-maximization and lead to irrationalities in economic markets. First, and most critically, human think about choices in *relative terms*; rather than focusing on our absolute payoffs, we instead make decisions with reference to arbitrary information that is typically irrelevant to the problem at hand. Second, we are *more sensitive to losses* relative to reference points than we are to equally sized gains. Such loss aversion can lead us to think about problems differently when they are framed in negative versus positive terms.

11.3 Irrational Equity-Seeking and the Emergence of Human Fairness Norms

The framing effects discussed above are not the only situations in which people exhibit loss aversion and relative preference switches across contexts. Another situation in which people exhibit strikingly irrational tendencies to forgo earnings is when thinking about their own payoffs relative to those of others. Behavioral economists have long observed that one of the most salient reference points for our own decisions is "what others are getting." Indeed, researchers have observed that people are often willing to give up much in terms of their absolute happiness and wealth in order to be better off than others. In one striking example, Solnick and Hemenway (1998) gave people the choice between earning $50,000 while others are earning $25,000 or earning $100,000 while others are earning $250,000. Surprisingly, almost half of the respondents were willing to take the first choice, despite the fact that this choice would cut one's actual wealth level and purchasing-power in half.

Human decision-makers' sensitivity to the relative payoffs of others is central to another way that human economies violate self-interested utility-maximization:

we care a bit more than a *Homo economicus* should about equity. For example, Kahneman et al. (1986) identified a number of economic scenarios in which people's interpretation of what should be done depends not on a decision's profitability, but instead on a decision's perceived equitability. Consider the following scenario:

> *A small company employs several workers and has been paying them average wages. There is severe unemployment in the area and the company could easily replace its current employees with good workers at a lower wage. The company has been making money. The owners reduce the current workers' wages by 5%.*

Kahneman and colleagues observed that 77% of people found the company's action in this case to be unacceptable. Interestingly, people's perceptions seem to change depending on the payoff received by the company; when the researchers changed the above scenario to read that the company "has been losing money," only 32% of people thought the company's wage cuts were unacceptable. In this way, people seem to use fairness constraints over economic constraints when judging the acceptability of economic decisions; as in the above, people judge a wage-cut for the employees as more acceptable when the company is also experiencing a loss than in cases when it is not.

Our human concern for equitable outcomes seems to lead to a number of real-world violations of selfish utility-maximization. First, people often give more than is minimally required in experimental giving or trust games. One such scenario involves a well-known economic game known as the dictator game (e.g., Camerer 2003; Henrich et al. 2004). In this game, two anonymous individuals play a one-shot game in which one individual, the dictator, must decide how to split a cash offer (e.g., $10). Because the game is anonymous and played only once, there is little incentive from a utility maximization perspective for the dictator to give any of the cash allotment to the second player. Nevertheless, participants do not selfishly keep all of the money. Indeed, most people give nonzero offers with many people splitting the allotment 50–50.

A second set of cases in which people exhibit a preference for fair behaviors concerns altruistic punishment – instances in which people are willing to sacrifice individual gain in order to punish wrongdoers (e.g., Kahneman et al. 1986; Zizzo and Oswald 2001; Camerer 2003; Fehr and Rockenbach 2003). Using experimental markets, researchers have found time after time that participants are willing to exact costly punishment even in cases where these behaviors yield no material gain for the punisher or gift-giver (Fehr and Gächter 2002). For example, consider the ultimatum game, a modified form of the dictator game. In this game, the first individual (the proposer) can again split the money any way he sees fit, but the second individual (the receiver) can then choose either to accept or reject the proposer's offer. If the receiver rejects the offer, then neither the proposer nor the receiver receives any money. From the perspective of self-interest, one might expect receivers to accept any nonzero offer. After all, any offer – even one of $0.01 – is better than nothing. It, therefore, follows that we would expect extremely low offers from proposers in anonymous one-shot games. In contrast, researchers

robustly observe that offers lower than 25% are nearly always rejected, and proposers frequently offer much higher than this threshold (Güth et al. 1982).

Clearly, neither the proposer nor the receiver is maximizing his own personal payoffs in this anonymous one-shot game. If they were, then proposers would give away as little as possible (e.g., $0.01 out of a possible $10), and receivers would be willing to accept these extremely small offers. Nevertheless, the fact that receivers deviate from this profit-maximizing strategy indicates that they may actually be reacting to the relative fairness of proposers' offers. Indeed, it seems that participants exhibit a cognitive capacity to detect the unfairness of certain rewards – namely, they possess the ability to compare their reward to that of another individual, to react negatively to unfair cases, and to forego small offers in order to punish those who created the inequity.[3]

11.4 The Evolution of Primate Economic Strategies: Monkey Markets

As reviewed above, a wealth of empirical work has established that loss-aversion – which requires sensitivity to others' rewards, and at least a minimal capacity to understand the relative quality of a reward – is robust in adult humans. A similarly large body of work has demonstrated that human decision-makers attend to and obey fairness constraints when making choices. Are these capacities specific to our own species? Or do other species possess similar tendencies? Unfortunately, less work to date has addressed whether similar biases are shared across the animal kingdom and, more specifically, whether they are present in the decision-making strategies of other species within the primate order. The remainder of this chapter will review the work that has been done to date exploring whether similar irrationalities exist in the decision-making of closely related primates.

