CHAPTER

7

Evolutionary Anthropological Insights into Neuroeconomics: What Non-Human Primates can Tell us About Human Decision-Making Strategies

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INTRODUCTION: HOW AN EVOLUTIONARY PERSPECTIVE IS IMPORTANT FOR NEUROECONOMICS

One of the central goals of neuroeconomics is to understand the neural mechanisms that allow people to make decisions and act in ways that satisfy their preferences. In order to do so, neuroeconomists face something of a challenge – they must strive to understand all aspects of our species' decision-making strategies, including our systematic biases and seemingly irrational tendencies. Unfortunately, as much work in the field of behavioral economics has demonstrated, many aspects of human choice work in ways that violate the assumptions of rationality. People, for example, change their decisions depending on framing (e.g., Tversky and Kahneman, 1981) and exhibit a number of paradoxical sets of preferences that would appear to violate expected utility theory (e.g., Ellsberg, 1961). Although the study of neuroeconomics would be far more convenient if people had perfectly stable preferences and made choices that maximized utility in the classical sense, neuroeconomists who want to understand real human choice must find ways to try to understand it as it is, no matter how irrational, biased, clunky, or inelegant it may be.

It is in the context of understanding even the inelegant aspects of human choice that this chapter aims to introduce the importance of non-human primate studies for the field of neuroeconomics. Recognizing that human choice is not perfect begs the question of where our biased decision-making strategies come from in the first place. Are our irrational decision-making strategies the result of learning over the course of a lifetime of decisions? Do these biased strategies result from specific environmental experiences or contexts? Or could these decision-making strategies be more universal, perhaps resulting from mechanisms that arose over evolution and operate regardless of context or experience?

This chapter argues that comparative work with non-human primates can provide an important tool for answering these questions. Specifically, we will argue that comparative work can yield insights into the nature of human decision making in two distinct ways. First, the comparative approach can suggest

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unique inferences about the origins of our own decision-making strategies. By determining whether human-like decision-making biases are shared by our closest living evolutionary relatives – the extant non-human primates – researchers can gain some insight into how these biases might arise in the first place. Humans share a recent evolutionary history with other primate species, yet we differ from them experientially – other primates lack human-like market experience, human-specific cultural training, and explicit economic teaching. In this way, any cognitive systems shared between human and non-human primates are likely to have a common evolutionary origin and therefore to rely little on the sorts of economic or cultural experiences that are unique to growing up as a human decision maker.

But there is a second way that studies of non-human primate biases can inform neuroeconomics. In order to fully understand the mechanisms that underlie human choice, neuroeconomists often turn to investigating the nature of choice and decisions at the level of single neurons in the brain. Although much work has used animal models to study the neural basis of the more rational aspects of our decision making (e.g., Padoa-Schioppa and Assad, 2006; Platt and Glimcher, 1999; Sugrue *et al*., 2005), these models have been less-frequently applied the more biased aspects of our decision making (but see Louie and Glimcher, 2012; McCoy and Platt, 2005). Behavioral work on non-human primate decision-making biases has the potential to overcome this limitation by developing an animal model of human irrational decision making that could be imported for use in neurophysiology. In doing so, researchers will gain much more specific traction on how biased decision-making strategies are implemented through the use of more refined neuroscientific techniques like those discussed in Chapter 6 (e.g. single-cell recordings, pharmacological inactivation, optogenetics, etc.).

This chapter will therefore review recent discoveries concerning whether other primates share human-like decision-making strategies. It begins by introducing the comparative approach and providing a quick general introduction to primate research, focusing specifically on two primate species that have been especially important for the study of human behavioral biases: *macaque* and *capuchin* monkeys. We then review two domains in which non-human primates have provided insight into the nature of human choice. We first explore whether capuchin monkeys exhibit strategies consistent with prospect theoretic accounts of human choice (as described in Chapters 3, 4 and the Appendix; for other reviews of non-human primates and prospect theory see Santos and Chen, 2009). We will then turn to work exploring ambiguity aversion in macaque monkeys and will examine whether monkeys share human-like paradoxes in their responses to ambiguous situations (see Hayden *et al*., 2010). In all three cases, monkeys demonstrate strategies that are qualitatively similar to the biases observed in human choice. This work thus argues that the biases that pervade human choice may be more deeply imbedded in our nervous systems than researchers have previously thought.

Before turning to work in primates, however, it is worth noting that primate researchers were not the first to take a principled economic approach with non-human subjects. Indeed, elegant early work in the 1970s by the American economist John Kagel and his colleagues found support for the stability of preferences and the applicability of economic choice theory in standard non-human psychological subjects, namely rats and pigeons. In a series of elegant 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 the behavior of rats and pigeons, like that of human consumers, appears to obey both the laws of demand and a number of other fundamental properties of traditional economic decision making (Battalio *et al*., 1981a, 1981b, 1985; Kagel *et al*., 1975, 1981, 1990, 1995).

