The Evolutionary Roots of Human Decision Making

Laurie R. Santos and Alexandra G. Rosati

Department of Psychology, Yale University, New Haven, Connecticut 06511;
email: Laurie.Santos@yale.edu

Annu. Rev. Psychol. 2015. 66:321–47

The *Annual Review of Psychology* is online at psych.annualreviews.org

This article's doi:
10.1146/annurev-psych-010814-015310

Keywords

preference, bias, rationality, cognitive evolution, primates

Abstract

Humans exhibit a suite of biases when making economic decisions. We review recent research on the origins of human decision making by examining whether similar choice biases are seen in nonhuman primates, our closest phylogenetic relatives. We propose that comparative studies can provide insight into four major questions about the nature of human choice biases that cannot be addressed by studies of our species alone. First, research with other primates can address the evolution of human choice biases and identify shared versus human-unique tendencies in decision making. Second, primate studies can constrain hypotheses about the psychological mechanisms underlying such biases. Third, comparisons of closely related species can identify when distinct mechanisms underlie related biases by examining evolutionary dissociations in choice strategies. Finally, comparative work can provide insight into the biological rationality of economically irrational preferences.

Contents

INTRODUCTION

> *De toutes les définitions de l'homme, la plus mauvaise me paraît celle qui en fait un animal raisonnable [Of all the definitions of man, the worst is that he is a rational animal].*
>
> *Anatole France*, Le Petit Pierre (*1918*)

Our species has long been heralded as "the rational animal," but you might not know it from a quick glimpse into a psychology textbook. Indeed, after the past 50 years of work in judgment and decision making, we now know that human choice is often not as rational as one might expect. In a number of contexts, human decisions tend to systematically deviate from what rational choice models would predict. For example, we consistently attend too much to irrelevant information (see reviews in Kahneman 2011), fall prey to contextual and situational variables (see Danziger et al. 2011), and even rationalize our bad decisions (see review in Harmon-Jones & Mills 1999). Moreover, many of these irrational biases operate quickly, effortlessly, and outside of our awareness—which means that merely recognizing that we have a bias does not always make that bias go away (Santos & Gendler 2014).

These so-called irrationalities in human decision making have garnered much attention in social psychology and behavioral economics. Indeed, there are many reasons to study the psychological mechanisms that underlie irrational decision making in humans: to make better predictions about how people will act in the real world, to generate new hypotheses about the factors that may lead human decisions astray, or even to create or refine economic policy based on evidence. But in this review, we argue that if psychologists want to truly understand human decision making, we should also be interested in the evolutionary origins of these decision-making biases. That is, we should explore whether animals—particularly our closest living evolutionary relatives, the nonhuman primates—share our decision-making biases.

Of course, animals must also make decisions about rewards in their natural lives—many other species face decision trade-offs where they must account for costs, such as temporal delays and uncertainty, as well as the potential payoffs in pursuing different courses of action. In this way, the decisions that humans face in economic contexts often have clear analogues with the problems that animals face when foraging for food or seeking mates. Consequently, the types of choices that psychologists and behavioral economists focus on in humans—such as intertemporal preferences and risk preferences—are also ubiquitous in biology and behavioral ecology. Indeed, there have been major theoretical and empirical advances in our knowledge of animal decision making from studies of distantly related species such as birds, rodents, and insects (Bautista et al. 2001, Caraco 1981, Kacelnik & Bateson 1997, Kamil et al. 1987, Krebs & Davies 1978, Real 1991, Stephens & Anderson 2001, Stephens et al. 2004). In the current review, however, we focus on more recent work investigating the roots of human biases in nonhuman primates, our closest phylogenetic relatives. Our goal in reviewing primate work specifically is to integrate behavioral economic work on human preference violations with methods from comparative psychology that are used to carefully tease apart the cognitive mechanisms underlying these observed behaviors, as well as biological theories that allow researchers to assess the evolutionary impact of different choice strategies.

Throughout this review, we argue that comparative research on decision-making biases in primates is critical for understanding the decision-making biases observed in humans. In particular, we argue that comparative research can provide four types of insights into human decision-making biases. First, comparative studies can illuminate the phylogeny of biases: which human decision-making biases are shared with other primates, and which are instead unique to our species. Second, comparative research can inform the particular cognitive mechanisms that are necessary for a given decision-making bias to emerge by examining decision-making processes in species that lack relevant mechanisms. Third, studies of closely related primate species can disentangle the psychological processes underlying different types of choices by assessing whether they evolve in tandem across species—that is, such studies can provide a new window into dissociations between different decision-making strategies. Finally, comparative work can generate new theories about why different decision-making biases emerged in the first place by evaluating their evolutionary function. In this way, comparative work provides an important theoretical framework for considering the optimality (or lack therefore) of different strategies from a biological perspective.

ARE HUMAN BIASES SHARED WITH OTHER PRIMATES?

One important question nonhuman primates can answer about the nature of human decision making concerns whether human biases are unique to our species. Despite our shared biological endowment, humans are quite different from other primates—humans have larger brains, use sophisticated technology, and engage in extensive cooperative endeavors. Identifying the reasons that humans show these salient differences is of fundamental importance not just in psychology and the social sciences, but in philosophy and biology as well (Hare 2011, Herrmann et al. 2007, Hill et al. 2009, Rosati et al. 2014, Sterelny 2012, Tomasello et al. 2005). However, for psychologists interested in the nature of human decision-making biases, the question of uniqueness has a different character. Typically, debates about the psychological processes that are uniquely derived in humans focus on cognitive capacities that appear to be more advanced in humans than in other species, such as our capacity for human speech, complex tool use, and mathematical reasoning. Exploring whether the irrational biases seen in humans are unique therefore turns the typical comparative cognition debate on its head: When using comparative cognition techniques to study the origin of human biases, we are not examining whether humans are uniquely smart in some capacity, but rather whether we are uniquely irrational.

Despite this important difference, an empirical investigation into the evolutionary origins of our less rational tendencies shares many commonalities with studies of human exceptionality (Santos & Chen 2009). In both cases, a major approach for understanding why humans possess such abilities (or fallibilities) is examining the roots of human cognitive systems. Comparative cognition therefore investigates the evolutionary origins of human cognition by examining the patterns seen in other species. Doing so is critical to illuminate the phylogenetic history of such biases: If a particular bias is widely shared among other primates, this indicates that the heuristic in question is evolutionarily ancient. Such data on phylogenetic patterns can begin to shed light on differences between economic rationality, or violations of rational choice theory, and biological rationality—a distinction discussed further in later sections. Furthermore, understanding whether a particular bias is unique (or what other species share that bias) provides important insights about the types of experiences that are necessary for that pattern of decision making to emerge. For example, if many other primates share a given bias, this suggests that the human bias might not be learned through experience with economic markets—much like inferences from developmental research on decision making in children (Harbaugh & Krause 2002). In this way, comparative research can tell us about the psychological mechanisms that underlie different traits.

Framing Effects

Decades of research in judgment and decision making have revealed that human choices are routinely subject to framing: We tend to view choice options not in absolute terms but rather relative to salient reference points (for a review, see Kahneman 2011). For example, when considering different options for combating a deadly disease, people respond differently when the same options are presented in terms of losses (i.e., lives lost) versus gains (i.e., lives saved; Tversky & Kahneman 1981). Such framing effects have long been observed in human behavior in both the lab (Kahneman & Tversky 2000) and field studies (Genesove & Mayer 2001, Odean 1998). These studies indicate that encoding the value of alternative options relative to some reference point is a pervasive component of how humans make choices. Although these effects are thought to stem from widely shared neurobiological mechanisms (De Martino et al. 2006), until recently little research has examined framing effects in nonhumans (see Marsh & Kacelnik 2002). Are humans unique in their tendency to see their decisions in relative terms, or are other primates also affected by the way different decision options are presented?

Chen and colleagues (2006) were the first to explore whether nonhuman primates were also susceptible to framing effects. To test this question, they developed an experimental token economy in which brown capuchin monkeys (*Cebus apella*) could trade tokens with human experimenters in exchange for food. The monkeys then could choose between two experimenters who gave the same average number of apple pieces across trials but differed in terms of how this final payoff was framed. In one study, monkeys had a choice between one experimenter (the gains experimenter) who started by showing the monkey one piece of apple and sometimes added an extra piece of apple, and a second experimenter (the losses experimenter) who started by showing the monkey two pieces of apple and sometimes removed one. Monkeys showed an overwhelming preference for the gains experimenter over the losses experimenter—even though they received the same payoff from both. In this way, capuchins appear to avoid options that are framed as a loss, just as humans do.

In a later study, Lakshminarayanan and colleagues (2011) tested whether monkeys' loss aversion would lead them to take on more risk in an attempt to avoid losses. Capuchins were presented with a choice between a safe experimenter (who always provided a reliable amount of food) and a risky experimenter (who sometimes varied the amount of food that they provided from trial to trial). However, this choice varied in whether it was framed as a loss or a gain. In one condition, monkeys were presented with a choice between safe and risky gains—the risky experimenter initially presented one apple piece and sometimes added two extra apple pieces, whereas the safe experimenter always started with one apple piece and always added one extra piece. In the other condition, monkeys received a choice between safe and risky losses—the risky experimenter started with three apple pieces but sometimes reduced it to one piece, whereas the safe experimenter always started with three apple pieces and always reduced it to two pieces. Although the expected value and risk levels were the same across the gain and loss conditions, monkeys did not treat these conditions similarly. All monkeys chose the risky over the safe experimenter in the losses condition, but they showed the opposite preference in the gains condition. In this way, monkeys exhibited a reflection effect: They tended to seek out more risk when dealing with losses compared to gains (Lakshminarayanan et al. 2011). Overall, capuchins exhibited qualitatively similar framing effects as human tested in similar framing studies (Kahneman 2011, Kahneman & Tversky 1979, Tversky & Kahneman 1981). Importantly, this capuchin work indicates that framing—a bias that at first glance might appear to be unique to human decisions—also plagues the decisions of other primates. This suggests that human framing biases might have deep roots in cognitive systems that are broadly shared across species (see also Marsh & Kacelnik 2002).

Peak-End Effect

Another set of psychological heuristics that humans exhibit concerns the strategies we use to evaluate past events. Rather than evaluating a past episode in terms of all available time points, people tend to evaluate events by focusing only on their subjective reactions to two time periods: the event's peak goodness (or badness) and the conclusion of the event. This well-documented heuristic is referred to as the peak-end effect. In one example, participants were asked to recall a painful event: holding their hands in cold water (Kahneman et al. 1993). However, both the length of this event and how well the event ended were varied in order to assess how this impacted the participant's memories. Surprisingly, participants tended to remember longer painful events that ended well as less bad than shorter painful events that ended poorly. In this way, people tend to ignore the duration of an event—how long it was—when subjectively evaluating it. Instead, they seem to focus solely on the event's peak and ending when assessing it after the fact (Redelmeier et al. 2003).

Are humans the only creatures to subjectively evaluate events using this peak-end heuristic? Many researchers have argued that humans differ from other animals in the extent to which we can think about and explicitly evaluate past episodes (see review in Roberts 2002). Under this view, humans might have a unique set of heuristics for subjectively evaluating past events. On the other hand, nonhumans are clearly capable of making choices between sequences of rewards over time (Brunner 1999, Brunner & Gibbon 1995) and thus may share human-like heuristics. To test these alternatives, primate researchers have begun to evaluate whether primates treat sequences differently depending on their peak and endpoints. Although results for a consistent peak-end effect are somewhat mixed (Xu et al. 2011), recent work suggests that some primates may use a peak-end heuristic like that of humans. Blanchard and colleagues (2014), for example, tested whether rhesus monkeys (*Macaca mulatta*) shared a human-like peak-end effect. They familiarized monkeys with different reward sequences and then gave monkeys a choice between the sequence they had just experienced and a standard neutral sequence. The authors found that monkeys' choices were affected by how the sequence ended. In one striking example, merely adding an extra low-valued reward to the end of an otherwise high-value sequence reduced the monkeys' subjective preference. Similarly, the authors also found evidence that monkeys tended to overweight sequences with a highly valued peak. Thus, there is increasing evidence that biased sequence evaluations are not unique to humans: Like humans, rhesus monkeys appear to overweight the peak and end point of an episode. In this way, the heuristics that humans use to think about and evaluate the past appear to be shared by other nonhuman primates as well.