To begin, do primates share our human economic sensitivity to relative rewards and payoffs? Researchers have known for some time that primates seem to evaluate their rewards not merely in absolute terms, but also on the basis of expectations. In a famous early example, Tinklepaugh (1928) presented macaques monkeys with a memory game in which they had to wait for a hidden reward over a delay period. During some trials, he switched the kind of hidden reward while the monkey was waiting. When monkeys found a reward that was smaller than the one they had originally seen hidden, they reacted negatively (see Watanabe 1996; Santos et al. 2002 for a more recent version of this hiding expectancy task). Monkeys were happy to accept a small reward (e.g., a slice of lettuce) if they were expecting a small reward, but refused to eat a small reward if they were expecting a tastier one

[3] Interestingly, recent work suggests that the cognitive precursors of inequity aversion emerge quite early in human development (Fehr et al. 2008; Lobue et al. in press). For example, using a simplified ultimatum game, Fehr et al. (2008) showed that children as young as eight years exhibit an aversion to inequity in anonymous one-shot games.

(e.g., a banana). These results suggest that monkeys might also evaluate payoffs in terms of reference points.

To get at this issue more carefully, we (Chen et al. 2006) decided to explore the possibility that primates might be reference-dependent in a context more similar to that of human economic choices. Specifically, we examined whether primates would evaluate relative payoffs in a real economic market – one that used "monetary" gambles similar to the scenarios presented to humans. To this end, we trained a group of capuchin monkeys (*Cebus apella*) to trade small metal tokens with human experimenters in order to obtain food (see Westergaard et al. 1998; Brosnan and de Waal 2003, 2004; Addessi et al. 2007 for similar token trading methodologies). In each study, we gave monkeys a "wallet" of small metal tokens, and reinforced them with food rewards for handing these tokens back to a human experimenter. Once subjects understood that they could "buy" food with tokens, we looked at whether they exhibited the same kinds of strategies as humans do in their experimental markets. We gave monkeys a limited budget of tokens and measured how they allocated these tokens across two experimenters, each of whom offered different kinds of foods at different prices. In this way, we could establish a measure of the monkeys' "preference" for each of the experimenters, and could thus explore how those preferences changed based on prices and framing.

We first explored whether monkeys paid attention to the "price" of different kinds of food. In our experiment, monkeys could use each token to purchase either an apple piece from one experimenter or a grape from a second experimenter. In this way, the experimenters initially sold different goods at equal prices. Because monkeys like apples and grapes equally, they spent approximately half of their token budget on each good. Once monkeys had gotten used to this price, we introduced what economists call a "price shock," and observed whether the monkeys adjusted their spending. Essentially, one of the two goods – say, apples – went on sale such that a single token now bought two units of the same item. We predicted that if monkeys reacted rationally to the price shock – that is, if their purchasing habits were related to the price of the goods, then they should change their pattern of purchasing in order to buy more of the cheaper good. Our subjects did just this, showing that their monkey token economy shared at least some features of human economies.

In a second study, we established that capuchins rationally spend more resources to obtain a greater reward. To do so, we adapted our experimental market so that the two experimenters provided the same type of reward for a token – apples – but differed in the number of apple pieces they delivered and the frequency that they provided these rewards. We again gave subjects a choice between two experimenters with whom they could trade their limited budget of tokens. The first experimenter initially displayed two pieces of apple before receiving a token from the subject, but then when paid sometimes removed one of these pieces and gave the monkey only one piece of apple. In contrast, the second experimenter always displayed one piece of apple and delivered exactly this quantity in exchange for a token (neither adding nor subtracting from it). This resulted in a situation in which the risky experimenter provided an average payoff that was one and half times the

payoff of the safe experimenter. Given this choice between a gamble with an average payoff of one and a half apple pieces and a sure choice of only one apple, capuchins preferred the gamble with the larger expected value (Chen et al. 2006). In this way, capuchins behaved rationally in at least some aspects of our trading market: they spent more resources on a cheaper food than an equally valuable but more expensive alternative, and chose options which maximize expected value even when this required choosing a risky choice over a safe one.

