Neuroeconomics

DECISION MAKING AND THE BRAIN

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CHAPTER

7

The Evolution of Rational and Irrational Economic Behavior: Evidence and Insight from a Non-human Primate Species

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INTRODUCTION

Modern economics as it is currently practiced is an exercise in applying three basic principles to nearly all settings. First, it entails positing agents with simple, stable preferences. Workers are assumed to maximize earnings net their disutility of labor, consumers are assumed to maximize a stable utility function given their budgets, and family members are assumed to bargain with each other given their competing goals. Second, people are endowed with effortlessly rational, error-free cognition. This assumption may entail agents simply understanding their own preferences, or it may ask that they solve arbitrarily complex signal-extraction problems. Finally, modern economics assumes that people interact with each other in ways that are relatively frictionless and thus yield equilibrium behavior. That is, people are assumed to maximize their own interests given the behavior of others, equalizing their personal returns across activities.

All three of these assumptions have proven deeply useful to economists. Assuming simple preferences limits the degree to which the analyst might "overfit" behaviors, and stable preferences are necessary if current observations are to bear any predictions about different contexts or future events. Assuming rational agents and equilibrium outcomes likewise disciplines analysts, making sure their predictions depend more on observable facts about the environment than they do on unobservable psychological properties, which are undoubtedly more difficult to measure and quantify. Unfortunately, although assumptions about stable preferences have proven formally useful to economists, it is clear that human decision makers do not always live up to the modern economists' high standards. Behavioral economists have spent the last few decades documenting a number of systematic ways in which human consumers violate standard economic assumptions (see reviews in Camerer, 1998; Kahneman *et al*., 1982).

Given the systematic errors and biases that psychologists and behavioral economists study, it may at first glance seem foolish to embark on a study of economic behavior and preferences in other species. If humans can't perform fast and error-free computations, achieve equilibrium reliably, or maintain stable and frame-invariant preferences, it seems unlikely that other, presumably less computationally-savvy, species will be able to do so. Nevertheless, this chapter will argue that modern economics – and, importantly, the emerging field of neuroeconomics – can gain insight into the nature of human preferences through the study of other species, particularly other closely related primates. While we agree that the behavior of non-human primates may have little hope of shedding light on such hyper-rational agents and their economies, we will argue that research examining non-human primate preferences may have something important to teach us about the deep structure of human preferences, and the way that less-than-perfect agents with those preferences respond to incentives.

This chapter will review our recent discoveries about preferences in one model primate species – the capuchin monkey. We begin by reviewing a number of different economic approaches to non-standard choice behavior in humans. We will then turn to our own work exploring whether capuchin monkeys (*Cebus apella*) also exhibit non-standard choice behavior in situations analogous to those seen in human markets. We will use this work to argue that many of the central lessons of price theory hold in (presumably) less than fully rational capuchin economies, and that many of the aspects of the prospect-theoretic preferences we observe in humans also appear in capuchin behavior. Observing that non-human primates display the same fundamental biases that humans do, and that these biases respond similarly to incentives, suggests both an expanded role for these biases in positive accounts of human economies, and that these biases may form the basis for a stable set of deeper preferences towards which economic tools can be applied.

NEOCLASSICAL APPROACHES TO NON-STANDARD BEHAVIOR

Although economists often formally assume that humans are hyper-rational agents, most economists recognize that humans commonly fail to live up to the standard of *Homo economicus*. Indeed, neither Adam Smith, the founder of classical economics, nor Alfred Marshall thought that humans were perfectly rational agents, and neither thought that rationality was a necessary condition for the usefulness of price theory. Instead, classical economists hypothesized that agents had and were motivated by simple, stable, self-interested preferences, and that such preferences acted to equalize returns across different activities, eliminating arbitrage opportunities and inducing efficient markets. As Smith famously wrote, "it is not from the benevolence of the butcher, the brewer, or the baker that we expect our dinner, but from their regard to their own interest."

Price-Theoretic Treatments

Neoclassical economists realized that their insights did not require agents to be hyper-rational; agents simply needed to respond to incentives. Under this view of agents, then, behavioral biases and cognitive limitations can be fruitfully studied using neoclassical economic techniques. One of the classic examples of this approach is the work of Gary Becker. As Becker (1962) himself put it, "the important theorems of modern economics result from a general principle which not only includes rational behavior and survivor arguments as special cases, but also much irrational behavior." Consistent with this idea, Becker and co-authors have used price-theoretic tools in settings which economists had previously thought not amenable to rational analysis. In the essays collected in his seminal *Economic Approach to Human Behavior* (1976), Becker applies price theory to understand such diverse phenomena as racial discrimination, family dynamics, and crime and punishment. In perhaps the most pure example of this approach, Becker and Murphy (1988) analyzed addictive behavior by positing that such behavior may arise from underlying stable preferences in which consumption of an addictive good today is a complement to consumption of that same good tomorrow. This price-theoretic framework yields important insights into addictive behavior, including rapidly increasing or declining (yet perfectly rational) consumption of addictive goods, "cold-turkey" quitting strategies, and the prediction that addicts will respond much more to permanent than to temporary price changes.