Counterfactual Reasoning

So far we have seen that nonhuman primates share human-like heuristics for evaluating options when making choices (framing) and evaluating experiences after the fact (peak-end effect). Yet when humans make decisions, we account for not only what did happen, but also what could have happened (Platt & Hayden 2011). Reasoning about such counterfactual (or hypothetical) events is especially common after failures to achieve a desired outcome: When people are faced with bad outcomes, they often consider what they might have done differently to achieve their goals (Byrne 2002). Such counterfactual reasoning tends to bias people to learn about appropriate courses of action and adjust their future behaviors, especially after making a poor choice. Moreover, counterfactual learning often seems driven by a particular emotional experience: the feeling of regret. That is, people feel regret when they realize that things would have turned out better had they acted differently, and this experience can cause people to shift their patterns of choice (Coricelli et al. 2007, Zeelenberg et al. 1996). Importantly, this ability to derive pain or pleasure from events that are not directly experienced stands in contradiction to traditional conceptions of utility, which depend entirely on learning from the actual outcome one received from a particular option (Bell 1982, Loomes & Sugden 1982). That is, classical economic models suggest that it is rational to feel disappointed if you gamble and lose, but it is irrational to additionally kick yourself for not choosing a different slot machine (but note that accounting for both actual and hypothetical outcomes over sequences of choices may improve learning efficiency and therefore be biologically rational; see discussion in Lee 2008).

Humans are biased to account for not only outcomes that actually did occur, but also simulated possible events that did not occur. Do animals reason about hypothetical outcomes in the same way? Recent studies on reinforcement learning in primates indicate that humans are not alone in our ability to think about hypothetical outcomes. For example, Lee and colleagues (Abe & Lee 2011, Lee et al. 2005) presented rhesus monkeys with a computer-based version of the game rock-paper-scissors. When Lee and colleagues examined the strategies that the monkeys used over time, they found that monkeys did not simply adjust their choices based on what they received on the previous trial. Surprisingly, monkeys also adjusted their strategy to account for rewards they would have received had they chosen a different option. Using a similar computer-based setup, Hayden and colleagues (2009) presented rhesus monkeys with a risky decision-making task with eight possible choices. Whereas seven of the options consistently provided small juice rewards, the final option was variable: Sometimes it provided a much larger reward, and sometimes it provided a much smaller reward. Critically, monkeys were given feedback about what the risky option would have provided on every trial. In this way, monkeys could see how much juice they would have gotten from the risky option, regardless of whether they had chosen it. As in the rock-paper-scissors task, modeling of the monkeys' behaviors showed that the monkeys adjusted their future strategies on the basis of what they would have received. In cases where the risky option would have provided the high-value outcome on one trial, monkeys were especially likely to seek this option out in future trials. In this way, monkeys—like humans—change their future choices according to counterfactual situations that could have happened but did not.

Although these findings indicate that rhesus monkeys also account for hypothetical outcomes when making decisions, they do not show why monkeys do so. In particular, do nonhumans attend to hypothetical outcomes for human-like reasons? Do monkeys also experience regret? Some initial evidence suggests that primates may also react to bad decisions with emotional responses. Rosati & Hare (2013) examined the emotional reactions that chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) exhibited when making choices between a risky gamble and a safe option. The main question was how the apes responded in trials in which the apes gambled but discovered that they had lost out and received the bad outcome. In fact, both species were more likely to exhibit behavioral markers of negative emotions—including negative vocalizations, tantrum-like banging, and scratching (an arousal or stress response in primates)—when they received the bad outcome but did so rarely after receiving the good risk outcome or choosing the safe alternative. Such emotional responses might reflect either disappointment (at not receiving the good outcome) or regret (at not having chosen differently). Notably, chimpanzees and bonobos were also more likely to attempt to switch their choice after discovering that they had received bad outcomes—that is, they spontaneously tried to correct their action, which is consistent with regretting their poor choice. Indeed, the more an individual bonobo tried to correct his or her choice after bad outcomes, the more that individual tended to avoid the risky option overall—similar to the patterns of regret avoidance seen when humans make decisions (Zeelenberg 1999; Zeelenberg et al. 1996, 1998). Together with the findings from monkeys (Hayden et al. 2009, Lee et al. 2005), these results suggest that at least some primates are biased to incorporate counterfactual events when making decisions, which might be driven by regret-like emotional experiences.

DO HUMANS HAVE UNIQUE MECHANISMS FOR DECISION MAKING?

The previous sections indicate that nonhumans exhibit several biases characteristic of human economic decision making. One possibility is that these biases stem from cognitive systems that are phylogenetically ancient and widely shared. In other cases, humans are hypothesized to display biases because of cognitive abilities—such as language or a rich sense of self—that animals are thought to lack. Consequently, primate studies can provide insight beyond merely identifying which human decision-making strategies are unique. Primate studies can also tell us more about the particular psychological mechanisms that are needed for those biases to emerge. That is, comparative studies can pinpoint the necessity of those capacities for the development of human-like biases. If species that lack specific capacities—such as a rich human-like sense of self—nonetheless exhibit a human-like bias, this would provide evidence that the cognitive mechanisms that underlie human decision making may be simpler and more parsimonious than judgment and decision-making researchers previously thought. In other cases, nonhuman primates and humans may exhibit similar behaviors, but such behaviors may reflect different underlying processes. In all cases, careful experiments are often needed to tease apart whether similar performance is truly supported by similar cognitive mechanisms.

The Endowment Effect

One example of nonhuman studies that have provided insight into human psychological mechanisms concerns the endowment effect. The endowment effect is a bias in which people overvalue a good that they own compared to one that they do not own (Thaler 1980). In a classic demonstration of this effect, Kahneman and colleagues (1990) gave participants a mug and asked how much money they demanded to sell it; other participants were asked how much they were willing to pay for the same mug. In fact, the participants who were endowed with the mug required twice as much money to sell the mug as the other participants were willing to pay for it. This finding, as well as many others (Franciosi et al. 1996, Johnson et al. 1993, Kahneman et al. 1991), demonstrates that people value objects more when they already own those objects. What is unclear from this robust set of findings, however, is why people overvalue owned objects. Researchers in judgment and decision making have therefore proposed a number of different accounts for why people show an endowment effect. For example, some have argued that the endowment effect relies on cognitive capacities such as a rich and motivated sense of self (Belk 1988, 1991; Lerner et al. 2004) or an understanding of ownership (Beggan 1992, Franciosi et al. 1996, Morewedge et al. 2009)—many of which are likely to be uniquely human. In contrast, other researchers have argued that the endowment effect results from simpler cognitive processes, such as loss aversion (Johnson et al. 2007, Kahneman et al. 1991, Rozin & Royzman 2001), ones that are known to be shared with nonhuman primates. Although many studies of human endowment effects do not directly address which of these possible mechanisms account for the results (but see Morewedge et al. 2009), research with nonhuman primates can tease apart the role that uniquely human cognitive processes play in this bias. That is, comparative studies can address the extent to which uniquely human concepts—such as a sense of self and an understanding of ownership—are actually necessary for the development of an endowment effect.

To this end, comparative cognition researchers over the past decade have observed that a number of nonhuman primate species exhibit what appears to be an endowment effect—at least in some contexts. For example, Brosnan and colleagues have observed that chimpanzees, gorillas (*Gorilla gorilla*), and orangutans (*Pongo pygmaeus*) are reluctant to exchange an item in their possession for another item—even if the new item was normally more preferred (Brosnan et al. 2007, 2008; Drayton et al. 2013; Flemming et al. 2012). Similarly, capuchin monkeys fail to trade a piece of food they own for an equally valued alternative kind of food (Lakshminarayanan et al. 2008). Capuchins' aversion to trading owned goods persisted even when the task controlled for the transaction cost of trading the food–that is, the extra time and effort necessary to make the trade.

These data at first glance suggest that nonhuman primates exhibit a bias much like the endowment effect. Consequently, these findings suggest that uniquely human concepts such as a rich sense of self and an understanding of ownership cannot be necessary for an endowment effect to emerge because nonhuman primates who lack these elaborated concepts also show hints of an endowment effect. However, at least one critical difference appears to exist between the endowment effect observed in nonhuman primates and the effect commonly observed in humans. Although humans exhibit an endowment effect with a variety of different kinds of goods, the nonhuman primate endowment effect seems limited relative to that of humans—primates exhibit an endowment effect when given possession of food but not when they are made owners of others kinds of objects such as toys and tools (Brosnan et al. 2007, Flemming et al. 2012). For example, great apes exhibit an endowment effect for food but not for functional items such as tools (Kanngiesser et al. 2011). Similarly, although chimpanzees exhibit an endowment effect for tools that they can use immediately to obtain food, they fail to show a similar effect when food is currently inaccessible or absent (Brosnan et al. 2012). Together, this work suggests that although nonhuman primates do exhibit a bias much like the endowment effect by refusing to trade an owned food for an equally valued alternative, this bias may be more limited than the one seen in humans. Cognitive capacities that are unique to humans may allow the endowment effect to encompass a broader variety of artifacts and goods for our species, whereas for other primates this effect is more specific to food items.

Choice-Induced Preference Changes

Research with nonhuman primates has also suggested that simpler cognitive mechanisms may underlie certain human biases, such as those studied by researchers interested in the phenomenon of cognitive dissonance. One example is known as choice-induced preference changes: People

Figure 1

Choice-induced preference changes in capuchins. In the Egan et al. (2007) study, (*a*) monkeys are given a choice between two differently colored chocolate candies: blue and green. (*b*) The monkey makes her choice, in this case blue. (*c*) Later, she is given a second choice between the unchosen option (green) and a novel but equivalent color (red). Egan and colleagues found that monkeys consistently avoided the unchosen option in the second choice, which suggests that capuchins may derogate unchosen options just as humans do (e.g., Brehm 1956).

tend to shift their preferences to match their own previous decisions (for reviews, see Egan et al. 2010, Harmon-Jones & Mills 1999). In a classic demonstration of this bias, Brehm (1956) had participants rate the value of different household items and then forced participants to choose between two of the items that they rated equally. Following this difficult choice, participants were asked to rerate all of the items, and Brehm then explored whether the act of making a choice affected participants' later ratings of the two items involved in the choice. In fact, participants tended to shift their ratings to match their choice, devaluing the object they had not selected.

Decades after these original observations, psychologists recognize that the bias to devalue unchosen options is quite robust. However, there is still much debate concerning the mechanisms that underlie this tendency. Some researchers have postulated that choice-induced preference changes require abilities that are unique to humans, such as possessing a self-concept (Steele 1988) or a motivation to be the type of person who makes consistent decisions (Aronson 1968). Others (Bem 1967, Egan et al. 2010) have argued that choice-induced preference changes may not require such rich capacities. To distinguish between these different alternatives, Egan and colleagues (2007) presented capuchin monkeys with a version of the choice test developed by Brehm (1956). After finding food items that monkeys rated equally (differently colored chocolate candies), monkeys were presented with a choice between two identically preferred items. After this initial choice, monkeys were given a second choice between the previously rejected food item and an equally valued novel third item (see **Figure 1**). In the second choice test, monkeys tended to devalue the candy they had chosen against in the initial choice test. Importantly, this devaluation of the previously unchosen item did not occur when the experimenter made the choice for the monkey: Capuchins only devalued unchosen options when they played a causal role in the decision.