Unfortunately, while rats and pigeons have taught us much about the nature of learning and economic choice, these distantly related species are not as helpful for informing claims about the *phylogeny* – the evolutionary history – of human choice behavior. Although rats and pigeons are commonly used in psychological studies, they represent extremely distantly related species from a human evolutionary perspective. For this reason, choice experiments involving rodents and birds are largely silent on questions regarding the evolutionary history of human choice behavior and on issues related to the neural architecture underling these behaviors.

The goal of recent work on primate economic choice, then, has been to bridge this divide, providing a set of behavioral measures in species that can both provide insights into the neural architectures that support human economic choices as well as the evolutionary origins of these strategies. Are our biases solely 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? Here, we try to tackle these questions by reviewing work examining whether our patterns of economic behavior – both our stable preferences and our behavioral biases – are shared by our closest living evolutionary relatives, the extant non-human primates. First, however, we provide a brief introduction to primates.

UNDERSTANDING EVOLUTIONARY HOMOLOGIES ACROSS PRIMATES

Any introduction to work with primates for economists and neuroscientists must begin by clearing up the common misconception that all non-human primates are the same. When neuroeconomists, or other neuroscientists for that matter, think about work in non-human primates, they sometimes make reference to the brain or cognitive processes of "the monkey". This is the sort of statement that grates on the ears of primate researchers, as those who use this term are 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 over 260 extant monkey species separated by up to 60 million years of evolution, all of whom inhabit different environments, eat different things, and presumably possess different cognitive specializations with different neural substrates (see 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. Indeed, 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) recently observed that cotton-top tamarins (*Saguinus oedipus*) and common marmosets (*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. 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 monkeys possess discounting functions that might be specific to their own species (and in the case of marmosets and tamarins, specific to their species-unique foraging behavior).

First, it is worth taking a step back to think about how primate species fit into the larger comparative picture. All primate species, including humans, are part of a single taxonomic group – known as an *order*. As you may remember from your high school biology class, researchers classify all organisms within a hierarchical classification system that explains how animals are related to one another evolutionarily. This classification system categorizes all organisms hierarchically using different taxonomic ranks that span from the most general to the most specific. The taxonomic ranks we use today to classify animals are nearly identical to the one developed by Linneaus back in the 1700s. In order from most general to specific, these ranks are: kingdom, phylum, class, order, family, genus, and species. Humans and other primates make up the primate *order*, which by definition means we share a number of more general taxonomic ranks as well. Humans and other primates are all members of the animal *kingdom*, the chordate (or backboned) *phylum*, and the *class* of mammals. We begin branching off from other primates at the level of the taxonomic rank of *family*. Humans and great apes (chimpanzees, bonobos, gorillas, and orangutans) are part of the family *Hominidae*, but all monkey species are part of different families. It is only at the level of our *genus*, *Homo*, that we become taxonomically separated[1] from all other living primates.

Most neuroscientists, however, will be most familiar with the most specific level of classification – the level of *species*. Typically, when neuroscientists talk about research with "monkeys" they tend to mean one genus of monkeys, the genus *Macaca*, that is typically used in neurophysiological studies of decision making. One species, in particular, the rhesus macaque (*Macaca mulatta*), is the most widely used neurophysiological model species (see Figure 7.1).[2] Macaques are Old World monkeys, meaning that they are native to Africa and Asia. (More distantly, related New World monkeys, in contrast, are native to Central and South America.) Macaques are the mostly widely distributed genus of primates (with the exception of our own human genus *Homo*) and are thus an extremely flexible group of species. Because of their adaptability, macaques live well in captivity and have thus long served as one of the successful animal models 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 late 1800s. This early

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[1] Historically, there were other species in our genus *Homo* (e.g., *Homo erectus, Homo neanderthalensis*), but all of these other species have been extinct for some time.

[2] Although macaques have predominated as neuroscientific models, some of the most important neuroscientific findings in decision making have also used a marmoset monkey model (e.g., Dias et al., 1996, 1997).

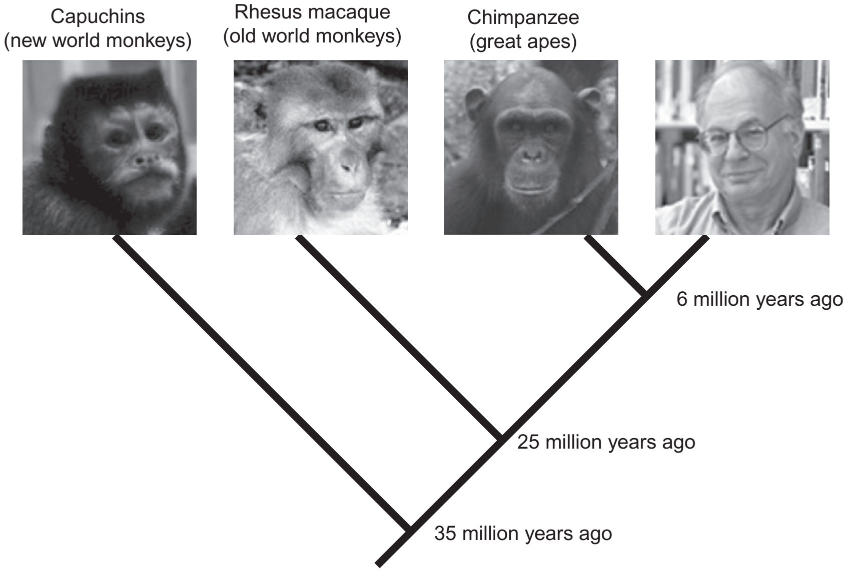

FIGURE 7.1 A depiction of the primate evolutionary tree. The above tree represents a few of the species most relevant for neuroeconomics work: the rhesus macaque (which branched off from the human line about 25 million years ago) and the capuchin (which branched off about 35 million years ago).