Becker's approach relies on assuming that what might seem transient, unstable, and irrational behavior may actually arise from stable, underlying preferences. These preferences may include terms not normally included in the arguments of utility – terms such as altruism, fairness, tastes, habits, and prejudices. Positing these more basic, stable preferences is fundamental to the application of neoclassical tools to non-standard settings. For example, Becker writes that "generally (among economists) … preferences are assumed not to change substantially over time, nor to be very different between wealthy and poor persons, or even between persons in different societies and cultures." Indeed, coupled with maximizing behavior and market equilibrium, Becker asserts that the assumption of stable preferences "forms the heart of the economic approach."

More recently, Ed Glaeser (2004) has argued that even if researchers were to show that human decision making is driven more by temporary, fleeting, situational factors than it is by stable preferences, this would only serve to increase the importance of classic price-theoretic techniques. This is because "many topics require both psychological insight into the power of local influence and economic reasoning about the supply of that influence" (Glaeser, 2004). Thus, even if it were the case that people made decisions based strongly on temporary and situational cues, in most market situations those cues will be provided by self-interested entrepreneurs such as marketers or politicians. Glaeser argues that price-theory is essentially the only tool we have to understand the supply of such frames and persuasive messages. The payoff to such an approach, Glaeser asserts, is powerful in that predictions arise from an equilibrium analysis of the supply of such messages. For example, Glaeser (2004) notes that:

> The applications of economics to the formation of aggregate cognitive errors suggest a number of comparative statics. These errors will be more common when the costs of making mistakes to the individual are low. As a result, we should expect more errors in the political arena (because no one's vote directly matters) than in the market arena (because making foolish purchases is at least somewhat costly). These errors will be more common when mistaken beliefs strongly complement supplier's returns. Mistaken beliefs will be more common when errors increase the current flow of utility. Thus, if people enjoy anticipating a rosy future, they should believe stories that make them overly optimistic and in particular, they should happily accept stories about a life after death.

Axiomatic Approaches

Another way neoclassical economists have dealt with non-standard behavior is through the use of axiomatic approaches. Where the price-theoretic approach to non-standard behavior focuses more on the role of incentives and market discipline in shaping (possibly non-standard) behavior, the axiomatic approaches focuses on weakening the assumptions underlying utility theory so as to allow the analysis of non-standard behavior. Kreps and Porteus (1978) used a classic axiomatic approach to study agents who appear to prefer earlier resolution of uncertainty rather than later (or *vice versa*), even though the timing of the resolution has no consequential effects. The Kreps-Porteus approach deals with this temporal inconsistency by applying the classic axioms of choice under uncertainty to dated lotteries – lotteries that specify not just what information will be revealed, but when that uncertainty will be revealed. Kreps-Porteus establishes a representation result that allowed for the prices definition of preferences for early resolution of uncertainty, allowing standard tools of economics to be applied to markets where the timing of information revelation is key, with broad applications in macroeconomics and finance.

More recently, Gul and Pesendorfer applied axiomatic choice theory to the phenomena of dynamic inconsistency and temptation preferences, with hyperbolic discounting being the most widely studied example. For instance, Gul and Pesendorfer (2001) used classic choice theory to study *choice sets*, rather than choices *per se*. A decision maker might, for example, strictly prefer the choice set B to the choice set A, even if A offers strictly more options (B is strictly a subset of A), because some of those options in A might produce temptation costs. Similar to the Kreps-Porteus approach, Gul and Pesendorfer derived a set of axioms which many simple forms of temptation satisfy and showed that, under those axioms, a simple representation of preferences in terms of linear functions suffices. This allows for the rigorous definition and study of markets in which temptation and a demand for self-control may exist. Fundamental to both axiomatic and price-theoretic approaches, however, is a strict neoclassical emphasis on positive economics; alternative axioms and utility functions are to be judged solely by their parsimony and ability to predict choice behavior. Most notably, this de-emphasizes any appeal to psychological realism, one of the main distinctions between neoclassical and behavioral economics.

Behavioral Economics Approaches

In contrast to these neoclassical approaches, much of modern behavioral economics starts by scanning the nearby disciplines of social psychology and sociology for robust biases that may manifest themselves in economically important settings. Economists using this approach have tried to incorporate psychological and sociological findings into economic analysis by finding a functional form for preferences that captures many of the stylized facts that these biases present. Most prominently, Kahneman and Tversky (1979) attempted to unify several stylized deviations from expected utility in a single theory of choice under uncertainty called *prospect theory*. Prospect theory represents choice as a function of the value of the choices rather than as a function of a person's overall utility. These values are assessed as either gains or losses (i.e., positive or negative differences) relative to an arbitrary reference point. A major implication of prospect theory, then, is that decision makers naturally frame their decisions as gains or losses relative to a particular reference point. Prospect theory's value function passes through the reference point as S-shaped, with a kink in the curve at the reference point, such that a given absolute-sized loss (e.g. a $5 loss) will decrease value more than an identically-sized gain (e.g. a $5 gain) will increase value. This feature of the value curve leads to loss-aversion: decision makers are more sensitive to a loss than they are to an equally-sized gain, which can lead to odd and often irrational framing effects in which decision-makers' responses may vary with how the choice is presented, worded, or described. The structure of the value curve also leads to a phenomenon known as the *reflection effect*: decision makers treat changes from a reference point differently depending on whether they are gains or losses. More specifically, decision makers tend to be risk-seeking when dealing with perceived losses, but risk-averse when dealing with perceived gains.