11.5 Primate Economic Irrationalities: Do Monkeys Exhibit Human Economic Biases?

Having established these basic similarities with our own markets, we then investigated whether capuchins shared some of the irrational preferences that commonly influence how people allocate resources – in particular, reference dependence and loss aversion. Specifically, we wanted to see whether capuchins base their choices not only on the absolute outcome of their choice but also on their initial expectation. To begin investigating whether capuchins share our human irrational purchasing tendencies, we again used our experimental two-trader market but this time did not vary either the kind or amount of food that was given to the subjects; both experimenters delivered food of *the same expected value*. Instead, we varied whether the experimenters added to or subtracted from the amount of food that they initially showed to the subject. Sometimes the experimenters gave more apples than they originally showed to the subject, and sometimes they gave less. This allowed us to explore whether subjects base their choices on the expectation (or *reference point*) created before each trade. In one study, we gave the monkeys a choice between two experimenters who both delivered the same average expected payoff of one and a half pieces of apples. For one experimenter, this average payoff was less than the monkeys' expectation. This first experimenter began every trade by showing the monkey two pieces of apple, but when paid either delivered two pieces of apple as shown or removed one to deliver only a single apple piece. The second experimenter, in contrast, gave more on average than the monkeys expected. This second experimenter began by showing the monkey only one piece of apple, but then when paid either delivered that one piece as promised or added a second piece for a payoff of two apple pieces. Despite the fact that the average payoff was identical across the two experimenters, our monkeys traded more tokens with the second experimenter, the one who offered more than the monkeys' initial expectation. This pattern of performance suggests that capuchins take into account reference points, just as humans do.

But do capuchins also exhibit loss aversion? To investigate this, we again had both experimenters deliver an identical final payoff (in this case, a single apple piece). The first experimenter, however, initially began by displaying two pieces of apple at the start of each trial, but then subtracted one piece before giving the

monkey his payoff. The second experimenter began each trial with a single piece of apple, and provided exactly this quantity. Again, despite the fact that the final outcome of trading was the same across the two experimenters, the monkeys traded more of their tokens with the second experimenter and avoided the first experimenter who initially offered a larger quantity and then subtracted during the trade (Chen et al. 2006). Like humans, monkeys appear to avoid choices that involve perceived losses.

In a final demonstration of how capuchin monkeys share our biased choices, we gave the monkeys an opportunity to be the "owner" of one good that they could barter for an equally priced good. Our aim was to see whether monkeys, like humans, exhibited an endowment effect, overvaluing the goods that they owned. To do so, we (Lakshminarayanan et al. 2008) set up a new market in which capuchins received foods that they could either keep and eat, or trade away for an equally valuable alternative. In the first phase of our experiment, we found two foods that the capuchins preferred equally. That is, given a small budget of tokens, they spent approximately half of their tokens on one these goods (e.g., cereal pieces) and half of their tokens on the other good (e.g., fruit pieces). We then made the monkeys owners of one of the two goods, say cereal, which they could then trade for the equally valuable fruit pieces. Like humans, capuchins preferred to retain the kind of food they owned, and rarely traded away food from their budget even for an equally preferred kind of food. Even across control conditions in which monkeys were compensated for any perceived transaction costs, our capuchin participants failed to trade goods they owned for equally preferred or slightly more valuable goods. Brosnan and colleagues (Brosnan et al. 2007, 2008) reported a similar endowment effect in chimpanzees (*Pan troglodytes*). Chimpanzees also refused to trade owned objects for equally valued alternatives. Like humans, capuchins and chimpanzees seem to avoid losing owned objects even if it means foregoing the gain of an equally valued alternative object.

The capuchin trading studies highlight the fact that at least one species of primate seems to share our human economic biases. Like humans, capuchin monkeys tested in an economic market exhibited reference dependence, loss aversion, and endowment effect. They too appear to evaluate their payoffs in relative terms and weigh losses more heavily than equally sized gains. The demonstration that other primates react similarly to humans in these market studies raises the question of whether nonhuman primates also share our relative evaluations in the social domain. Do primates also compare their payoffs to those of others? Do they react negatively when they get less than their equitable share? In short, do primates share our human concerns for equity and fairness considerations?

11.6 Are Primates Irrationally Equity-Seeking?

Excitingly, recent work in primate cognition has devoted considerable attention to the question of whether primates share a sense of equity and fairness (see reviews in