work functionally established macaques as the primate brain model for the next century. Indeed, many chapters in this volume focus on neuroeconomic insights gleaned from macaque brains (e.g., Chapters 13, 19, 20, 22, 23, 24 and 25).

Although much of the neurophysiological work in neuroeconomics has used a macaque model, much of the behavioral work on monkey preferences – particularly work studying heuristics and biases – has not focused on macaques. Instead, much of the recent comparative behavioral work on economic preferences has focused on a species believed to represent a cognitive rather than a neuroscientific model of human cognition – the brown capuchin monkey (*Cebus apella*)[3] (see Brosnan, 2006). In contrast to macaques, which are members of the Old World monkey lineage, capuchins are members of the New World monkey branch to which humans are more distantly related. New World monkeys split from the Old World primate line around 35–40 million years ago. While Old World monkeys inhabit Africa and Asia, New World monkeys, like capuchins, are native to South and Central America, and thus have evolved in wholly different ecological niches than other Old World species.

Despite millions of years of evolutionary separation from our own species, the cognition of capuchin monkeys is quite similar to that of humans in a number of respects. Capuchins have extremely large brains relative to their body size (e.g., Fragaszy *et al.*, 2004a,b). 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 large as 40 individuals. Despite this large group size, however, capuchins are an extremely tolerant primate maintaining only a loosely defined dominance hierarchy that permits sharing food with many members of the group (e.g., de Waal, 2008; 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 (Phillips *et al.*, 2009) and can socially learn from the actions of others, though the specifics of how much they can learn continue to be debated (Adams-Curtis and Fragaszy, 1995; Bonnie and de Waal, 2007; Brosnan and de Waal, 2004; Custance *et al.*, 1999; Ottoni and Mannu, 2001; Ottoni *et al.*, 2005; Visalberghi and Addessi, 2001; see elegant reviews in Addessi and Visalberghi, 2006 and Fragaszy *et al.*, 2004a).

[3] Again, it is worth noting that capuchins are not the only primate species used in behavioral work on economic preferences. Some researchers have focused on great ape species – particularly chimpanzees and bonobos – in recent studies on economic behavior (e.g., Brosnan *et al.*, 2007; Heilbronner *et al.*, 2008; Rosati and Hare, 2011; Rosati *et al.*, 2007), as well as other New World species, such as tamarins and marmosets (e.g., Rosati *et al.*, 2006; Stevens *et al.*, 2005a,b).

Finally, capuchins are known for their elaborate tool-use. They use a variety of tools 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 for use as a mosquito repellant (Fragaszy *et al.*, 2004a, Valderrama *et al.*, 2000; Visalberghi *et al.*, 2009).

Having provided this brief introduction to primates generally, this chapter now turns to a few specific domains in which researchers have probed the origins of our behavioral biases by exploring decision making in non-human primates. We next review two domains in which researchers have tried to use a comparative approach to the study origins of our biases.

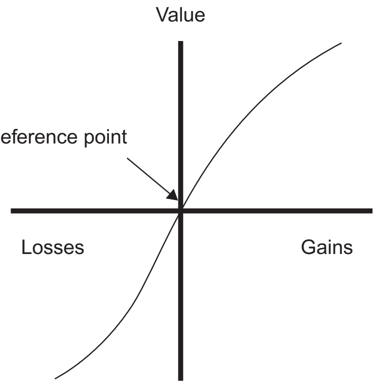

FIGURE 7.2 A diagram of the value function in prospect theory. The S-shaped value function passes through the reference point with a "kink," such that a given absolute-sized loss will decrease in value more than an identically sized gain will increase value.