Prospect theory has been widely applied across numerous fields in economics, including finance (explaining the disposition effect and the equity premium), labor supply (income targeting), and consumer choice (asymmetric price elasticities, the endowment effect). (See Camerer (1998) for an elegant and comprehensive review of the applications of prospect theory in economics.)

Another widely used model in behavioral economics is David Laibson's model of time-inconsistent choice. Laibson (1997) modeled inter-temporal inconstancy with a beta-delta model of hyperbolic discounting, and demonstrated how agents with such preferences could be imbedded in economic models of choice over time. By doing this and demonstrating how to solve such the dynamic-programming problem that these agents face when trying to optimize, economists could model the effects of present-biased preferences and how they might interact with different types of illiquid assets, market structures, or public policies.

THE ROLE OF NON-HUMAN PRIMATE STUDIES IN MODERN ECONOMICS

Common to all the approaches reviewed is that, by and large, they take the origins and structure of behavioral biases as given. To date, far less direct attention has been paid to understanding how basic or fundamental these biases are. Put differently, most of the approaches reviewed above explicitly model the external market forces and technologies which shape the supply of cues, yet the cognitive systems and constraints that lead to these biases are worked around, often in one of two ways. Most behavioral economists leave these biases to social psychologists to study, acting essentially as importers of psychological insights. In turn, the models that behavioral economists use are based on assumptions judged not only by their ability to organize economic data, but also by their psychological realism. Axiomatic approaches, in contrast, tend to disregard the latter of these two goals, instead treating the minds of people as black boxes that are approachable through observing choice data alone. In both behavioral economic and axiomatic approaches, however, little work has examined how our behavioral biases arise in the first place.

What, then, are the origins and deeper structure of our systematic economic biases? Are our biases the result of social or cultural learning and specific environmental experiences? Or could they be more universal, perhaps resulting from mechanisms that arose over evolution and operate regardless of context or experience? We and our colleagues have begun addressing these questions by exploring whether the roots of our economic behavior – both our stable preferences and our behavioral biases – are shared by our closest living evolutionary relatives, the extant non-human primates. Since humans and capuchins are closely related biologically, yet lack similar market experience, any shared cognitive systems are likely to have a common origin.

Note, however, that our work on primate economic biases was not the first to take a principled economic approach with non-human subjects. Indeed, some elegant early work in the 1970s by Kagel and colleagues found support for the stability of preferences and the applicability of economic choice theory in standard non-human psychological subjects: rats and pigeons. In a series of studies, Kagel and colleagues trained their subjects on a lever-pressing task in which subjects had a "budget" of different lever presses, each of which delivered different rewards at different rates. The researchers then used a standard revealed-preference approach in which the subjects' choices were identified via their lever choices. Using this approach, Kagel and colleagues demonstrated that rat and pigeon behavior, like that of human consumers, appears to obey the laws of demand (Battalio *et al*., 1981a, 1981b, 1985; Kagel *et al*., 1975, 1981, 1990, 1995).

Unfortunately, while rats and pigeons are easy subjects to work with, their limited cognitive abilities make it difficult to investigate more subtle aspects of economic choice, including many important and systematic human biases. More importantly, rats and pigeons lack one of the hallmarks of human economies: trade. Indeed, Adam Smith famously argued that the behavior of animals was not relevant to economics because they lacked the capacity to master trade. As he put it in *The Wealth of Nations*, "Nobody ever saw a dog make a fair and deliberate exchange of one bone for another with another dog. Nobody ever saw one animal by its gestures and natural cries signify to another, this is mine, that yours; I am willing to give this for that."

Another problem with the exclusive use of rats and pigeons as models for human economic choice concerns their potential for informing claims about the evolution of human choice behavior. Although rats and pigeons are commonly used in psychological studies, they represent extremely distantly related species from an evolutionary perspective. For this reason, choice experiments involving rodents and birds are silent, both on questions regarding the evolutionary history of human choice behavior and on issues related to the neural architecture underling these behaviors. In short, although previous work with animals has adeptly demonstrated the robustness of revealed-preference techniques, the field of economics is still far from an evolutionary-history based understanding of human decision making.

The goal of our recent work on capuchin economic choice is to bridge this evolutionary divide. To do so, we have developed an experimental method for presenting choice problems to capuchin monkeys in a situation that is as analogous as possible to the markets in which humans exhibit economic choice. Before turning to these studies, we'll take a brief pause to introduce the reader to the subjects of our experiments. Since many economists (and possibly some neuroscientists) are not all that familiar with primate evolution and taxonomy, we first provide a brief introduction on the phylogenetic history of primates.