In a later study, Egan et al. (2010) showed that capuchins exhibit similar choice-induced preference changes even when merely given the illusion of choice (for a similar finding in humans, see Sharot et al. 2010). Here, Egan and colleagues allowed capuchins to think they made a choice when in fact that choice had been surreptitiously predetermined by the experimenter. Despite merely having the illusion of choice, capuchins still showed the same choice-induced preference changes, which suggests that preexisting preferences between the two options could not account for the monkeys' performance (for a discussion of this alternative explanation, see Chen & Risen 2009). In addition, West and colleagues (2010) demonstrated that these choice-induced preference changes may be specific to primate psychology: Although West and colleagues replicated the basic preference change effect with several different primate species, they found no such choice-induced shifts in several other nonprimate mammal and bird species. Taken together, these findings of choice-induced preference changes in primates provide important hints about the mechanisms that may underlie these preference changes in humans. In particular, the primate work to date suggests that at least some of the potential mechanisms that could underlie this bias—such as the possibility of a threatened self-concept in the face of inconsistent decisions (Aronson 1968, Steele 1988)—are unlikely to fully explain the phenomenon. Although more complex uniquely human mechanisms may be involved in the phenomenon of choice-induced preference changes in humans, primate work demonstrates that such mechanisms are not necessary for this tendency to emerge.

ARE THERE EVOLUTIONARY DISSOCIATIONS IN CHOICE?

The previous section examined how comparative studies can illuminate which specific cognitive mechanisms are necessary for the biases we observe in human decision making. Yet comparisons between different primates can also illuminate the extent to which such biases operate independently. Much debate in judgment and decision making concerns the extent to which a given heuristic is either an independent cognitive strategy or instead a constituent part of other kinds of heuristics. As with neurobiological research, cross-species comparisons can therefore provide critical insight into the cognitive systems supporting decision making by examining when these systems are dissociated. Because distinct systems can evolve independently across species (Barton 1996, 2006; Striedter 2005), examining whether particular components of complex behaviors are coherent from an evolutionary perspective can help address whether those skills are independent. For example, if two economic biases are manifestations of the same basic psychological phenomenon, then they should generally co-occur within a species and covary across species. In contrast, if two biases result from two separate cognitive mechanisms, then it is possible for a species to exhibit one tendency but not the other.

Risk and Ambiguity Aversion

Using this evolutionary dissociations approach, comparative researchers have begun examining whether different sets of biases can be distinguished across species. One important example involves decisions under uncertainty, or situations in which individuals do not know for certain what outcome will follow from their choice (Platt & Huettel 2008). Although uncertainty has been defined in many ways, two manifestations of uncertainty are of major importance in economic theory: risk and ambiguity (Ellsberg 1961, Hsu et al. 2005, Huettel et al. 2006). Risk refers to a form of uncertainty in which there is probabilistic variation in reward outcomes, but the distribution of these different probabilities is known. For example, consider a decision maker who must bet on whether a black ball will be pulled from an urn that she knows contains exactly 50 black balls and 50 red balls. This hypothetical decision maker faces a decision under risk because she is sure that the probability of pulling a black ball from the urn is 50%. In contrast, ambiguity refers to situations in which the probability distribution of different outcomes is unknown—for example, when the decision maker does not know the actual numbers of red versus black balls in the urn. Theoretical models from economics suggest that decision makers should choose between different options based on the value they expect to receive, regardless of whether they are certain of the probability distribution. However studies that disentangle risk and ambiguity suggest that people exhibit aversion to ambiguity above and beyond their aversion of risk (Camerer & Weber 1992). That is, people have a bias against choosing the unknown.

Are risk aversion and ambiguity aversion simply two manifestations of the same psychological phenomenon, reflecting different points on a continuum between perfect certainty and perfect uncertainty? Or do distinct cognitive mechanisms underlie these two kinds of biases? To examine this issue, comparative researchers have examined chimpanzees and bonobos, two closely related species. Several studies to date have shown that chimpanzees are more risk prone than bonobos are (Haun et al. 2011; Heilbronner et al. 2008; Rosati & Hare 2012, 2013). If risk aversion and ambiguity aversion are supported by the same system, then chimpanzees should also be more willing than bonobos to accept ambiguity when making decisions. To test this, Rosati & Hare (2011) presented chimpanzees and bonobos with a decision task in which a certain option was pitted against an alternative across four situations. In three trial types, apes had complete knowledge of the probability of receiving good rewards from the alternative: a 100% chance (good trials), a 0% chance (bad trials), and 50% chance (risk trials). In the fourth trial type, subjects faced ambiguity because they did not know which situation they were in (the apes' view of the potential payoffs was blocked before they chose). The critical question was how the apes responded to the ambiguous option in comparison to the risky option. In fact, apes were less likely to choose the ambiguous option than the risky option, even though the ambiguous option was functionally equivalent to the risky option in terms of its average payoff. Yet a comparison of the two species showed that both chimpanzees and bonobos exhibited similar levels of ambiguity aversion when accounting for their different risk preferences. That is, although bonobos are more risk averse than chimpanzees are, they are not relatively more ambiguity averse. Similarly, although rhesus macaques are risk seeking under many circumstances (McCoy & Platt 2002), they also tend to exhibit ambiguity aversion (Hayden et al. 2010). Taken together, this work suggests that the cognitive system supporting risk preferences and the cognitive system supporting ambiguity preferences may be evolutionarily distinct and that these two heuristics are supported by separate cognitive mechanisms.

Temporal and Effort Discounting

Another area in which dissociations across species have provided insight into the cognitive mechanisms underlying economic biases concerns how individuals make trade-offs between the benefits and costs of acquiring resources. One such trade-off involves temporal costs: People tend to devalue rewards that are delayed. (Frederick et al. 2002, Loewenstein et al. 2003). However, differences in the timing of benefits are just one type of cost that decision makers face—sometimes people pay costs not in terms of time but rather in terms of the amount of effort or work that is required to gain the reward (Rudebeck et al. 2006, Walton et al. 2007). For example, consider a man who is trying to lose weight. The man in question could try to achieve his goal by paying a temporal cost through changes in diet: foregoing the immediate temptation of a piece of cake now for the long-term benefit of health and longevity. But this hypothetical man could also make a different trade-off, accomplishing the same goal through effort costs: He could decide to exercise in order to avoid the temptation of being lazy and having a relaxing afternoon. Although both of these scenarios involve problems of temptation, the first involves a discounting problem presented in terms of time, whereas the other involves a discounting problem with a different currency: effort.

Are effort and temporal costs psychologically similar, or do these different decisions actually involve distinct cognitive systems? Although effort and time costs are often confounded in real-world situations (because effortful behaviors typically also take up time), recent comparative studies have revealed dissociations in terms of how different species treat these costs. Stevens and colleagues (2005a) have compared temporal and effort discounting in cotton-top tamarins (*Saguinus oedipus*) and common marmosets (*Callithrix jacchus*), two closely related New World primates. When faced with delay costs when making temporal discounting choices, marmosets tend to outwait tamarins (Rosati et al. 2006, Stevens et al. 2005a). At first glance, this might suggest that marmosets generally have a higher tolerance for decision costs. However, in another study tamarins and marmosets were presented with a decision in which rewards were displaced in space rather than time (Stevens et al. 2005b). Here, monkeys could either approach a smaller, closer reward or a larger reward that was farther away. In this context, tamarins were more willing than marmosets to travel longer distances to acquire food. That is, although marmosets were more willing to accept temporal costs than tamarins, tamarins were more willing to accept effort costs than marmosets. Indeed, marmosets avoided paying energetic costs to acquire larger rewards, even though the time necessary to travel to those locations was less than the durations they were quite willing to wait in the temporal tasks. This pattern of performance suggests that trade-offs involving delays and trade-offs concerning work effort are dissociable and can evolve independently (see also Kralik & Sampson 2012).

CAN ANIMALS OVERCOME THEIR BIASES?

Thus far we have reviewed cases in which work in nonhuman primates has illuminated the mechanisms underlying decision-making biases in humans. Yet although it is important to understand a particular bias, sometimes it is also critical to be able to intervene on biases once they have been identified. Although it may not always be possible to completely eradicate biases, work from psychology and behavioral economics has increasingly identified situations that encourage people to act against their typical dispositions (Thaler & Sunstein 2008). In this section, we therefore identify contexts that maximize nonhuman primates' abilities to overcome their biases, which we argue can provide new windows on when and why people succumb to their biases. In particular, we focus on several examples of how researchers are beginning to gain insight into the ways that primates solve problems of self-control.

Intertemporal Choice

Intertemporal choices—or decisions that involve trade-offs between the rewards accrued and the time spent waiting for them—are ubiquitous in human decision making. From decisions about dieting and health (as discussed previously) to decisions about saving money for retirement, humans are faced with decisions involving such temporal trade-offs across all domains of life. Decades of research with humans have revealed that people have a preference for immediate gratification: People tend to overvalue rewards they could have right now compared to rewards they must wait to acquire. This overvaluing of immediate rewards sometimes results in economically irrational preference reversals, in which a person's preferred option changes as access to both options is pushed farther into the future. For example, people tend to prefer receiving $10 today to $11 tomorrow but will also prefer receiving $11 in 366 days to $10 in 365 days. This pattern of preferences is inconsistent because the person must wait one extra day for the extra dollar in both cases (Frederick et al. 2002).

Despite the potency of our bias for immediate rewards in many situations, humans are quite skilled at holding out for future gains in some contexts—we can wait weeks or even months for larger rewards in certain situations (Rachlin 2000). Famous work by Mischel and colleagues (1989) has shown that an individual's ability to avoid temptation early in life is predictive of a suite of measures of adult success such as educational attainment, highlighting the importance of this skill for modern humans. Can animals overcome their bias for immediate gratification as well? Some of the first studies to examine this question focused on measuring discounting rates in more distantly related nonprimate species such as birds and rodents (Green et al. 1994, 2004; Mazur 1987; Rachlin 2000; Tobin & Logue 1994). These studies found that animals exhibited hyperbolic discounting patterns with inconsistent preferences, much like humans. However, these studies also observed that birds and rodents discounted the future much more steeply than humans did (for a discussion of differences in hyperbolic discounting rates in humans and other species, see Hwang et al. 2009). For example, when offered a choice between a smaller, sooner reward and a delayed reward that was three times as large, animals preferred the larger rewards when the delay was quite short. However, if the delay was increased—so that animals had to wait in the range of 10 seconds—they switched to preferring the immediate alternative. These results have been used as evidence that nonhumans are even more biased toward pursuing immediate gratification than are humans (although see later sections for a discussion of the potential biological rationality for such seemingly shortsighted decision rules). Indeed, this pattern of results suggests that nonhumans sometimes act as though rewards that are delayed more than a few seconds do not even exist. More broadly, these findings concord with theoretical claims that humans are unique in their ability to engage in prospection and consider the future impact of their actions (McClure et al. 2004; Roberts 2002; Stevens & Stephens 2008; Suddendorf & Corballis 2007a,b).