PROSPECT THEORY AND FRAMING EFFECTS IN NON-HUMAN PRIMATES

One of the first domains in which researchers explored the origins of our behavioral biases was in the domain of choice under uncertainty. Kahneman and Tversky (1979) famously presented a set of cases in which people deviate from expected utility, which they tried to unify under their single theory of choice known as prospect theory (see Chapter 3 and the Appendix for a detailed description of prospect theory). Unlike expected utility theory (Chapter 1) which assumes choices maximize average utility, prospect theory proposes that choices are guided by a more complex set of representations of gains, losses and probabilities. Perhaps more importantly, prospect theory argues that all of these representations are framed relative to a particular wealth or aspiration level, often called the *reference point*. A major implication of prospect theory, then, is that decision makers naturally frame their decisions as gains or losses relative to a reference point. Prospect theory's *value function* (which relates objective value to subjective value) passes through the reference point with a "kink," such that a given absolute-sized loss (e.g., a \$5 loss) will decrease in value more than an identically sized gain (e.g., a \$5 gain) will increase in value (see Figure 7.2). This feature of the value function 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 (see review in Kahneman *et al.*, 1982). The S-shape of the value function 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 (e.g., Tversky and Kahneman, 1981). 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. For example, prospect theory has been used in behavioral finance to explain what is known as the *disposition effect*, in which investors tend to keep shares that have recently gained in value and sell shares that have recently lost value, as well as the *equity premium puzzle*, in which people invest more in bonds than stocks given the relative value of each. Prospect theory has also been important for exemplifying aspects of consumer choice, such as cases of asymmetric price elasticities (see Camerer, 1998, for an elegant and comprehensive review of the applications of prospect theory in economics). Unfortunately, little work to date had addressed where the biases described by prospect theory come from in the first place.

In one of the first attempts to explore behavioral biases in non-human primates, Chen *et al.* (2006) investigated whether capuchin monkeys' economic choices exhibited the framing and context effects observed in humans. The initial goal of this project was to first design a task that could reveal capuchins' preferences. The problem, of course, was that capuchin monkeys do not typically perform the tasks that experimental economists employ to reveal human preferences. Monkeys' preferences cannot be assessed using written surveys concerning their willingness to pay for certain gambles or bundles of goods, nor can one use monkeys' behavior as consumers in a market since they do not naturally act as consumers in markets. Chen *et al.* therefore had to design a novel method that permitted capuchins to reveal their preferences in 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, Chen and colleagues (2006) 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, Addessi *et al.*, 2007; Brosnan and de Waal, 2003, 2004; Liv *et al.*, 1999; Westergaard *et al.*, 1998, 2004). A number of different laboratories have successfully taught capuchins this trading technique using an individual experimenter who would reward a capuchin subject for handing her the token. Chen and colleagues used a similar trading method 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 (see Figure 7.3). In this way, capuchins could be put into a situation much like an economic market, one in which they could express preferences over different bundles of goods. With this set-up, Chen and colleagues were able to introduce price and wealth changes and examine how such changes affected capuchins' purchasing behavior. Further, they 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, they could examine whether capuchins' preferences obeyed prospect-theoretic predictions, and thus were affected by reference points and framing.

Chen and colleagues (2006) introduced adult capuchins to this economic market. Each capuchin began testing by leaving its homeroom and entering a small testing enclosure. In the testing enclosure, monkeys found a small wallet of small disc-shaped metal tokens. Two experimenters then positioned themselves on either side of the enclosure. 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 enclosure. 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. Monkeys could therefore check their options and trade with the experimenter who gave the best kind or amount of the good.

Using this set-up, Chen and colleagues first examined whether the capuchins' preferences in this token economy mirrored that 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, the researchers 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, capuchins were introduced to a compensated price shift. Chen and colleagues gave each monkey 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 would need to shift some of their consumption to the cheaper good; they should spend more of their token budget on the cheaper good than they did before the price shift. The majority of the

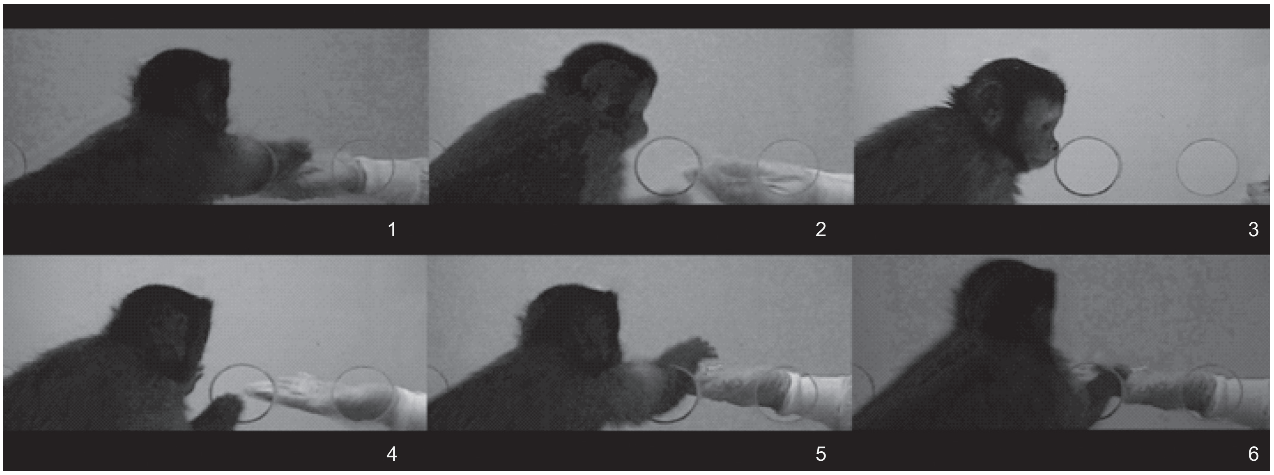

FIGURE 7.3 A frame by frame demonstration of a single trading event involving one of Chen *et al.*'s (2006) capuchin actors (Jill). The capuchin begins by placing a token in the experimenter's hand (1). The experimenter then takes the token away (2–3) and delivers a piece of food (4) which the capuchin then takes from the experimenter's hand (5–6).

capuchins tested did just this, suggesting that they, like humans, obey the core principle of classical economic *price theory*.