PRIMATE EVOLUTION 101

When neuroeconomists reference the brain or cognitive processes of "the monkey," they are – probably without realizing it – being incredibly imprecise. To researchers in primate cognition, the term "monkey" does not pick out a coherent natural kind – a "monkey" could mean any one of the 264 extant monkey species, all of whom inhabit different environments, eat different things, come from different genera, and presumably possess different cognitive specializations with different neural substrates (see the review in Ghazanfar and Santos, 2004). Such differences can have important consequences for the cognitive and neural capacities that these different species utilize in decision-making contexts. Even very closely related monkey species can differ drastically in fundamental cognitive processes and decision-making strategies. To take one elegant example, Stevens and colleagues (2005a, 2005b) recently observed that cotton-top tamarins (*Saguinus oedipus*) and common marmosts (*Callithrix jacchus*) – two extremely closely related New World monkey species – exhibit robust differences in their discounting behavior, with marmosets valuing future rewards more than tamarins do. As this example demonstrates, it would make little sense to talk about discounting behavior in "the monkey," as such a generalization would miss out on the fact that different kinds of monkey possess discounting functions that might be specific to their own species (or, in the case of marmosets and tamarins, specific to their species-unique feed ecology).

Typically, however, when neuroscientists refer to research with monkeys they tend to mean the species of monkey most typically used in neurophysiological studies of decision making, namely the macaque, one of several species within the genus *Macaca*[1]. Macaques are an Old World monkey species, meaning that they are native to Africa and Asia. Macaques are the mostly widely distributed genus of primates (with the exception of humans), and are thus an extremely flexible species. Because of their adaptability, macaques live well in captivity and have thus long served as a successful

[1]It should be remembered, however, that although macaques have predominated as neuroscientific models, some of the most important neuroscientific findings in decision making have also used a marmoset monkey model – for example, Dias *et al*., 1996, 1997.

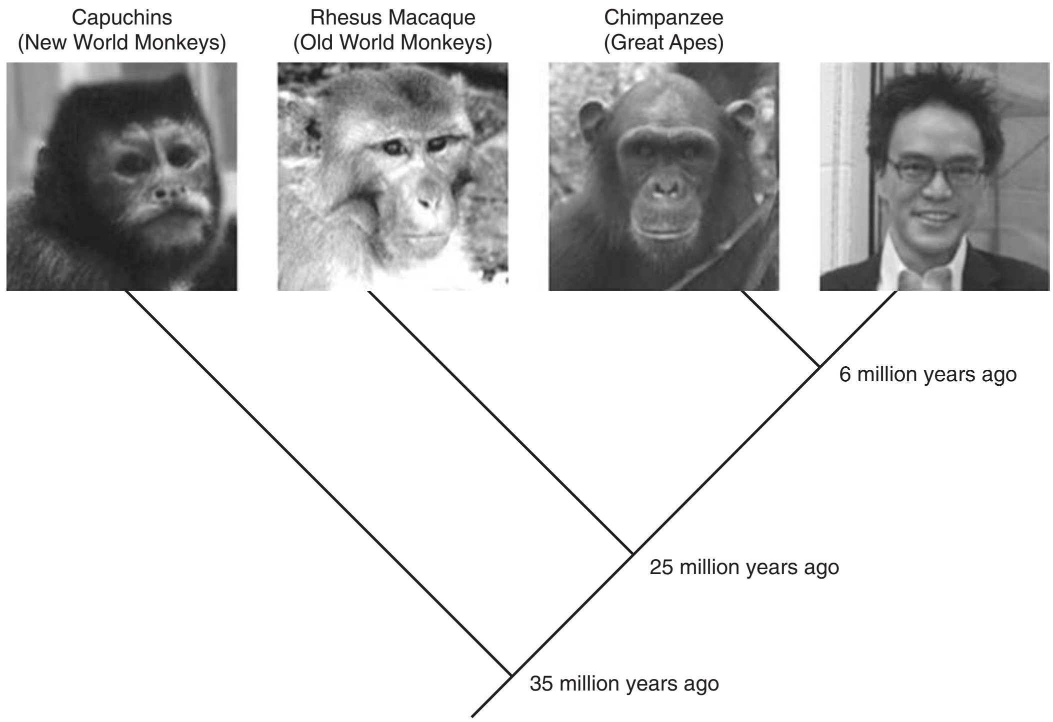

FIGURE 7.1 A schema of the primate evolutionary tree. Our subject species, the capuchin monkey, branched of from the human Old World primate line about 35 million years ago.

animal model in medical studies. Due to their prominence in early medical research, macaques were quickly imported for use in early neuroscientific investigations. Some of the first approaches to detailing the structure and function of primate motor cortex were performed on macaques in the 1800s. This early work functionally established macaques as the primate brain model for the next two centuries. Indeed, many chapters in this volume specifically focus on neuroeconomic insights gleaned from macaque brains – for example, Chapters 29 and 31.

Our behavioral work on monkey preferences does not focus on macaques, however. Instead, we work with a species believed to represent a cognitive rather than a neuroscientific model of human cognition – the brown capuchin monkey (see Chapters 18 and 19). In contrast to macaques, who are members of the Old World monkey lineage, capuchins are members of the more distantly related New World monkey branch, a group of primates that split from the Old World primate line around 35–40 million years ago (Figure 7.1). While Old World monkeys inhabit Africa and Asia, New World monkeys, like capuchins, are native to South and Central America, and thus evolved in different ecological niches than did other Old World species.