But is this bias toward the immediate reward true of nonhuman primates as well? Some studies indicate that nonhuman primates may also have difficulties waiting for larger payoffs. For example, when long-tailed macaques (*Macaca fascicularis*) are presented with a delay-adjusting task—in which the delay to receive a larger reward is systematically adjusted over trials until the individual chooses equally between the smaller reward and larger reward that offers three times as much—they are willing to wait approximately 40 seconds for the delayed reward before they switch to preferring the smaller, immediate reward (Tobin et al. 1996). Cotton-top tamarins and common marmosets show even less willingness to wait—they hold out less than 10 to 20 seconds across individuals before succumbing to the temptation of an immediate reward compared with a delayed reward that is three times as large (Stevens et al. 2005a). These studies of monkeys' immediacy bias fit with a long-standing claim that humans may be unique in their capacity to overcome a bias for succumbing to immediate gratification. However, more recent work examining great apes, our closest living relatives, suggests that at least some primates are quite skilled at foregoing immediate temptation in order to reap future riches. For example, Beran and colleagues (Beran 2002, Beran & Evans 2006, Beran et al. 1999) have shown that apes can exhibit high levels of patience in delay-of-gratification tasks if doing so pays off. In one task, Beran and colleagues allowed chimpanzees to decide when to take a reward that accumulated slowly over time: More rewards would continue to accumulate as long as the ape could resist touching them, similar to the tasks developed for use with children by Mischel and colleagues (1970, 1972, 1989). Surprisingly, Beran and colleagues observed that apes were sometimes able to wait upward of 10 minutes to increase their payoffs.

Across the diverse set of tasks devised to study patience in nonhumans (Addessi et al. 2013), apes are consistently more willing to wait than are other primates when tested on matched comparisons. For example, apes outwait monkeys on accumulation tasks (Evans & Beran 2007b, Evans et al. 2012, Parrish et al. 2014, Stevens et al. 2011), exhibit higher indifference points in delay-adjusting tasks compared with a variety of monkey and lemur species (Addessi et al. 2011, Amici et al. 2008, Rosati et al. 2007, Stevens et al. 2005a, Stevens & Muhlhoff 2012, Tobin et al. 1996), and wait longer than monkeys in exchange situations (Dufour et al. 2007; Pelé et al. 2010, 2011; Ramseyer et al. 2006). Even more remarkable, however, is the fact that great apes appear to overcome their biases toward immediate rewards using some of the same self-control strategies as humans do. For example, chimpanzees will spontaneously exhibit self-distraction behaviors, such as looking away from an accumulating reward or playing with toys, in order to refrain from temptation while waiting (Evans & Beran 2007a). These behaviors are quite similar to those of human children, who find that self-control is more difficult when they attend to the arousing motivational qualities of food rewards and who are more successful when they are able to distract themselves (Mischel & Ebbesen 1970, Mischel et al. 1972). Further converging evidence that apes are capable of thinking about their future selves comes from planning studies in which apes must anticipate that saving a tool now will allow them to use it in the future. Indeed, some apes successfully plan to use a tool as long as 14 hours in advance (Mucalhy & Call 2006; see also Osvath & Osvath 2008). Overall, these results suggest that humans and other great apes may share similar capacities to overcome immediate temptation and to act in ways that benefit their future selves as well as similar strategies for doing so.

Self-Control and Abstract Rewards

Intertemporal choices present a conflict between one's prepotent desire for immediate satisfaction and the goal of maximizing one's total payoffs. Viewed in this light, the bias toward immediate rewards may be just one of a larger group of self-control biases that individuals must overcome in order to make effective decisions. Are nonhuman primates able to overcome biases of self-control more generally, and what strategies do they use to do so? To examine this, comparative psychologists have developed several nonverbal tasks aimed specifically at exploring whether primates can overcome their prepotent biases. One of the most famous of these methods is known as the reverse contingency task—a situation that requires primates to inhibit their bias to approach the best of possible rewards. In one version of this task, Boysen and colleagues (Boysen & Berntson 1995; Boysen et al. 1996, 1999) gave chimpanzees a choice between different sizes of foods. The trick was that chimpanzees had to point to the reward they did not want in order to get the reward they did want. Chimpanzees therefore could only succeed in this task if they found ways to inhibit their prepotent response to point at the larger reward. In their initial study, Boysen and colleagues found that chimpanzees were unable to overcome their bias to reach for the best reward, thus failing to get the best food in this task. Since then, researchers have assessed the performance of numerous primate species on this task, and their results suggest that this bias to reach for a preferred reward is one that is quite difficult for most primate species to overcome (Anderson et al. 2000, Genty et al. 2004, Kralik 2005, Shifferman 2009, Uher & Call 2008).

Are there psychological strategies that allow primates to overcome their initial biases and maximize their rewards in the reverse contingency task? The chimpanzee studies by Boysen and colleagues suggest one answer: Although chimpanzees showed poor performance when making decisions about food, the same chimpanzees succeeded when faced with symbolic representations of the rewards. For example, chimpanzees that had been previously trained to comprehend Arabic numerals were tested on the reverse contingency task both when faced with real pieces of food and when choosing between Arabic numerals (that symbolized different amounts of food). When tested on the symbolic version of the task, chimpanzees were better able to control their initial bias to point toward the visibly bigger option (Boysen & Berntson 1995; Boysen et al. 1996, 1999). More recent studies have shown that other primate species also improve on reverse contingency tasks when they do not have immediate visual access to the rewards. For example, primates are more successful when they have learned that certain cues (such as color) predict different amounts of food (Anderson et al. 2000, Genty et al. 2004, Kralik 2005, Uher & Call 2008, Vlamings et al. 2006) or when they make choices about food rewards symbolized by different tokens (Addessi & Rossi 2011). Together, these tasks suggest that primates can succeed in inhibiting their prepotent response biases when they are not directly confronted with visible food rewards. In this sense, other primates perform much like the children in Mischel and colleagues' studies (Mischel & Ebbesen 1970; Mischel et al. 1972, 1989): Both children and primates can overcome their biases by diverting their attention from the salient aspects of the rewards in front of them.

Does the success of primates at using symbols to solve reverse contingency tasks also translate into improvements in their ability to delay gratification more generally? Here results are less conclusive. For example, Evans and colleagues (2012) presented chimpanzees and capuchin moneys with the delay-of-gratification task described previously. In their task, chimpanzees and capuchins were tested with either accumulating food or with accumulating symbolic tokens (which could then be traded for food). Chimpanzees exhibited a similar ability to wait regardless of which item was accumulating, but capuchins waited significantly longer when tested with food than when tested with tokens. Similarly, capuchins were somewhat more willing to wait for food rewards than various types of tokens in a temporal choice task (Addessi et al. 2014). Overall, these results suggest that although abstract rewards can sometimes allow primates to overcome their prepotent biases, they may not improve primates' self-control in all contexts. These results also highlight a critical difference between the methods used to test decision-making biases in humans and those used to test other primates: Whereas human tasks typically require participants to make choices involving abstract rewards such as money, nonhuman studies typically require that participants make choices about biologically relevant rewards such as food, which may involve different motivations or reward salience. Indeed, these differences in reward type could be one reason why humans seem better able than other primates to inhibit their prepotent responses in many contexts.

Given that primates sometimes show improved self-control when making decisions about abstract rewards (such as in the reverse contingency task) but more inconsistent responses in other situations (such as when foregoing their bias toward an immediate reward), this raises an important question: Do nonhuman primates represent abstract rewards such as tokens in the same way as humans represent money? Early comparative research illustrated that primates can learn to treat tokens as rewards (Cowles 1937, Kelleher 1957, Wolfe 1936), and more recent work has shown that primates can recognize that different tokens can take different values as well as quantitatively compare them (Addessi et al. 2007). However, important differences exist between how primates treat these abstract tokens and how humans represent money (for reviews of the psychology of money in humans, see Lea & Webley 2006; Vohs et al. 2006, 2008). For example, humans recognize that money can be stored and that it holds its value over time, but to date there is little evidence that primates can represent tokens as a storable resource (but see Sousa & Matsuzawa 2001). Moreover, money facilitates efficient trades between individuals who differ in the goods that they have and the goods they want (Davies 2002), but primates seem to be unable to engage in more human-like exchange. For example, chimpanzees prefer a high-value token that can be used to acquire a more preferred food over a low-value token that can be used to acquire a less-preferred food—even when the preferred food is unavailable and the high-value token therefore is worthless (Brosnan & de Waal 2004, 2005). There is also limited evidence that primates will exchange tokens with other conspecifics when it is beneficial to do so. Rather, nonhuman primate exchange seems highly dependent on the presence of human experimenters (Brosnan & Beran 2009, Dufour et al. 2009, Parrish et al. 2013, Pelé et al. 2009, Tanaka & Yamamoto 2009). Together, these findings suggest that primates do not represent tokens in the rich and flexible way that humans represent money. Consequently, abstract rewards may be a less potent solution for overcoming self-control biases in animals than in humans.

ARE SOME "IRRATIONAL" BIASES ADAPTIVE?

From the review presented above, it is clear that nonhuman primates exhibit many of the same economic biases that are seen in humans; various other species are loss averse and reference dependent, exhibit endowment effects and peak-end biases, and sometimes fall prey to the availability of small but immediate rewards. Yet these widely shared choice patterns are also thought to be irrational by many psychologists and economists (for a discussion of this issue, see the debate between Gigerenzer & Goldstein 1996 and Kahneman & Tversky 1996). The question of why individuals show these so-called irrational biases is difficult to answer when considering just the human species, but it becomes even more puzzling when viewed from an evolutionary perspective. Why would such error-prone decision-making capacities evolve and be maintained across numerous species, including our own?

We argue that the answer to this question lies in thinking more critically about whether these decision-making biases actually constitute errors or irrationalities in the first place. Humans and animals are thought to exhibit a bias when their patterns of decision making violate principles of economic rationality—that is, when their choices do no concord with theoretic axioms defining how an ideal decision maker should behave to maximize utility. But these same patterns of decision making may actually accord with principles of biological rationality. For example, individuals may act in a way that maximizes fitness from the perspective of natural selection, or they may use strategies that display good fit with the environment in which they evolved. Considering the biological consequences, or functions, of different choice strategies can therefore illuminate psychological investigations into the mechanisms supporting these behaviors.

Redefining Optimality

Economics and biology have a core commonality: Both fields assume that optimal behavior should maximize some currency (Hammerstein & Hagen 2005). Economic theory consists of a series of mathematical axioms describing how people should act to maximize their personal utility or goodness (von Neumann & Morgenstern 1947). According to rational choice theory, one important component of maximizing utility is consistency: If a decision maker has a certain preference in one context, then that individual should exhibit this same preference in another context (Shafir et al. 2002; Waite 2001a,b). Thus, many of the biases discussed previously violate rational choice theory because decision makers do not have consistent preferences. For example, humans and capuchins prefer to play it safe for gains, but gamble for losses—even though the utility (as indexed by the amount of food or money received) in both contexts seems identical (Lakshminarayanan et al. 2011, Tversky & Kahneman 1981). Similarly, humans and other animals have a preference for immediacy, but this preference reverses when all possible alternatives are pushed into the future (for example, Frederick et al. 2002).

Evolutionary theory also assumes that organisms try to maximize a currency. However, the important currency for biological analysis is not an animal's (subjective) utility but rather its reproductive fitness. Thus, biological models focus on how choices influence an animal's reproductive success over the life span. Importantly, natural selection does not need to prioritize consistency in the way rational choice theory does. Fitness is not an intrinsic characteristic of a particular individual—it is a measure of success relative to other variants in the population. Moreover, from the perspective of natural selection, it is critical to examine the actual consequences of different strategies across contexts rather than whether such strategies are internally consistent. Indeed, sometimes it may be biologically rational for organisms to express inconsistent preferences if those preferences work to maximize fitness. In this way, inconsistent "biased" preferences can be optimal in the sense that they produce the best-case behavior from a biological perspective (Kacelnik 2006, Model. Anim. Decis. Group et al. 2014). Theoretical models in behavioral ecology also account for the real-world complexity seen in natural environments and support the claim that decision-making strategies should be sensitive to contextual information across many contexts (Houston 1997; Houston & McNamara 1999; Houston et al. 2007a,b; Rosati & Stevens 2009).