de Waal 1996, 2008; Brosnan 2006; Silk 2007, Silk and Boyd this volume). Much of this work has examined whether primates are also averse to inequitable outcomes. In a landmark series of studies, Brosnan and colleagues (Brosnan and de Waal 2003; Brosnan et al. 2005; Brosnan 2006; van Wolkenten et al. 2007) investigated whether two primate species – capuchins and chimpanzees – would forego an otherwise desired food reward that was delivered unfairly in a trading task. In the original capuchin study (Brosnan and de Waal 2003), monkeys watched an experimenter trade with a conspecific and pay that conspecific either a low-valued (e.g., cucumber) or high-valued food reward (e.g., a grape). After seeing the conspecific's payoff, the subject monkey got its own chance to trade and was paid only the low-valued reward. Although capuchins were happy with a low-valued cucumber payoff when the other monkey also got a cucumber, capuchins rejected the cucumber when the other monkey got a grape. Surprisingly, in this and other studies (e.g., Brosnan et al. 2005; Brosnan 2006; van Wolkenten et al. 2007), capuchins and chimpanzees were willing to reject an otherwise desired food reward if they previously observed another conspecific obtaining a better reward for the same amount of work (but see Dubreuil et al. 2006; Roma et al. 2006 for failures to replicate this effect with a different paradigm). In a similar vein, capuchins have been shown to spontaneously share food with the individuals that helped to work for that food (de Waal and Berger 2000).

Taken together, capuchins and chimpanzees tested in token trading tasks seem to act in ways that are consistent with notions of inequity aversion, even when doing so results in losing an otherwise valued piece of food (e.g., Brosnan and de Waal 2003). Like humans, these primate species seem to evaluate their own payoff relative to that of others and react negatively when others "earn" more than they do for equal amounts of work. To summarize, then, basic components of equity – for example, judging one's own reward against the payoffs of others – are present in several primate species.

That said, there does appear to be some potentially important differences between the equity seeking strategies observed in human and nonhuman primates. As reviewed above, humans often act in ways that promote equity not just for their own outcomes, but also for those of others. In the parlance of experimental economics, humans are averse not just to *disadvantageous inequity* – situations in which an actor gets relatively less than other individuals – but also to *advantageous inequity* – situations in which the actor gets relatively more than other individuals. Human decision-makers often act to reduce inequity even in cases in which they themselves are not negatively effective (e.g., providing equitable offers in one-shot dictator games, giving to charity, working for social justice, etc.). To date, there is relatively little evidence that any nonhuman primate does the same. Brosnan (2006) reported, for example, that capuchins who received the grape in her task never rejected it or offered to share it with the monkey who received the unfair cucumber payoff. In fact, she noted that higher-paid monkeys occasionally stole rejected cucumbers from their lesser-paid cagemates. Failures to observe advantageous inequity aversion in these and other tasks (see Silk and Boyd this volume for an elegant review of striking demonstrations of primates' failures to provide equitable

rewards to others even at low cost to themselves) suggest that humans may be unique in their advantageous inequity concerns.

11.7 Conclusions About the Evolution of Human Economic Strategies

Like humans, nonhuman primates also violate at least some of the standard tenets of expected utility maximization. Several primate species show economic preferences that are consistent with loss aversion, reference dependence, and disadvantageous inequity aversion. To summarize, nonhuman primates seem to share many human-like irrational decision-making biases, despite the fact that making choices in this way would not lead to economically rational choices in the long run.

The fact that researchers have observed decision-making biases, such as inequity-aversion, loss-aversion, and prosocial-giving outside of our species, is striking for at least two reasons. First, these findings suggest that despite the fact that human irrational decision-making violates the norms of rational economic behavior, these behaviors seem to represent cognitive strategies that have been in place for millions of years of evolutionary history. Even though loss-aversion and inequity norms may not contribute straightforwardly to better economic choices, these strategies have still been around for quite a long time. Indeed, results demonstrating economic irrationalities and fairness-like norms in capuchin monkeys suggest that similar biases may have existed in our common ancestor with New World primates over 35 million years ago.

Second, the existence of several of these biases in nonhuman primates may provide a valuable hint for understanding *why* these biases may be so persistent and robustly demonstrated in our own species. Although the biases we have discussed in this chapter are typically considered non-normative from a classical economic perspective, several researchers have argued that such irrational strategies may in fact be rather smart in certain contexts (e.g., Gigerenzer and Goldstein 1996; Gigerenzer et al. 1999; Gigerenzer and Selten 2001). Gigerenzer and colleagues, for example, have long speculated that seemingly "irrational" decision-making biases may allow decision-makers to quickly navigate what would normally be cognitively-taxing complicated computations. In this way, the irrational strategies we have observed may be better from an evolutionary perspective than originally thought in part because they are faster and cheaper than a more rational approach. Our observation that such strategies are evolutionarily ancient provides credence to this view, and suggests that researchers might need to rethink what should be considered the best normative model of decision-making.

Finally, we end with an exciting implication of the recent work on primate irrationalities. Although the nature of nonhuman primate economic strategies is still far from understood, researchers now have a variety of methods in place that can be tweaked to investigate many aspects of primates' social and economic preferences.

These methods create exciting possibilities for future research across human and nonhuman species. The hope, then, is that the next decade of work in this area can determine not just whether primates share different human economic behaviors, but also whether the mechanisms that underlie these behaviors are also shared broadly across the primate order.

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