Despite millions of years of separation from our own species, the cognition of capuchin monkeys is, in many ways, quite similar to that of humans in a number of domains. Capuchins are often considered among primate researchers to be "the chimpanzee" of the New World primates. Capuchins have extremely large brains relative to their body size (see, for example, Fragaszy *et al.*, 2004a). In addition to these physical attributes, capuchins live in relatively large social groups, particularly compared to other New World species, with groups in the wild becoming as larger as 40 individuals. Despite this large group size, however, capuchins are an extremely tolerant species of primate, maintaining only a loosely defined dominance hierarchy that permits sharing food with many members of the group (de Waal, 2000; de Waal and Berger, 2000). For this reason, capuchins are extremely socially adept. Recent research suggests that they can successfully represent the goals of other individuals (Santos, personal communication) and can learn socially from the actions of others – though the specifics regarding how much they can learn continue to be debated (Adams-Curtis and Fragaszy, 1995; Custance *et al.*, 1999; Ottoni and Mannu, 2001; Visalberghi and Addessi, 2000, 2001; Brosnan and de Waal, 2004; Ottoni *et al.*, 2005; Bonnie and de Waal, 2007; see elegant reviews in Adessi and Visalberghi, 2006 and Fragaszy *et al.*, 2004b). Finally, capuchins are known for their elaborate tool-use. They use a variety of tools

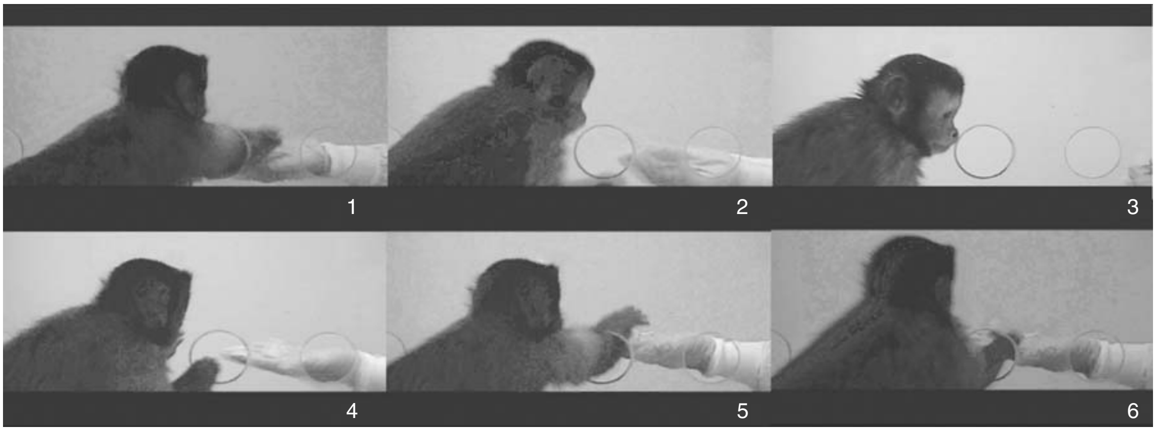

FIGURE 7.2 A frame-by-frame demonstration of a single trading event involving one of our capuchin actors (Jill). The capuchin begins by placing a token in the experimenter's hand (1). The experimenter then takes the token away (2–3) and delivers a piece of food (4) which the capuchin then takes from the experimenter's hand (5–6).

both in the wild and in captivity, including using pushing and pulling tools to gain out-of-reach food, dipping tools to gain access to out-of-reach liquids, combinations of stone hammers and anvils for opening palm nuts, and even crushed millipedes as a mosquito repellant (Fragaszy *et al*., 2004b, Valderrama *et al*., 2000).

REVEALING CAPUCHIN PREFERENCES: THE TOKEN TRADING METHODOLOGY

Our goal was to design a task with which we could reveal capuchins' preferences. The problem, of course, is that capuchins would presumably have some difficulty performing the tasks that experimental economists typically employ to reveal human preferences. Monkeys' preferences concerning their willingness to pay for certain gambles or bundles of goods can't be assessed using written surveys; nor can monkeys' behavior as consumers in a market be used, since they do not naturally act as consumers in markets. We therefore had to design a novel method that permitted capuchins to reveal their preferences in something like a market, a situation that was as analogous as possible to the methods used to test preferences in humans; specifically, one that involved relatively little training and also permitted formal price-theoretic analyses.

To do this, we capitalized on the fact that capuchin monkeys (as well as other primates) can be quickly trained to trade tokens for small food rewards (see, for example, Westergaard *et al*., 1998, 2004; Liv *et al*., 1999; Brosnan and de Waal, 2003, 2004; Adessi *et al*., 2007). A number of different labs have successfully taught capuchins this trading methodology using an individual experimenter who would reward a capuchin subject for handing her the token. In our set-up, we hoped to give capuchins choices *between multiple different traders*, each of whom would deliver different kinds or amounts of goods when presented with a single token. In this way, we were able to put capuchins into a situation much like an economic market – one in which they could establish preferences across different bundles of goods. With this set-up, we could introduce price and wealth changes and examine how such changes affected capuchins' purchasing behavior. Further, we could observe whether capuchins preferred options that stochastically dominated all others (i.e., ones in which they unconditionally received the most food). Finally, and perhaps most importantly, we could examine whether capuchins' preferences obeyed prospect-theoretic predictions, and thus were affected by reference points and framing.