When these context-sensitive models are tested in experimental studies, behavioral ecologists have found that a variety of bird and insect species exhibit relevant shifts in their choices depending on the context (Kacelnik & Marsh 2002, Pompilio et al. 2006, Schuck-Paim & Kacelnik 2002, Schuck-Paim et al. 2004). One important piece of contextual information identified by behavioral ecologists (but often absent from economic models) is energetic state or satiation level (Pompilio et al. 2006, Schuck-Paim et al. 2004). Animals sometimes show state-dependent preferences because the impact of energetic increases on an individual's fitness is not linear: A given unit of food has a large impact on individuals in an energetically low state, but there are diminishing returns when the individual is already in a high state. Thus, many of the seemingly irrational inconsistent preferences that animals (and humans) exhibit—such as risk preferences that change across contexts—might actually be fitness maximizing from a biological optimality perspective.

The biological view also allows for a different explanation of primates' decision-making biases: Some biases may not be optimal per se but may instead represent the best possible solution given the other sorts of computational limitations real organisms must face. Organisms often lack the time and information-processing capacity necessary to determine perfect mathematically accurate solutions to different decision problems. Consequently, it could make sense for individuals to use less computationally intensive heuristics that occasionally get the answer wrong but mostly get it right (Gigerenzer & Selten 2001, Gigerenzer et al. 1999, Tversky 1969). That is, biased decision-making mechanisms might not be perfect but still might be good enough to work properly in most real-world circumstances given the environments animals typically face. Under this view, biased heuristics still cause "irrational" decisions, as organisms may not be making choices in a way that a decision maker with perfect knowledge and infinite time might. However, such decision rules are still the best solution that natural selection can achieve given constraints.

This biological view has some important implications for evaluating why such decision-making biases may have evolved in the first place. Consider the example of the bias toward immediate rewards that we discussed previously. Many studies of self-control suggest that organisms maximize their utility overall by acquiring the most possible rewards, and thus failures to do so represent an irrational bias for immediate gratification. However, the pitfalls of always waiting for the largest reward are clear when taken to the extreme. Consider the situation of a foraging animal choosing what food resource to pursue. Holding out for a larger, delayed reward might be a good strategy if it only involves giving up a few minutes of time, but foregoing immediate temptation might not be such a good idea if it requires waiting years for the payoff. In such extreme cases, decision makers may die of starvation waiting for the windfall. As this example suggests, a biological perspective indicates that individuals should not try to maximize the amounts of rewards they acquire over their entire life—extreme patience risks the possibility of huge windfalls that are delivered too late to be of use. A better strategy might be to maximize one's own rate of consumption over some more biologically relevant interval. This means that organisms may sometimes prefer immediacy for biologically rational reasons (Fawcett et al. 2012, Kacelnik 2003, Stephens & Anderson 2001, Stephens et al. 2004). This view also predicts that individuals might ignore certain temporal periods when making decisions because those periods do not factor into their biologically relevant rate-maximization calculations (Bateson & Kacelnik 1996, Blanchard et al. 2013, Rosati et al. 2006, Stephens & McLinn 2003). Indeed, humans also seem to exhibit temporal strategies that allow them to maximize rate of gain by preferring immediate options when it is optimal to do so (Schweighofer et al. 2006). As this example suggests, the optimal biological solution to problems involving temporal trade-offs does not necessarily accord with the solution that economic choice models predict is the most rational.

Biases in Comparative Perspective

Assessing the biological rationality of decision making also highlights the importance of understanding the context in which particular choice strategies are used. One such approach for assessing the relationship between decision making and environments is the comparative method, one of the powerful tools in evolutionary biology. The comparative method can help identify the influence of natural selection and assess the potential adaptive value of different traits by relating the traits of different organisms to differences in their ecological or social niche (Clutton-Brock & Harvey 1979, Endler 1986, Mayr 1982). In terms of cognitive traits such as decision-making strategies, this comparative method involves relating variation in choice strategies between species to differences in those species' natural history (MacLean et al. 2012). Specifically, researchers can test whether different animals show specific choice biases that are tailored to their particular environments and social problems (sometimes referred to as ecological rationality).

Is there evidence that primates' decision-making biases vary with their socioecology? Increasing evidence suggests that differences in species' biases might map on to differences in their ecology. To take one example, different species show variation in how susceptible they are to the temptation of immediate rewards. As described previously, two species of New World primates—cotton-top tamarins and common marmosets—show different patterns of choice in temporal and spatial discounting. Whereas marmosets are more willing to wait out temporal delays to acquire larger rewards, tamarins are more willing to travel longer distances (Rosati et al. 2006; Stevens et al. 2005a,b). Importantly, tamarins and marmosets are closely related species that have similar body sizes, live in similar pair-bonded groups with cooperative breeding, and even consume similar types of foods. But there is one major difference in these two species' ecologies: The diets of these species vary in their dependence on gum versus insects. Marmosets are obligate gummivores with specialized dental and gut adaptations to allow them to gouge holes in trees so they can access the gum or sap inside after it leaks out (Stevenson & Rylands 1988). Thus, marmosets spend much of their time waiting for sap to exude from trees. Tamarins, in contrast, only feed on gum opportunistically. Instead, tamarins spend more time ranging in order to locate fruit and insects—more ephemeral resources. The differences in these species' decision-making strategies that we described previously now make more sense in light of the two species' feeding ecologies: Marmosets might need greater tolerance for temporal delays in order to acquire gum, whereas tamarins might need the motivation to travel large distances to find their most important food resources. That is, differences in these species' typical diet may drive the differences seen in their respective decision-making biases.

Studies of ape decision making also support the hypothesis that differences in biases may be related to a species' natural history. Chimpanzees and bonobos—our two closest living relatives—diverged from each other less than one million years ago (Won & Hey 2005). Despite their evolutionary relatedness, these two species differ in their feeding ecology (Kano 1992; Malenky & Wrangham 1993; White 1989, 1998; White & Wrangham 1988; Wrangham & Peterson 1996). Relative to bonobos, chimpanzees are thought to live in environments that exhibit more risk (as evidenced by more seasonal variation and a greater dependence on risky hunting) and more temporal costs (as evidenced by longer search times between patchy resources and their use of temporally costly extractive foraging techniques). Moreover, some researchers have argued that these ecological changes account for differences in these species' social behaviors (Hare et al. 2012, Parish 1996, Wrangham 2000, Wrangham & Peterson 1996, Wrangham & Pilbeam 2001). In terms of decision making, these ecological data further predict that chimpanzees and bonobos should differ in their willingness to accept risk and put up with temporal costs to acquire rewards. Indeed, increasing evidence indicates that although chimpanzees and bonobos generally show quite similar patterns of cognitive skills (Herrmann et al. 2010), they exhibit a suite of differences in their decision-making biases. In particular, chimpanzees are more risk seeking and more patient than bonobos are (Haun et al. 2011; Heilbronner et al. 2008; Rosati & Hare 2012, 2013; Rosati et al. 2007), which concords with the greater variation and temporal delays chimpanzees are thought to face in the wild. Taken together, these studies indicate that the different economic biases seen in different species may in fact be tailored to their socioecological context (see also Stevens 2014). As such, comparative studies suggest that what appear to be violations of economic "rationality" might actually reflect rational responses to a given species' natural history.

CONCLUSIONS

The goal of this review was to examine the potential commonalities—and differences—between human and nonhuman primate decision making. We first reviewed evidence concerning whether nonhuman primates exhibit the sort of heuristics and biases readily observed in human choice behavior. We have argued that many primate species show biases that are qualitatively similar to those shown by humans in classic judgment and decision-making studies. Indeed, biases ranging from framing, choice-induced preference changes, peak-end heuristics, the endowment effect, and ambiguity aversion all seem to affect the choices of our primate relatives in much the same way that they affect human choices. That is, many of the classic biases that fill textbooks are not solely the hallmark of human decisions but rather are widely shared with other primate species.

In exposing these commonalities between human and nonhuman choice biases, we also hope to have provided new insight into the nature of human decision biases as well as how these biases got to be there in the first place. First, we have argued that understanding patterns of decision making in other primates can help identify the sorts of cognitive mechanisms that underlie human choice biases. Indeed, we have argued that comparative studies may be especially useful in constraining hypotheses about the types of psychological capacities that likely underlie behavioral biases in humans. Second, we have explored how comparative studies of related primate species can provide new insight into the mechanisms underlying human decision making by revealing evolutionary dissociations in biases. That is, comparative studies can disentangle whether some decision biases are manifestations of a single cognitive mechanism or whether they instead depend on distinct mechanisms that can vary independently across species. Third, we examined the contexts that allow some primates to overcome their biases, particularly in the domain of biases related to immediate gratification and self-control. Finally, we examined how evolutionary theory provides insight into the origins of decision biases as well as how comparative studies that relate decision strategies to particular ecological contexts can provide new insights into the biological function of these strategies. In doing so, we have questioned whether it is always appropriate to call these strategies irrational. Indeed, increasing evidence suggests that many biases that look irrational (from the perspective of rational choice theory) may be quite rational from the perspective of biology.

Although more work remains to be done in terms of understanding the phylogenetic origins of human judgment and decision-making biases, we hope this review has demonstrated the unique way that the comparative approach can inform our understanding of the psychology underlying human choice biases. We anticipate that understanding the biased decisions of some of our closest relatives can continue to provide an important empirical tool for judgment and decision-making researchers. By understanding how other species' choices go awry, we may be better able to both understand and improve the decisions of our own species.

SUMMARY POINTS

1. Nonhuman primates exhibit many human-like economic biases, including framing effects, peak-end effects, endowment effects, and a preference for immediacy.

2. Comparative research can pinpoint which aspects of human decision making are widely shared with other primates or are unique to our species.
3. Other species exhibit similarities and differences relative to humans in both their experiences and cognitive abilities, so primate studies can disentangle the psychological mechanisms that generate different biases.
4. A comparative perspective on decision making can illuminate whether some human economic biases are biologically rational.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Daeyeol Lee and the members of the Yale Comparative Cognition Laboratory for helpful comments and discussion on an earlier version of the manuscript. L.R.S. was supported by a McDonnell Scholar Award and Yale University. A.G.R. was supported by an NIH grant (R01MH096875).