In a further study, Chen and colleagues 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 who's payoff stochastically dominated (i.e. the one that gave the most food overall)? To look at this, Chen and colleagues 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 apple pieces they initially offered and in the number they actually gave the monkey after payment. 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 handing over only one piece after the monkey had made her payment. On average, however, this risky experimenter represented a good deal – he gave 1.5 pieces of apple on average while the other experimenter gave only one piece. Like rational actors, the capuchin traders reliably preferred the risky experimenter whose offer stochastically dominated that of the riskless trader. In this way, capuchins not only shift consumption rationally in response to price shifts, but also prefer trading for gambles that provide the highest average payoffs.

Chen and colleagues' (2006) findings that capuchins obey price theory and chose options that stochastically dominate suggests 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 non-standardly in the ways that humans do. As decades of work in behavioral economics have shown, human consumers appear to evaluate their choices not in terms of the final impact of those choices on their overall wealth (e.g., Ariely and Norton, 2008; Kahmeman *et al*., 1982), but rather appear to evaluate different gambles with regard to apparently arbitrary reference points. Of particular relevance here is that human participants tend to be loss averse – they avoid payoffs that appear as losses relative to their reference points more than they seek out gains relative to those same reference points (e.g., Kahneman and Tversky, 1986; Tverky and Kahneman, 1981). The phenomena of reference dependence and loss aversion have now been demonstrated in countless experimental scenarios and gambles (e.g., Tversky and Kahneman, 1986), but also appear to have real-world manifestations in situations as diverse as unemployment patterns (Akerlof and Yellen, 1990; Krueger and Summers, 1988), housing market changes (Odean, 1998), and asymmetric consumer elasticities (Hardie *et al*., 1993). Further, reference dependence also affects participants' intuitions about fairness and moral concerns in some contexts (Kahneman *et al*., 1991). Is reference dependence a uniquely human phenomenon, or does it extend more broadly across the animal kingdom?

To examine this, Chen *et al*. (2006) presented monkeys with trading situations in which they had the opportunity to consider their final trading payoffs relative to a reference point. In the first study, Chen *et al*. (2006) tested for reference dependence by independently varying what monkeys were initially shown and then what they eventually received in exchange for a token. In this way, the researchers were able to set up situations in which the monkeys could get more or less than they expected.

In the first experiment, they examined whether capuchins attended to this reference point. Monkeys got to choose between two experimenters who both delivered the same average expected payoff of 1.5 pieces of apples. One experimenter, however, gave this average payoff of 1.5 apples by way of a perceived loss. This experimenter began every trade by showing the monkey 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 monkey less than what she expected based on the reference point. The second experimenter, in contrast, gave more on average than the monkey 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 1.5 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, capuchins 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.

Chen *et al.* then went on to examine whether capuchins avoid losses in the same way as humans. To test this hypothesis, they gave monkeys a choice between one experimenter who always delivered a loss – he consistently promised two pieces of apple and gave one – and an experimenter who always gave what was expected – he promised one piece of apple and delivered exactly that piece. As in the previous study, 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 addition to avoiding choices that are framed as losses, there is also evidence that capuchin monkeys' risk preferences are affected by framing. Lakshminarayanan and colleagues (2011) presented the capuchins with 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 low payoff. What differed across the two conditions was how the experimenters framed the monkeys' choices. In the first condition, both of the experimenters framed their 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 Tversky and Kahneman (1981), 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 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,[4] capuchins are more risk tolerant when gambling over losses than over gains.

The fact that capuchins exhibit loss aversion and framing effects has allowed this species to become a good model for testing the role that phenomena like loss aversion plays in the development of other behavioral biases. For example, Lakshminarayanan *et al.* (2008) were able to examine the mechanisms underlying a bias known as the *endowment effect* using this capuchin trading set-up. The endowment effect is a bias in which ownership appears to increase an object's value. In 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 in the context of a mug-trading economy. Kahneman *et al.* found that participants who owned (or had been "endowed with") the mug demanded a higher price to sell their mug than was required for identical mugs being traded in the parallel experimental economy. This discrepancy between owners' willingness-to-accept and buyers' willingness-to-pay was christened the endowment effect.