Chen *et al*. (2006) introduced five adult capuchins to this economic market. Each capuchin began testing by leaving its homecage and entering a small testing box. In the box, monkeys found a small wallet of small, disc-shaped metal tokens. Two experimenters then positioned themselves on either side of the cage. The two experimenters differed in their clothing (each wore differently colored medical scrubs) and also in the kind of good offered. On each trial, the monkey had a chance to trade a token with one of the two experimenters. Each trial began when the two experimenters were in position on either side of the cage. In one hand the experimenters held the good that they were offering to the monkey; their other hand remained open for the monkey's token (Figure 7.2). Monkeys could therefore check their options and trade with the experimenter who gave the best kind or amount of the good. Each session lasted until the monkey had spent all of its tokens.

DO CAPUCHINS OBEY PRICE THEORY AS HUMANS DO?

Our first goal was to examine whether the preferences capuchins established in the token economy we had set up mirrored those of a human economy. That is, having allocated their budget of tokens across a set of possible goods, would capuchins respond rationally to price and wealth shocks? To do this, we first found two goods that the capuchins liked equally – pieces of jello and apple slices – spending about half their budget on each of the goods. Once capuchins' choices stabilized across sessions, we introduced a compensated price shift.

In our compensated price shift, we assigned each subject a new budget of tokens and then dropped the price of one of the two goods by half. In order to respond as humans would to this price shift, capuchins must shift their consumption to the cheaper good; namely, they should spend more of their token budget on the cheaper good than they did before the price shift. The majority of our capuchins actors did just this, suggesting that they, like humans, obey the tenets of price theory.

In a further study, we examined whether capuchins also try to maximize their expected payoff in the market. If capuchins had a choice between two traders offering the same kind of good, would they choose the experimenter whose payoff stochastically dominated, the one that gave the most food overall? To look at this, we (Chen *et al*., 2006) again presented capuchins with a choice between two traders, but this time the traders offered the same kind of good – apples. The traders differed both in the number of apples they initially offered and in the number they gave over. The first experimenter always offered the monkey one piece of apple and then handed over that one piece. The second experimenter, in contrast, was risky – he did not always hand over what he promised. This second experimenter began with two pieces of apple and then, with 50% probability, either handed over both pieces or took one of the two pieces away for an offer of only one piece. On average, however, this risky experimenter represented a good deal – he gave one-and-a-half pieces of apple on average, while the other experimenter gave only one piece. Like rational actors, our capuchin traders appeared reliably to prefer the risky experimenter who stochastically dominated. In this way, capuchins not only shift consumption rationally in response to price shifts, but also prefer trading gambles that provide the highest average payoffs.

DO CAPUCHINS DISPLAY THE SAME BIASES AS HUMANS?

Our findings that capuchins obey price theory and choose options that stochastically dominate suggest that capuchins behave rationally in their token market in some of the same ways that humans behave rationally in their economies. This work, then, set the stage for examining whether capuchins also behave *nonstandardly* in the ways that humans do. Specifically, we wanted to examine whether capuchins share some of the biases that pervade human choice behavior. As decades of work in behavioral economics have shown, human consumers appear to evaluate their choices not only in terms of their expected payoffs. Instead, consumers also appear to evaluate different gambles in terms of arbitrary reference points. In particular, human participants tend to be loss averse – they avoid getting payoffs that appear as losses relative to their reference points more than they appear to seek out gains relative to their reference points (e.g., Kahneman and Tversky, 1986; Tverky and Kahneman, 1981). The phenomena of reference dependence and loss aversion have been demonstrated in countless experimental scenarios and gambles (e.g., Tversky and Kahneman, 1986), but also have demonstrated real-world manifestations in situations as diverse as unemployment patterns (Krueger and Summers, 1988; Akerlof and Yellen, 1990) housing-market changes (Odean, 1998), and asymmetric consumer elasticities (Hardie *et al*., 1993). Further, reference dependence also affects participants' intuitions regarding fairness and moral concerns (Kahneman *et al*., 1991).

Is reference dependence a uniquely human phenomenon, or does it extend more broadly across the animal kingdom? To examine this, we presented monkeys with trading situations in which they had the opportunity to consider their final trading payoffs relative to a reference point. We could therefore examine whether framing also affects capuchin choice and preferences.

Are Capuchins Reference Dependent and Loss Averse?

In our first study (Chen *et al*., 2006), we explored whether capuchins, like humans, set up expectations relative to an arbitrary reference point. To do this, we independently varied what monkeys were initially shown and then what they eventually received in exchange for a token, thereby setting up situations in which the monkeys could get more or less than they expected. In the first experiment, we examined whether capuchins attended to this reference point. Monkeys got to choose between two experimenters who both delivered the same average expected payoff of one-and-a-half pieces of apples. One experimenter, however, gave this average payoff of one-and-a-half apples by way of a perceived loss. This experimenter began every trade by showing the monkeys two pieces of apple. When this experimenter was paid, he either delivered these two pieces of apple as promised, or removed one to deliver only a single apple piece. In this way, the first experimenter gave the monkeys less than they had expected based on their reference point. The second experimenter, in contrast, gave more on average than the monkeys expected. This second experimenter always began by displaying a single piece of apple but then, when paid, either delivered this one piece as promised or added a second piece for a payoff of two apple pieces. Monkeys thus had a choice of obtaining an average of one-and-a-half pieces of apple by way of a perceived loss or by way of a perceived gain. Although the average payoff was the same across the two experimenters, our monkey consumers did not prefer the two experimenters equally. Instead, they reliably preferred the experimenter who delivered his apple pieces by way of a gain. Like humans, capuchins appear to take into account reference points – in this case, what they initially are offered.