LITERATURE CITED

Abe H, Lee D. 2011. Distributed coding of actual and hypothetical outcomes in the orbital and dorsolateral prefrontal cortex. *Neuron* 70:731–41

Addessi E, Bellagamba F, Delfino A, De Petrillo F, Focaroli V, et al. 2014. Waiting by mistake: Symbolic representation of rewards modulated intertemporal choice in capuchin monkeys, preschool children, and adult humans. *Cognition* 130:428–41

Addessi E, Crescimbene L, Visalberghi E. 2007. Do capuchin monkeys (*Cebus apella*) use tokens as symbols? *Proc. R. Soc. B* 274:2579–85

Addessi E, Paglieri F, Beran M, Evans T, Macchitella L, et al. 2013. Delay choice versus delay maintenance: different measures of delayed gratification in capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* 127:392–98

Addessi E, Paglieri F, Focaroli V. 2011. The ecological rationality of delay tolerance: insights from capuchin monkeys. *Cognition* 119:142–47

Addessi E, Rossi S. 2011. Tokens improve capuchin performance in the reverse-reward contingency task. *Proc. R. Soc. B* 278:849–54

Amici F, Aureli F, Call J. 2008. Fission-fusion dynamics, behavioral flexibility and inhibitory control in primates. *Curr. Biol.* 18:1415–19

Anderson JR, Awazu S, Fujita K. 2000. Can squirrel monkeys (*Saimiri sciureus*) learn self-control? A study using food array selection tests and reverse-reward contingency. *J. Exp. Psychol.: Anim. Behav. Process.* 26:87–97

Aronson E. 1968. Dissonance theory: progress and problems. In *Theories of Cognitive Consistency: A Sourcebook*, ed. RP Abelson, WJ McGuire, TM Newcomb, MJ Rosenberg, PH Tannenbaum, pp. 5–27. Chicago: Rand McNally

Barton RA. 1996. Neocortex size and behavioral ecology in primates. *Proc. R. Soc. B* 263:173–77

Barton RA. 2006. Primate brain evolution: integrating comparative, neurophysiological, and ethological data. *Evol. Anthropol.* 15:224–36

Bateson M, Kacelnik A. 1996. Rate currencies and the foraging starling: the fallacy of the averages revisited. *Behav. Ecol.* 7:341–52

Shows that monkeys can learn that tokens are symbols of quantity and can flexibly compare the value of different tokens.

Bautista LM, Tinbergen J, Kacelnik A. 2001. To walk or to fly? How birds choose among foraging modes. *Proc. Natl. Acad. Sci. USA* 98:1089–94

Beggan JK. 1992. On the social nature of nonsocial perception: the mere ownership effect. *J. Personal. Soc. Psychol.* 62:229–37

Belk RW. 1988. Possessions and the extended self. *J. Consum. Res.* 15:139–68

Belk RW. 1991. The ineluctable mysteries of possessions. *J. Soc. Behav. Personal.* 6:17–55

Bell DE. 1982. Regret in decision-making under uncertainty. *Oper. Res.* 30:961–81

Bem DJ. 1967. Self-perception: an alternative interpretation of cognitive dissonance phenomena. *Psychol. Rev.* 74:183–200

Beran MJ. 2002. Maintenance of self-imposed delay of gratification by four chimpanzees (*Pan troglodytes*) and an orangutan (*Pongo pygmaeus*). *J. Gen. Psychol.* 129:49–66

Beran MJ, Evans TA. 2006. Maintenance of delay of gratification by four chimpanzees (*Pan troglodytes*): the effects of delayed reward visibility, experimenter presence, and extended delay intervals. *Behav. Process.* 73:315–24

Beran MJ, Savage-Rumbaugh ES, Pate JL, Rumbauh DM. 1999. Delay of gratification in chimpanzees (*Pan troglodytes*). *Dev. Psychobiol.* 34:119–27

Blanchard TC, Pearson JM, Hayden BY. 2013. Postreward delays and systematic biases in measures of animal temporal discounting. *Proc. Natl. Acad. Sci. USA* 110:15491–96

Blanchard TC, Wolfe LS, Vlaev I, Winston JS, Hayden BY. 2014. Biases in preferences for sequences of outcomes in monkeys. *Cognition* 130:289–99

Shows that monkeys exhibit peak-end biases by over-weighting the most extreme event and later-occurring events in reward sequences.

Boysen ST, Berntson GG. 1995. Responses to quantity: perceptual versus cognitive mechanisms in chimpanzees (*Pan troglodytes*). *J. Exp. Psychol.: Anim. Behav. Process.* 21:82–86

Boysen ST, Berntson GG, Hannan MB, Cacioppo JT. 1996. Quantity-based interference and symbolic representations in chimpanzees (*Pan troglodytes*). *J. Exp. Psychol.: Anim. Behav. Process.* 22:76–86

Boysen ST, Mukobi KL, Berntson GG. 1999. Overcoming response bias using symbolic representations of number by chimpanzees (*Pan troglodytes*). *Anim. Learn. Behav.* 27:229–35

Brehm JW. 1956. Postdecision changes in the desirability of alternatives. *J. Abnorm. Soc. Psychol.* 52:384–89

Brosnan SF, Beran MJ. 2009. Trading behavior between conspecifics in chimpanzees, *Pan troglodytes*. *J. Comp. Psychol.* 123:181–94

Brosnan SF, de Waal FBM. 2004. A concept of value during experimental exchange in brown capuchin monkeys, *Cebus apella*. *Folia Primatol.* 75:317–30

Brosnan SF, de Waal FBM. 2005. Responses to a simple barter task in chimpanzees, *Pan troglodytes*. *Primates* 46:173–82

Brosnan SF, Grady MF, Lambeth SP, Schapiro SJ, Beran MJ. 2008. Chimpanzee autarky. *PLOS ONE* 3:e1518

Brosnan SF, Jones OD, Gardner M, Lambeth SP, Schapiro SJ. 2012. Evolution and the expression of biases: situational value changes the endowment effect in chimpanzees. *Evol. Hum. Behav.* 33:378–86

Brosnan SF, Jones OD, Lambeth SP, Mareno MC, Richardson AS, Schapiro SJ. 2007. Endowment effects in chimpanzees. *Curr. Biol.* 17:1–4

First demonstration that chimpanzees exhibit an endowment effect, preferring items they possess to items they can acquire through exchange.

Brunner D. 1999. Preference for sequences of rewards: further tests of a parallel discounting model. *Behav. Process.* 45:87–99

Brunner D, Gibbon J. 1995. Value of food aggregates: parallel versus serial discounting. *Anim. Behav.* 50:1627–34

Byrne RMJ. 2002. Mental models and counterfactual thoughts about what might have been. *Trends Cogn. Sci.* 6:426–31

Camerer C, Weber M. 1992. Recent developments in modeling preferences: uncertainty and ambiguity. *J. Risk Uncertain.* 5:325–70

Caraco T. 1981. Risk sensitivity and foraging. *Ecology* 62:527–31

Chen MK, Lakshminarayanan V, Santos LR. 2006. How basic are behavioral biases? Evidence from capuchin monkey trading behavior. *J. Polit. Econ.* 114:517–37

First demonstration that other primates exhibit framing effects and loss aversion.

Chen MK, Risen JL. 2009. Is choice a reliable predictor of choice? A comment on Sagarin and Skowronski. *J. Exp. Soc. Psychol.* 45:425–27

Clutton-Brock TH, Harvey PH. 1979. Comparison and adaptation. *Proc. R. Soc. B* 205:547–65

Coricelli G, Dolan RJ, Sirigu A. 2007. Brain, emotion, and decision making: the paradigmatic example of regret. *Trends Cogn. Sci.* 11:258–65

Cowles JT. 1937. Food-tokens as incentives for learning by chimpanzees. *Comp. Psychol. Monogr.* 14(5):1–96

Danziger S, Levav J, Avnaim-Pessoa L. 2011. Extraneous factors in judicial decisions. *Proc. Natl. Acad. Sci. USA* 108:6889–92

Davies G. 2002. *A History of Money: From Ancient Times to the Present Day*. Cardiff, UK: Univ. Wales Press

De Martino B, Kumaran D, Seymour B, Dolan RJ. 2006. Frames, biases, and rational decision-making in the human brain. *Science* 313:684–87

Drayton LA, Brosnan SF, Carrigan J, Stoinski TS. 2013. Endowment effect in gorillas (*Gorilla gorilla*). *J. Comp. Psychol.* 127:365–69

Dufour V, Pelé M, Neumann M, Thierry B, Call J. 2009. Calculated reciprocity after all: computation behind token transfers in orangutans. *Biol. Lett.* 5:172–75

Dufour V, Pelé M, Sterck EHM, Thierry B. 2007. Chimpanzee (*Pan troglodytes*) anticipation of food return: coping with waiting time in an exchange task. *J. Comp. Psychol.* 121:145–55

Egan L, Bloom P, Santos LR. 2010. Choice-induced preferences in the absence of choice: evidence from a blind two-choice paradigm with young children and capuchin monkeys. *J. Exp. Soc. Psychol.* 46:204–7

Egan L, Santos LR, Bloom P. 2007. The origins of cognitive dissonance: evidence from children and monkeys. *Psychol. Sci.* 18:978–83

First demonstration that capuchins exhibit choice-induced preference changes, devaluing options they previously chose against.

Ellsberg D. 1961. Risk, ambiguity, and the Savage axioms. *Q. J. Econ.* 75:643–69

Endler JA. 1986. *Natural Selection in the Wild*. Princeton, NJ: Princeton Univ. Press

Evans TA, Beran MJ. 2007a. Chimpanzees use self-distraction to cope with impulsivity. *Biol. Lett.* 3:599–602

Shows that chimpanzees, like human children, are better able to delay gratification when they can divert attention from the temptation of immediate rewards.

Evans TA, Beran MJ. 2007b. Delay of gratification and delayed maintenance by rhesus macaques (*Macaca mulatta*). *J. Gen. Psychol.* 134:199–216

Evans TA, Beran MJ, Paglieri F, Addessi E. 2012. Delaying gratification for food and tokens in capuchin monkeys (*Cebus apella*) and chimpanzees (*Pan troglodytes*): When quantity is salient, symbolic stimuli do not improve performance. *Anim. Cogn.* 15:539–48

Fawcett TW, McNamara JM, Houston HI. 2012. When is it adaptive to be patient? A general framework for evaluating delayed rewards. *Behav. Process.* 89:128–36

Flemming TM, Jones OD, Mayo L, Stoinski T, Brosnan SF. 2012. The endowment effect in orangutans. *Int. J. Comp. Psychol.* 25:285–98

Franciosi R, Kujal P, Michelitsch R, Smith V, Deng G. 1996. Experimental tests of the endowment effect. *J. Econ. Behav. Organ.* 30:213–26

Frederick S, Loewenstein G, O'Donoghue T. 2002. Time discounting and time preference: a critical review. *J. Econ. Lit.* 2:351–401

Genesove D, Mayer C. 2001. Loss aversion and seller behavior: evidence from the housing market. *Q. J. Econ.* 116:1233–60

Genty E, Palmier C, Roeder JJ. 2004. Learning to suppress responses to the larger of two rewards in two species of lemurs, *Eulemur fulvus* and *E. macaco*. *Anim. Behav.* 67:925–32

Gigerenzer G, Goldstein DG. 1996. Reasoning the fast and frugal way: models of bounded rationality. *Psychol. Rev.* 103:650–69

Gigerenzer G, Selten R. 2001. *Bounded Rationality: The Adaptive Toolbox*. Cambridge, MA: MIT Press

Gigerenzer G, Todd PM, ABC Res. Group. 1999. *Simple Heuristics That Make Us Smart.* Oxford, UK: Oxford Univ. Press

Green L, Fristoe N, Myerson J. 1994. Temporal discounting and preference reversals in choice between delayed outcomes. *Psychon. Bull. Rev.* 1:383–89

Green L, Myerson J, Holt DD, Slevin JR, Estle SJ. 2004. Discounting of delayed food rewards in pigeons and rats: Is there a magnitude effect? *J. Exp. Anal. Behav.* 81:39–50

Hammerstein P, Hagen EH. 2005. The second wave of evolutionary economics in biology. *Trends Ecol. Evol.* 20:604–9

Harbaugh WT, Krause K. 2002. Risk attitudes of children and adults: choices over small and large probability gains and losses. *Exp. Econ.* 5:53–84

Hare B. 2011. From hominoid to hominid mind: What changed and why? *Annu. Rev. Anthropol.* 40:293–309

Hare B, Wobber V, Wrangam R. 2012. The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Anim. Behav.* 83:573–85

Harmon-Jones E, Mills J. 1999. *Cognitive Dissonance: Progress on a Pivotal Theory in Social Psychology*. Washington, DC: Am. Psychol. Assoc.