Although much work has established that people show an endowment effect, there is still considerable debate concerning the exact mechanisms underlying the phenomena. For example, some researchers have hypothesized that endowment effects follow from loss aversion (see Kahneman *et al.*, 1990). Under this view, people consider an owned object to be more valuable because they think about parting with the object (i.e., losing it) when estimating its worth. In this way, people's tendency to avoid losses causes them to overvalue objects already in their possession. In contrast, other researchers have hypothesized that endowment effects arise for reasons other than loss aversion; Morewedge *et al.* (2009), for example, argued that people overvalue owned goods because owned goods are more connected with the self and therefore are associated with a suite of positive associations connected to people's self biases. Under this view, then, people like owned objects not because they consider what it's like to lose them, but because such objects are a deeper part of who they are.[5]

To distinguish between these different classes of accounts, Lakshminarayanan *et al.* (2008) tested whether capuchins were also susceptible to endowment effects. If loss aversion is fully able to account for endowment effects in human participants, then capuchins – who exhibit loss aversion in an experimental market – may also show a bias towards over-valuing objects that they own over those they do not yet own. In contrast, if a rich self-concept or specific kinds of interpersonal interactions are

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[4] Interestingly, recent work suggests that capuchins are not the only non-human species to show a risk preference reversal that depends on framing. The European starling (*Sturnus vulgaris*) – shows a similar risk preference reversal on an analogous choice task (Marsh and Kacelnik, 2002). Combined with the capuchin studies, this work suggests that framing effects may extend broadly across the animal kingdom, and may also be present in a variety of different species.

[5] In fact, for this reason, some researchers have even questioned whether the endowment effect reflects some kind of artificial experimentally induced effect (e.g., Plott and Zeiler, 2005).

required to induce endowment effects, then it is likely that capuchins might not show such effects.

To get at this issue, Lakshminarayanan *et al*. made capuchins the "owner" of one of two equally preferred goods. Specifically, monkeys were provided with one kind of good and were then allowed to trade for another equally preferred kind of good. Since the two goods were equally preferred, one might expect the capuchins to trade about half their endowed goods and then keep the other half. In contrast to this prediction, capuchins reliably preferred to keep the food with which they were endowed. Control conditions later revealed that this effect was not due to 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 indicated that a non-human species[6] evinces a true endowment effect, one that cannot be explained by timing, inhibition, or problems with transaction related costs. In doing so, this work suggests that endowment effects are likely to be the result of loss aversion rather than more complex cognitive capacities or human-like cultural features.

Taken together, the results reviewed so far suggest that one non-human primate species – the brown capuchin – shares at least three 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 relative to those reference points. In addition, capuchins show a reflection effect, becoming more risky when they are dealing with perceived losses than when they are dealing with perceived gains. Finally, this species appears to show an endowment effect, overvaluing foods that are in their possession over ones that are not. Such results indicate that monkeys also succumb to a variety of the same biases as humans, with different descriptions of the same problem leading them to make different choices.

AMBIGUITY AVERSION AND THE ELLSBERG PARADOX IN NON-HUMAN PRIMATES

Having established that monkeys show behavioral biases in the domain of framing and risk, we now review evidence that a different species of monkey exhibits another human-like paradoxical preference: an aversion to unknown situations. As any student of human behavior probably realizes, people hate ambiguity. In economic terms, people tend to prefer a risky option with a fully specified reward probability distribution to an ambiguous option with an unspecific reward probability distribution, and will pay to avoid the ambiguous option even when it has lower expected value (Curley *et al*., 1986; Einhorn and Hogarth, 1985; Fox and Tversky, 1995). This economically irrational bias is often illustrated by the Ellsberg Paradox, in which people are offered a bet on drawing, say, a red ball from one of two urns, one in which the ratio of red to blue balls is known, and another in which the ratio of red to blue balls is unknown. Even when told that the ratio of red and blue balls in the second urn is selected randomly, people tend to prefer the unambiguous urn (Ellsberg, 1961).

Although much work has demonstrated that people are averse to ambiguity, less work has explored where this bias comes from in the first place. Indeed, from an evolutionary point of view, ambiguity aversion seems especially mysterious. After all, natural environments likely present a continuum of decision contexts, from risky ones in which outcome probabilities are well-known to more ambiguous ones. Why should people hate ambiguity so much? Is it fear of the unknown, a kind of compounded-uncertainty or a riskier form of normal risk? Or perhaps this bias stems from some uniquely human faculty-like language or the use of money?

Recent work in neuroeconomics provides partial answers to these questions. Brain imaging studies comparing people betting on risky gambles (in which probabilities are fully specified) and ambiguous gambles (in which specific probabilities have been obscured) generally have, in some studies, revealed that different networks of brain areas are activated when making decisions under risk compared with making decisions under ambiguity (see Platt and Huettel, 2008 for a review). In these studies, risky decisions were found to activate insula and parietal cortex, regions involved in anticipating losses and performing calculations, respectively (Hsu *et al*., 2005; Huettel *et al*., 2006). In one of these studies, ambiguity was associated with activation in the amygdala and lateral orbitofrontal cortex, possibly reflecting aversive processes (Hsu *et al*., 2005), whereas in the other ambiguous gambles specifically activated the inferior frontal gyrus. By contrast, Levy *et al*. (2010) found that activation in these areas, and others, was correlated with the subjective value of the chosen gamble, as estimated from participants' choices, for decisions made under both risk and ambiguity. Consistent with these findings, Huettel and colleagues (2006) found that *relative*

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[6] For a similar result in chimpanzees, see Brosnan *et al*. (2006).

activation in brain areas recruited during decision making under risk and ambiguity predicted individual differences in choice behavior. Thus, whether or not differences in human decision making under risk and ambiguity reflect the engagement of distinct neural circuits remains an open question.