We then went on to examine whether capuchins avoid losses in the same way as humans. Did capuchins avoid the experimenter who gave them perceived losses, or did they instead seek out the experimenter who gave them perceived gains. To test this, we gave monkeys a choice between one experimenter who always delivered a loss – he consistently promised two pieces of apple and gave one – versus an experimenter who always gave what was expected – he promised one piece of apple and delivered exactly that piece. As in the previous study, our monkeys seemed to avoid the experimenter who delivered the perceived loss. Interestingly, monkeys faced with this choice robustly preferred the experimenter who gave what they expected, despite the fact that both experimenters delivered a single piece of apple on every trial.

In this way, capuchins appear to share at least two of the fundamental biases that humans display. Capuchins represent their payoffs relative to arbitrary reference points and appear to avoid gambles that are framed as losses. Such results indicate that monkeys also succumb to framing effects, with different descriptions of the same problem leading them to make different choices.

Framing and Risk: Do Capuchins Exhibit a Reflection Effect?

In our next set of studies, we examined whether framing also affects monkeys' risk preferences. To do this, we presented the capuchins with a version of Tversky and Kahneman's (1981) well-known Asian Disease problem (Lakshminarayanan, Chen, and Santos, personal communication). In each condition, monkeys had a choice between two kinds of experimenters who delivered identical expected payoffs but differed in how much their payoffs varied. Monkeys could choose to trade with a safe experimenter who traded the same way on every trial, or a risky experimenter who represented a 50–50 gamble between a high and a low payoff. What differed across the two conditions was how the experimenters framed the monkeys' choices. In the first condition, each of the experimenters framed his payoff in terms of a gain; monkeys had a choice between a safe experimenter who promised one piece of food but always delivered two, and a risky experimenter who promised one piece of food but then delivered either one piece of food or three pieces of food. Like humans tested in the Asian Disease problem, monkeys presented with gains chose to avoid risk – they reliably preferred to trade with the safe experimenter over the risky experimenter. The second condition, in contrast, presented monkeys with safe and risky losses. Monkeys had a choice between a safe experimenter who always promised three pieces of food but always delivered two, and a risky experimenter who promised three pieces of food but either delivered one piece of food or three pieces of food. In contrast to their performance in the gains condition, monkeys in the losses condition preferred to trade with the risky experimenter. In this way, monkeys appear to change their risk preferences depending on whether they are expecting perceived losses or perceived gains. Like humans, capuchins get riskier when gambling over losses than gains.

Interestingly, recent work by Kacelnik and his colleagues suggests that capuchins are not the only non-human species to show a framing-based risk-preference reversal when depending on framing; another even more distantly related non-human species – the European starling (*Sturnus vulgaris*) – shows a similar risk-preference reversal on an analogous choice task. Marsh and Kacelnik (2002) presented starlings with a task in which they could choose either fixed or variable rewards. Starlings practiced this task with one expected payoff amount, and were then tested with outcomes that were either more or less than their expectations. Starlings preferred the risky option more when they received less than they expected rather than when they received more than they expected, suggesting that starlings also become more risk-prone when dealing with perceived losses than with perceived gains. Combined with our capuchin studies, this work suggests that framing effects may extend broadly across the animal kingdom, and may also extend to a variety of taxa.

Do Capuchins Exhibit An Endowment Effect?

We then went on to examine whether capuchins demonstrate an endowment effect (see Thaler, 1980), a phenomenon in which ownership increases an object's value. In what is now a classic paper, Kahneman *et al*. (1990) presented half of a group of human participants with a coffee mug, and then allowed participants to either buy or sell the new mug. Kahneman and colleagues found that participants that owned the mug demanded a higher price to sell the mug than non-owners would pay to buy it. This discrepancy between owners' willingness-to-accept and buyers' willingness-to-pay was christened the *endowment effect*. Although there is still considerable debate concerning the exact mechanisms underlying the endowment effect, many have hypothesized that this effect follows from loss aversion (see Kahneman *et al*., 1990). If this is the case, then capuchins – who exhibit loss aversion in our experimental market – may also show a bias towards over-valuing objects that they own over those they don't yet own.

In a recent study (Lakshminarayanan, Chen, and Santos, personal communication), we explored whether capuchins were also susceptible to endowment effects (see Chapter 19 for similar experiments with chimpanzees). We first determined two goods that the monkeys preferred about equally, splitting their budget of tokens across the two goods. We then made our capuchin subjects the "owners" of one of the two equally preferred goods. Rather than giving each monkey subject a wallet of tokens, we instead provided a wallet of goods and allowed them to trade for the other equally preferred good. Since the two goods were already shown to be equally preferred, it might be predicted that capuchins would trade about half their endowed goods and then keep the other half. However, in contrast to this prediction, our capuchin actors reliably preferred to keep the food with which they were endowed. Control conditions revealed that our observed effect was not due timing effects or transaction costs – monkeys failed to trade their endowed good even in cases in which they were compensated for the cost of the trade and the time it takes to wait for the trade to be completed. These results provide the first evidence to date that a non-human species demonstrates a true endowment effect – one that cannot be explained by timing, inhibition, or problems with transaction-related costs.