Haun DBM, Nawroth C, Call J. 2011. Great apes' risk-taking strategies in a decision making task. *PLOS ONE* 6:e28801

Hayden BY, Heilbronner SR, Platt ML. 2010. Ambiguity aversion in rhesus macaques. *Front. Neurosci.* 4:166

Hayden BY, Pearson JM, Platt ML. 2009. Fictive reward signals in the anterior cingulate cortex. *Science* 324:948–50

Heilbronner SH, Rosati AG, Hare B, Hauser MD. 2008. A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzees and bonobos. *Biol. Lett.* 4:246–49

Herrmann E, Call J, Hernandez-Lloreda MV, Hare B, Tomasello M. 2007. Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science* 317:1360–66

Herrmann E, Hare B, Call J, Tomasello M. 2010. Differences in the cognitive skills of bonobos and chimpanzees. *PLOS ONE* 5:e12438

Hill K, Barton M, Hurtado M. 2009. The emergence of human uniqueness: characters underlying behavioral modernity. *Evol. Anthropol.* 18:187–200

Houston AI. 1997. Natural selection and context-dependent values. *Proc. R. Soc. B* 264:1539–41

Houston AI, McNamara JM. 1999. *Models of Adaptive Behaviour: An Approach Based on State*. Cambridge, UK: Cambridge Univ. Press

Houston AI, McNamara JM, Steer MD. 2007a. Do we expect natural selection to produce rational behaviour? *Philos. Trans. R. Soc. B* 362:1531–43

Models the evolutionary consequences of decision making, showing that biologically optimal rules can produce economically "irrational" biases.

Houston AI, McNamara JM, Steer MD. 2007b. Violations of transitivity under fitness maximization. *Biol. Lett.* 3:365–67

Hsu M, Bhatt M, Adolphs R, Tranel D, Camerer C. 2005. Neural systems responding to degrees of uncertainty in human decision-making. *Science* 310:1680–83

Huettel SA, Stowe JC, Gordon EM, Warner BT, Platt ML. 2006. Neural signatures of economic preferences for risk and ambiguity. *Neuron* 49:765–75

Hwang J, Kim S, Lee D. 2009. Temporal discounting and inter-temporal choice in rhesus monkeys. *Front. Behav. Neurosci.* 3:9

Johnson EJ, Haubl G, Keinan A. 2007. Aspects of endowment: a query theory account of loss aversion for simple objects. *J. Exp. Psychol.: Learn. Mem. Cogn.* 33:461–74

Johnson EJ, Hershey J, Meszaros J, Kunreuther H. 1993. Framing, probability distortions, and insurance decisions. *J. Risk Uncertain.* 7:35–51

Kacelnik A. 2003. The evolution of patience. In *Time and Decision: Economics and Psychological Perspectives on Intertemporal Choice*, ed. G Loewenstein, D Read, R Baumeister, pp. 115–38. New York: Russell Sage Found.

Kacelnik A. 2006. Meanings of rationality. In *Rational Animals?*, ed. S Hurley, M Nudds, pp. 87–106. Oxford, UK: Oxford Univ. Press

Kacelnik A, Bateson M. 1997. Risk-sensitivity: crossroads for theories of decision making. *Trends Cogn. Sci.* 1:304–9

Kacelnik A, Marsh B. 2002. Cost can increase preference in starlings. *Anim. Behav.* 63:245–50

Kahneman D. 2011. *Thinking, Fast and Slow*. New York: Farrar, Straus & Giroux

Kahneman D, Fredrickson BL, Schreiber CA, Redelmeier DA. 1993. When more pain is preferred to less. *Psychol. Sci.* 4:401–5

Kahneman D, Knetsch J, Thaler R. 1990. Experimental tests of the endowment effect and the Coase theorem. *J. Polit. Econ.* 98:1325–48

Kahneman D, Knetsch JL, Thaler RH. 1991. Anomalies: the endowment effect, loss aversion, and status quo bias. *J. Econ. Perspect.* 5:193–206

Kahneman D, Tversky A. 1979. Prospect theory: an analysis of decision under risk. *Econometrica* 47:263–92

Kahneman D, Tversky A. 1996. On the reality of cognitive illusions. *Psychol. Rev.* 103:582–91

Kahneman D, Tversky A. 2000. *Choices, Values, and Frames*. Cambridge, UK: Cambridge Univ. Press

Kamil AC, Krebs JR, Pulliam HR. 1987. *Foraging Behavior*. New York: Plenum

Kanngiesser P, Santos LR, Hood BM, Call J. 2011. The limits of endowment effects in great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*). *J. Comp. Psychol.* 125:436–45

Kano T. 1992. *The Last Ape: Pygmy Chimpanzee Behavior and Ecology*. Stanford, CA: Stanford Univ. Press

Kelleher RT. 1957. Conditioned reinforcement in chimpanzees. *J. Comp. Physiol. Psychol.* 50:571–75

Kralik JD. 2005. Inhibitory control and response selection in problem solving: how cotton-top tamarins (*Saguinus oedipus*) overcome a bias for selecting the larger quantity of food. *J. Comp. Psychol.* 119:78–89

Kralik JD, Sampson WWL. 2012. A fruit in hand is worth many more in the bush: steep spatial discounting by free-ranging rhesus macaques (*Macaca mulatta*). *Behav. Process.* 89:197–202

Krebs JR, Davies NB. 1978. *Behavioural Ecology: An Evolutionary Approach*. Oxford, UK: Blackwell Sci.

Lakshminarayanan V, Chen MK, Santos LR. 2008. Endowment effect in capuchin monkeys. *Philos. Trans. R. Soc. B* 363:3837–44

Lakshminarayanan VR, Chen MK, Santos LR. 2011. The evolution of decision-making under risk: framing effects in monkey risk preferences. *J. Exp. Soc. Psychol.* 47:689–93

Lea SEG, Webley P. 2006. Money as tool, money as drug: the biological psychology of a strong incentive. *Behav. Brain Sci.* 29:161–209

Lee D. 2008. Game theory and neural basis of social decision making. *Nat. Rev. Neurosci.* 11:404–9

Lee D, McGreevy BP, Barraclough DJ. 2005. Learning and decision making in monkeys during a rock-paper-scissors game. *Cogn. Brain Res.* 25:416–30

First demonstration that monkeys engage in counterfactual reasoning: Monkeys adjust their behavior in response to what they could have received had they chosen differently.

Lerner JS, Small DA, Loewenstein G. 2004. Heart strings and purse strings: carryover effects of emotions on economic decisions. *Psychol. Sci.* 15:337–41

Loewenstein G, Read D, Baumeister R, eds. 2003. *Time and Decision: Economic and Psychological Perspectives on Intertemporal Choice*. New York: Russell Sage Found.

Loomes G, Sugden R. 1982. Regret theory: an alternative theory of rational choice under uncertainty. *Econ. J.* 92:805–24

MacLean EL, Matthews LJ, Hare BA, Nunn CL, Anderson RC, et al. 2012. How does cognition evolve? Phylogenetic comparative psychology. *Anim. Cogn.* 15:223–38

Malenky RK, Wrangham RW. 1993. A quantitative comparison of terrestrial herbaceous food consumption by *Pan paniscus* in the Lomako Forest, Zaire, and *Pan troglodytes* in the Kibale Forest, Uganda. *Am. J. Primatol.* 32:1–12

Marsh B, Kacelnik A. 2002. Framing effects and risky decisions in starlings. *Proc. Natl. Acad. Sci. USA* 99:3352–55

Mayr E. 1982. *The Growth of Biological Thought*. Cambridge, MA: Harvard Univ. Press

Mazur JE. 1987. An adjusting procedure for studying delayed reinforcement. In *Quantitative Analyses of Behavior: The Effect of Delay and of Intervening Events on Reinforcement Value*, ed. ML Commons, JE Mazur, JA Nevin, H Rachlin, pp. 55–73. Hillsdale, NJ: Erlbaum

McClure SM, Laibson DI, Loewenstein GF, Cohen JD. 2004. Separate neural systems value immediate and delayed monetary rewards. *Science* 306:503–7

McCoy AN, Platt ML. 2002. Risk-sensitive neurons in macaque posterior cingulate cortex. *Nat. Neurosci.* 8:1120–27

Mischel W, Ebbesen EB. 1970. Attention in delay of gratification. *J. Personal. Soc. Psychol.* 16:329–37

Mischel W, Ebbesen EB, Zeiss AR. 1972. Cognitive and attentional mechanisms in delay of gratification. *J. Personal. Soc. Psychol.* 21:204–18

Mischel W, Shoda Y, Rodriguez ML. 1989. Delay of gratification in children. *Science* 244:933–38

Model. Anim. Decis. Group, Fawcett TW, Fallenstein B, Higginson AD, Houston AI, et al. 2014. The evolution of decision rules in complex environments. *Trends Cogn. Sci.* 18:153–61

Morewedge CM, Shu LL, Gilbert DT, Wilson TD. 2009. Bad riddance or good rubbish? Ownership and not loss aversion causes the endowment effect. *J. Exp. Soc. Psychol.* 45:947–51

Mucalhy N, Call J. 2006. Apes save tools for future use. *Science* 312:1038–40

Odean T. 1998. Are investors reluctant to realize their losses? *J. Financ.* 53:1775–98

Osvath M, Osvath H. 2008. Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: self-control and pre-experience in the face of future tool use. *Anim. Cogn.* 11:661–74

Parish AR. 1996. Female relationships in bonobos (*Pan paniscus*): evidence for bonding, cooperation, and female dominance in a male-philopatric species. *Hum. Nat.* 7:61–96

Parrish AE, Perdue BM, Evans TA, Beran MJ. 2013. Chimpanzees (*Pan troglodytes*) transfer tokens repeatedly with a partner to accumulate rewards in a self-control task. *Anim. Cogn.* 16:627–36

Parrish AE, Perdue BM, Stromberg EE, Bania AE, Evans TA, Beran MJ. 2014. Delay of gratification by orangutans (*Pongo pygmaeus*) in the accumulation task. *J. Comp. Psychol.* 128:209–14

Pelé M, Dufour V, Micheletta J, Thierry B. 2010. Long-tailed macaques display unexpected waiting abilities in exchange tasks. *Anim. Cogn.* 13:263–71

Pelé M, Dufour V, Thierry B, Call J. 2009. Token transfers among great apes (*Gorilla gorilla*, *Pongo pygmaeus*, *Pan paniscus*, and *Pan troglodytes*): species differences, gestural requests, and reciprocal exchange. *J. Comp. Psychol.* 123:375–84

Pelé M, Micheletta J, Uhlrich P, Thierry B, Dufour V. 2011. Delay maintenance in Tonkean macaques (*Macaca tonkeana*) and brown capuchin monkeys (*Cebus apella*). *Int. J. Primatol.* 32:149–66

Platt ML, Hayden BY. 2011. Learning: not just the facts, ma'am, but the counterfactuals as well. *PLOS Biol.* 9:e1001092

Platt ML, Huettel SA. 2008. Risky business: the neuroeconomics of decision making under uncertainty. *Nat. Neurosci.* 11:398–403

Pompilio L, Kacelnik A, Behmer ST. 2006. State-dependent learned valuation drives choice in an invertebrate. *Science* 311:1613–15

Rachlin H. 2000. *The Science of Self-Control*. Cambridge, MA: Harvard Univ. Press

Ramseyer A, Pelé M, Dufour V, Chauvin C, Thierry B. 2006. Accepting loss: the temporal limits of reciprocity in brown capuchin monkeys. *Proc. R. Soc. B* 273:179–84

Real LA. 1991. Animal choice behavior and the evolution of cognitive architecture. *Science* 253:980–86

Redelmeier DA, Katz J, Kahneman D. 2003. Memories of colonoscopy: a randomized trial. *Pain* 104:187–94

Roberts WA. 2002. Are animals stuck in time? *Psychol. Bull.* 128:473–89

Rosati AG, Hare B. 2011. Chimpanzees and bonobos distinguish between risk and ambiguity. *Biol. Lett.* 7:15–18

Rosati AG, Hare B. 2012. Decision-making across social contexts: Competition increases preferences for risk in chimpanzees and bonobos. *Anim. Behav.* 84:869–79

Rosati AG, Hare B. 2013. Chimpanzees and bonobos exhibit emotional responses to decision outcomes. *PLOS ONE* 8:e63058

Rosati AG, Stevens JR. 2009. Rational decisions: the adaptive nature of context-dependent choice. In *Rational Animals, Irrational Humans*, ed. AP Watanabe, L Blaisdell, L Huber, A Young, pp. 101–17. Tokyo: Keio Univ. Press

Rosati AG, Stevens JR, Hare B, Hauser MD. 2007. The evolutionary origins of human patience: temporal preferences in chimpanzees, bonobos, and human adults. *Curr. Biol.* 17:1663–68

Shows that chimpanzees and bonobos, two closely related species, exhibit different levels of patience in line with predictions from their wild feeding ecology.