Whether the distinction between risk and ambiguity reflects uniquely human faculties requires knowing whether other animals also avoid ambiguity in similar contexts and, if so, whether the underlying biological processes are shared with humans as well. Although little work has addressed how animals deal with ambiguous situations, there is a relatively large literature on how animals deal with risky decisions (reviewed in Platt and Huettel 2008; Kacelnik and Bateson, 1997; Weber *et al.*, 2004). These studies show that animals as diverse as birds, bees, rats, and monkeys are sensitive to risk. Most animals appear to be risk averse in general, although this may vary with contextual factors such as hunger (Caraco *et al.*, 1990; but see also Bateson, 2002), the number and timing of decisions (Hayden and Platt, 2007), and species differences in ecology and social structure (Heilbronner *et al.*, 2008). Moreover, several recent neurophysiological studies in monkeys (Fiorillo *et al.*, 2003; McCoy and Platt, 2005; O'Neill and Schultz, 2010; Platt and Glimcher, 1999) found that risk and outcome probability modulate the activity of neurons in several cortical and subcortical areas implicated in decision making.

Despite this growing literature on risky decision making in animals, very little is known regarding the impact of ambiguity on decision making by animals. This gap reflects, in part, the perceived difficulty in training animals to make choices about ambiguous gambles. Although researchers have developed methods for giving animals information about risky choices, it has proven trickier to find methods to introduce animals to probabilities and then systematically obscure that information. Recently, Hayden and colleagues (2010) trained rhesus macaques to choose between two bars that explicitly cued probabilities of various reward outcomes and obscured that information on some trials (Figure 7.4A). The portion of each bar that was blue cued the probability of receiving a large juice reward if the monkey chose that option, whereas the portion of each bar that was red cued the likelihood of obtaining a small reward. All four monkeys quickly learned these cues, and reliably chose the option with a higher probability of obtaining a large reward when both options offered risky gambles.

Subsequently, the authors systematically obscured information about reward probability for one of the options by occluding the intersection of the red and blue portions of the bar. All four monkeys reliably preferred risky options to ambiguous ones, despite the fact that this bias was costly (Figure 7.4B). Just like people, when ambiguity was increased for one of the options monkeys avoided it more often. Finally, ambiguity aversion gradually declined as monkeys learned the underlying probability distribution of rewards associated with the ambiguous option over the course of several weeks. For comparison, human participants performing the same task for points showed similar ambiguity aversion (Figure 7.4C).

Rhesus monkeys, like humans, are thus sensitive to ambiguity, and prefer options with full information. These findings imply that the cognitive processes motivating human preferences for certainty are shared with at least some non-human primates. Thus, ambiguity aversion does not appear to arise from uniquely human faculties such as language, symbolic culture, or the use of an abstract currency, or putatively uniquely human motivations like the desire to avoid embarrassment or regret (Curley *et al.*, 1986; Heath and Tversky, 1991; Kühberger and Perner, 2003). Ambiguity aversion in rhesus monkeys and humans implicates evolutionarily conserved decision-making strategies embodied in shared neural circuitry, although this conclusion awaits further testing in other primate species.

WHAT COMPARATIVE WORK MEANS FOR TRADITIONAL ECONOMICS AND NEUROECONOMICS

When taken together, the comparative studies reviewed above suggest that two distantly related species of monkeys – brown capuchins and rhesus macaques – share a number of the non-standard preferences or biases that human decision makers show. First, although capuchins' decisions appear to obey the human-like standards of price theory, this species also exhibits the same systematic biases as humans – capuchins evaluate gambles in terms of arbitrary reference points, pay more attention to losses than to gains, change their risk preferences in different contexts, and show market anomalies like the endowment effect. Second, although macaques track expected value during a risky choice task, this species also falls prey to ambiguity aversion in much the same way as humans. A review of the comparative work to date thus suggests that human behavioral biases may 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 monkey species.