WHAT COMPARATIVE WORK MEANS FOR TRADITIONAL ECONOMICS AND NEUROECONOMICS

When taken together, our comparative studies to date suggest that capuchin monkey preferences operate in much the same way as those of human agents. First, capuchins appear to obey the standard tenets of price theory, just like humans. In spite of their obedience to price theory, however, capuchins also exhibit the same systematic biases as humans – they evaluate gambles in terms of arbitrary reference points, and pay more attention to losses than to gains. Finally, monkeys appear to show other market anomalies, like the endowment effect. Our work thus suggests that human behavioral biases result not from species-unique market experiences or cultural learning; instead, such biases are more likely to be far more basic, perhaps even evolved strategies present long ago in our common ancestor with other New World primate species.

This work further suggests that such biases may emerge in the absence of much market experience not just in capuchins, but in the human species as well. Indeed, our work provides hints about another possible and probably fruitful line of work on the origins of preference. Our studies to date have focused on the evolutionary origins of human preferences and incentives, but even less work has examined the *ontogenetic origins* of these phenomena – namely, how they develop over the human lifecourse (for review, see Santos and Lakshminarayanan, 2008). Although some work to date has examined the development of loss aversion (e.g., Reyna and Ellis, 1994) and the endowment effect (see Harbaugh *et al*., 2001) in children, there is still relatively little consensus concerning how and when behavioral biases emerge in human decision making. In addition, to our knowledge, all of the available evidence to date examining the development of revealed preferences has involved older children – participants who've had at least some experience making purchases in the real world. For this reason, older children are not the best subject pool if intending to examine the role of experience in the development of loss aversion and reference dependence. To really study the role of experience, researchers should focus their empirical effort on studying human infants – participants who are young enough to lack *any* market experience. Although human infants' preferences are not currently a standard focus for economic experimentation, there is no reason they cannot become one. In the past decade, developmental psychologists have established a number of empirical methods that can be easily imported for use in economic studies with preverbal infants. Infant-researchers have developed standard methods for assessing both infants' choices (e.g., Feigenson *et al*., 2002) and their preferences (e.g., Spelke, 1976), all using non-verbal techniques. Using these experimental methods, economists could potentially ask whether infants obey price theory (and thus examine whether an obedience to price theory can emerge in the complete absence of experience). Similarly, it would be possible to examine how and when biases like loss aversion and reference dependence begin emerging, and again explore the role of economic experience and other factors in the development of these heuristics.

Our finding that many behavioral biases are shared by closely related primates has a number of implications for practicing economists. The first of these involves how an economist might choose to treat behavioral biases in both positive and normative terms. For example, if biases observed in human behavior are the results of misapplied heuristics, then it seems natural to assume that what is learned can be unlearned, and that these mistakes are likely to disappear quickly in the face of market pressures – especially when stakes are high. Our work, however, suggests that these biases emerge in the absence of experience, and thus that biases are likely to manifest themselves in novel situations. Such findings also raise the hurdle that competitive pressure may need to pass to discipline behavior. From a positivist perspective, while it may still be reasonable to believe that in high-stakes settings where market participants are exposed to constant feedback markets will display extremely rational behavior, those settings might not represent the majority of economically relevant settings. Indeed, consistent with classical welfare analysis, if a bias repeatedly emerges in different market settings and represents a fundamental aspect of people's preferences, it may demand more normative weight than we might have otherwise thought.

Our work also has important implications for non-traditional economists – neuroeconomists interested in the neural basis of standard and non-standard economic behavior. In the past decade, macaque models have afforded neurophysiologists with a number of important discoveries concerning the neural basis of our representation of risk and value (see Chapters 29, 31, and 32). Many of the neurophysiological studies to date, however, have concerned themselves with more standard aspects of choice behavior. In contrast, fMRI research with humans has focused on the neural basis of more non-standard behaviors, namely behavioral biases. While such fMRI techniques have already provided tremendous insight into the neural basis of these framing effects (see, for example, Chapters 10 and 11), these methods would undoubtedly be complemented by neurophysiology work examining framing effects at the level of individual neurons. To date, however, little neurophysiological work has addressed the role of context and framing, in part because designing framing tasks for use in non-verbal primate subjects is a non-trivial task. The trading experiments we have developed for capuchins, however, demonstrate that such framing effects can and do occur in a non-verbal species. Our work suggests that a physiological investigation of framing is possible, and thus that it might be possible to examine prospect theoretic predictions in a primate neural model. Our work demonstrating that monkeys exhibit an endowment effect further suggests that physiologists might be able to examine even more subject changes in valuation – such as those due to ownership – in a primate model as well.

The field of neuroeconomics, though still in its infancy, has enjoyed much success in a relatively short amount of time. Undoubtedly, much of the success of this newly emerging field relies on the importance it places on interdisciplinary approaches to the study of economic behavior. Our goal in this chapter has been to point out how primate cognition studies of choice, preferences, and incentives can add to this empirical mix – both in their own right as a way of examining the origins of standard and non-standard economic behavior, and for their potential to give rise to new behavioral assays needed for neurophysiological insights into human economic behavior.

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