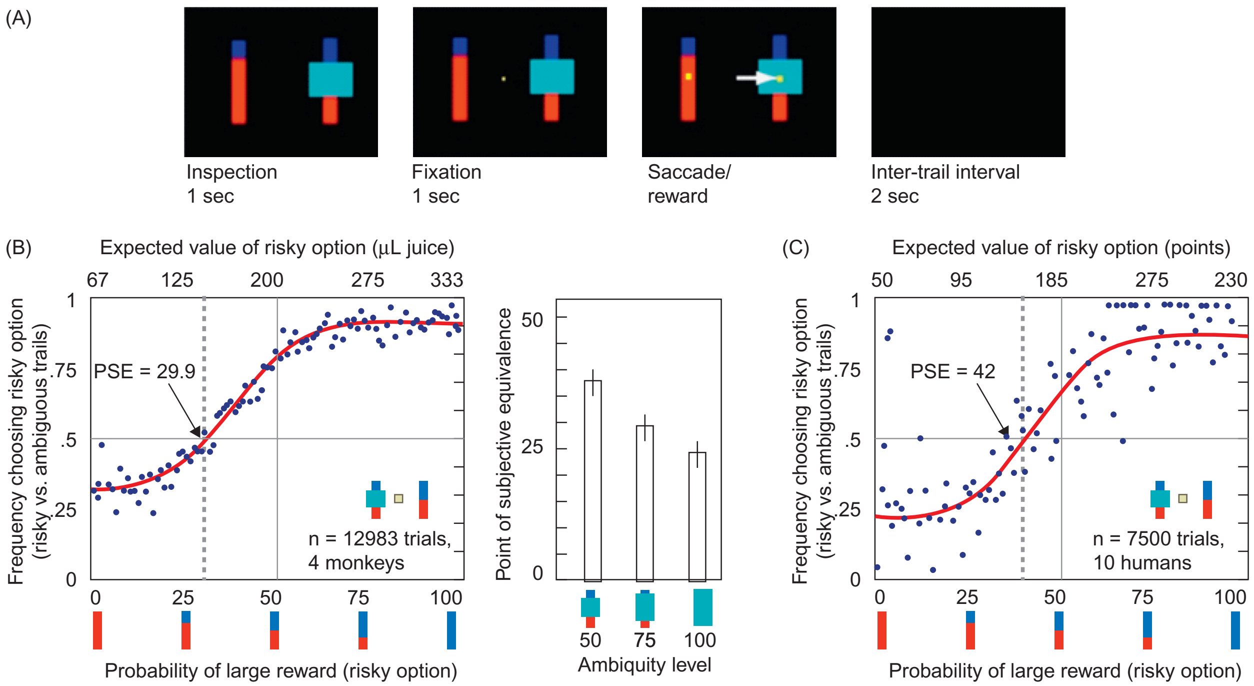

FIGURE 7.4 A depiction of the method and results of Hayden *et al.* (2010). (A) Monkeys were shown two bars that explicitly cued probabilities of various reward outcomes and obscured that information on some trials. (B) Monkeys' choice of risky versus ambiguous options. (C) Human participants' choices of risky versus ambiguous options.

The work reviewed here further suggests that decision-making biases may arise in the absence of market experience not just in monkeys, but in the human species as well. Indeed, the results presented here provide 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 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), the endowment effect (see Harbaugh *et al.*, 2001), and ambiguity aversion (e.g., Tymula *et al.*, 2012) in children and adolescents, there is still relatively little consensus concerning whether 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 have had at least some experience with purchases in the real world. For this reason, older children are not the best subject pool if one wants to examine the role of experience in the development of loss aversion and reference dependence. To better get at the role of experience, researchers should focus their empirical effort on populations that *really* lack experience with decisions. One such population is human infants. Infants are, by definition, so young that they 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 easily be 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 ask whether infants obey price theory (and thus, examine whether an obedience to price theory can emerge in the complete absence of experience — a point of some importance in developing economies). Similarly, one could examine how and when biases like loss aversion and reference dependence begin emerging and again, explore the role of economic experience (of the kind societies provide) and other factors in the development of these heuristics.

The fact that some behavioral biases are shared with non-human 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 un-learned, and that these mistakes are likely to disappear quickly in the face of market pressures, especially when stakes are high. The work we summarized here, however, suggests that these biases emerge in a relatively consistent fashion despite diverse experience, and thus hints that such biases are likely to manifest themselves powerfully in novel situations.

The findings reviewed here also have 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 (discussed throughout this volume). Many of the neurophysiological studies to date, however, have concerned themselves with aspects of choice behavior that follow from classical economic models. In contrast, fMRI research with humans has focused on the neural basis of a variety of economic behaviors including those characterized by behavioral biases. While such fMRI techniques have already provided tremendous insight into the neural basis of both framing effects (e.g., de Martino *et al.*, 2009; Tom *et al.*, 2007) and ambiguity aversion (e.g., Hsu *et al.*, 2005), these methods would undoubtedly be complemented by neurophysiology work at the level of individual neurons. Unfortunately, to date, little neurophysiological work in monkeys has addressed the mechanisms underlying behavioral biases, in part because designing framing tasks for use in non-verbal primate subjects is a non-trivial task (though see Seo and Lee, 2009). The behavioral methods reviewed here, however, demonstrate that such framing effects and paradoxical choices can and do occur in non-verbal species. These findings imply that a physiological investigation of behavioral biases is possible, and thus that it might be possible to examine prospect theoretic predictions in a primate neural model. Work demonstrating that monkeys exhibit an endowment effect further suggests that physiologists might be able to examine even more subjective changes in valuation — such as those due to ownership — in a primate model as well.

The field of neuroeconomics — though still relatively new — has enjoyed much success in a 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. The goal in this chapter has been to point out how studies of choice, preferences and incentives in non-human primates 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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PART II

NEURAL AND PSYCHOLOGICAL FOUNDATIONS OF ECONOMIC PREFERENCES