Rosati AG, Stevens JR, Hauser MD. 2006. The effect of handling time on temporal discounting in two New World primates. *Anim. Behav.* 71:1379–87

Rosati AG, Wobber V, Hughes K, Santos LR. 2014. Comparative developmental psychology: How is human cognitive development unique? *Evol. Psychol.* 12:448–73

Rozin P, Royzman EB. 2001. Negativity bias, negativity dominance, and contagion. *Personal. Soc. Psychol. Rev.* 5:296–320

Rudebeck PH, Walton ME, Smyth AN, Bannerman DM, Rushworth MSF. 2006. Separate neural pathways process different decision costs. *Nat. Neurosci.* 9:1161–68

Santos LR, Chen MK. 2009. The evolution of rational and irrational economic behavior: evidence and insight from a non-human primate species. In *Neuroeconomics: Decision Making and the Brain*, ed. PW Glimcher, CF Camerer, E Fehr, RA Poldrack, pp. 81–94. London: Elsevier

Santos, LR, Gendler TS. 2014. What scientific idea is ready for retirement? Knowing is half the battle. Edge.org. **http://edge.org/response-detail/25436**

Schuck-Paim C, Kacelnik A. 2002. Rationality in risk-sensitive foraging choices by starlings. *Anim. Behav.* 64:869–79

Schuck-Paim C, Pompilio L, Kacelnik A. 2004. State-dependent decisions cause apparent violations of rationality in animal choice. *PLOS Biol.* 2:e402

Schweighofer N, Shishida K, Han CE, Okamoto Y, Tanaka SC, et al. 2006. Humans can adopt optimal discounting strategy under real-time constraints. *PLOS Comput. Biol.* 2:1349–56

Shafir S, Waite TA, Smith BH. 2002. Context-dependent violations of rational choice in honeybees (*Apis mellifera*) and gray jays (*Perisoreus canadensis*). *Behav. Ecol. Sociobiol.* 51:180–87

Sharot T, Velasquez CM, Dolan RJ. 2010. Do decisions shape preference? Evidence from blind choice. *Psychol. Sci.* 21:1231–35

Shifferman EM. 2009. Its own reward: lessons to be drawn from the reversed-reward contingency paradigm. *Anim. Cogn.* 12:547–58

Sousa C, Matsuzawa T. 2001. The use of tokens as rewards and tools by chimpanzees. *Anim. Cogn.* 4:213–21

Steele CM. 1988. The psychology of self-affirmation: sustaining the integrity of the self. In *Advances in Experimental Social Psychology*, Vol. 22, ed. L Berkowitz, pp. 261–301. San Diego, CA: Academic

Stephens DW, Anderson D. 2001. The adaptive value of preference for immediacy: when shortsighted rules have farsighted consequences. *Behav. Ecol.* 12:330–39

Stephens DW, Kerr B, Fernandez-Juricic E. 2004. Impulsivity without discounting: the ecological rationality hypothesis. *Proc. R. Soc. B* 271:2459–65

Stephens DW, McLinn CM. 2003. Choice and context: testing a simple short-term choice rule. *Anim. Behav.* 66:59–70

Sterelny K. 2012. *The Evolved Apprentice*. Cambridge, MA: MIT Press

Stevens JR. 2014. Evolutionary pressures on primate intertemporal choice. *Proc. R. Soc. B* 289:20140499

Stevens JR, Hallinan EV, Hauser MD. 2005a. The ecology and evolution of patience in two New World monkeys. *Biol. Lett.* 1:223–26

Stevens JR, Muhlhoff N. 2012. Intertemporal choice in lemurs. *Behav. Process.* 89:121–27

Stevens JR, Rosati AG, Heilbronner SR, Muelhoff N. 2011. Waiting for grapes: expectancy and delayed gratification in bonobos. *Int. J. Comp. Psychol.* 24:99–111

Stevens JR, Rosati AG, Ross K, Hauser MD. 2005b. Will travel for food: spatial discounting in two New World monkeys. *Curr. Biol.* 15:1855–60

Compares effort discounting in two monkey species, showing that work trade-off problems may be distinct from temporal trade-off problems.

Stevens JR, Stephens DW. 2008. Patience. *Curr. Biol.* 18:R11–12

Stevenson MF, Rylands AB. 1988. The marmosets, genus *Callithrix*. In *Ecology and Behavior of Neotropical Primates*, Vol. 2, ed. RA Mittermeier, AB Rylands, AF Coimbra-Filho, GAB Fonseca, pp. 131–222. Washington, DC: World Wildl. Fund

Striedter GF. 2005. *Principles of Brain Evolution*. Sunderland, MA: Sinauer Assoc.

Suddendorf T, Corballis MC. 2007a. The evolution of foresight: What is mental time travel, and is it unique to humans? *Behav. Brain Sci.* 30:299–351

Suddendorf T, Corballis MC. 2007b. Mental time travel and the evolution of the human mind. *Genet. Soc. Pychol. Monogr.* 123:133–68

Tanaka M, Yamamoto S. 2009. Token transfer between mother and offspring chimpanzees (*Pan troglodytes*): mother-offspring interaction in a competitive situation. *Anim. Cogn.* 12:S19–26

Thaler RH. 1980. Toward a positive theory of consumer choice. *J. Econ. Behav. Organ.* 1:39–60

Thaler RH, Sunstein CR. 2008. *Nudge: Improving Decisions About Health, Wealth, and Happiness*. New Haven, CT: Yale Univ. Press

Tobin H, Logue AW. 1994. Self-control across species (*Columba livia*, *Homo sapiens*, and *Rattus norvegicus*). *J. Comp. Psychol.* 108:126–33

Tobin H, Logue AW, Chelonis JJ, Ackerman KT. 1996. Self-control in the monkey *Macaca fascicularis*. *Anim. Learn. Behav.* 24:168–74

Tomasello M, Carpenter M, Call J, Behne T, Moll H. 2005. Understanding and sharing intentions: the origins of cultural cognition. *Behav. Brain Sci.* 28:675–735

Tversky A. 1969. Intransitivity of preferences. *Psychol. Rev.* 76:31–48

Tversky A, Kahneman D. 1981. The framing of decisions and the psychology of choice. *Science* 211:453–58

Uher J, Call J. 2008. How the great apes (*Pan troglodytes*, *Pongo pygmaeus*, *Pan paniscus*, *Gorilla gorilla*) perform on the reversed reward contingency task II: transfer to new quantities, long-term retention, and the impact of quantity ratios. *J. Comp. Psychol.* 122:204–12

Vlamings PHM, Uher J, Call J. 2006. How the great apes (*Pan troglodytes*, *Pongo pygmaeus*, *Pan paniscus*, and *Gorilla gorilla*) perform on the reversed contingency task: the effects of food quantity and food visibility. *J. Exp. Psychol.: Anim. Behav. Process.* 32:60–70

Vohs KD, Mead NL, Goode MR. 2006. The psychological consequences of money. *Science* 314:1154–56

Vohs KD, Mead NL, Goode MR. 2008. Merely activating the concept of money changes personal and interpersonal behavior. *Curr. Dir. Psychol. Sci.* 17:208–12

von Neumann J, Morgenstern O. 1947. *Theory of Games and Economic Behavior*. Princeton, NJ: Princeton Univ. Press. 2nd ed.

Waite TA. 2001a. Background context and decision making in hoarding gray jays. *Behav. Ecol.* 12:318–24

Waite TA. 2001b. Intransitive preferences in hoarding gray jays (*Perisoreus canadensis*). *Behav. Ecol. Sociobiol.* 50:116–21

Walton ME, Rudebeck PH, Bannerman DM, Rushworth MSF. 2007. Calculating the cost of acting in frontal cortex. *Ann. N. Y. Acad. Sci.* 1104:340–56

West S, Jett SE, Beckman T, Vonk J. 2010. The phylogenetic roots of cognitive dissonance. *J. Comp. Psychol.* 124:425–32

White FJ. 1989. Ecological correlates of pygmy chimpanzee social structure. In *Comparative Socioecology: The Behavioral Ecology of Human and Other Mammals*, ed. V Standen, RA Foley, pp. 151–64. Oxford, UK: Blackwell Sci.

White FJ. 1998. Seasonality and socioecology: the importance of variation in fruit abundance to bonobo sociality. *Int. J. Primatol.* 19:1013–27

White FJ, Wrangham RW. 1988. Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. *Behaviour* 105:148–64

Wolfe JB. 1936. Effectiveness of token rewards for chimpanzees. *Comp. Psychol. Monogr.* 12:1–72

Won YJ, Hey J. 2005. Divergence population genetics of chimpanzees. *Mol. Biol. Evol.* 22:297–307

Wrangham R. 2000. Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In *Primate Males: Causes and Consequences of Variation in Group Composition*, ed. P Kappeler, pp. 248–58. Cambridge, UK: Cambridge Univ. Press

Wrangham R, Peterson D. 1996. *Demonic Males: Apes and the Origins of Human Violence*. New York: Houghton Mifflin

Wrangham R, Pilbeam D. 2001. African apes as time machines. In *All Apes Great and Small*, Vol. 1, *African Apes*, ed. BMF Galdikas, NE Briggs, LK Sheeran, GL Shapiro, J Goodall, pp. 5–17. New York: Springer

Xu ER, Knight EJ, Kralik JD. 2011. Rhesus monkeys lack a consistent peak-end effect. *Q. J. Exp. Psychol.* 64:2301–15

Zeelenberg M. 1999. Anticipated regret, expected feedback, and behavioral decision making. *J. Behav. Decis. Mak.* 12:93–106

Zeelenberg M, Beattie J, van der Plight J, de Vries NK. 1996. Consequences of regret aversion: effects of expected feedback on risky decision making. *Organ. Behav. Hum. Decis. Process.* 65:148–58

Zeelenberg M, van Dijk WW, van der Plight J, Manstead ASR, van Empelen P, Reinderman D. 1998. Emotional reactions to the outcomes of decisions: the role of counterfactual thought in the experience of regret and disappointment. *Organ. Behav. Hum. Decis. Process.* 75:117–41

Annual Review of Psychology
Volume 66, 2015

Contents

Indexes

Errata

An online log of corrections to *Annual Review of Psychology* articles may be found at http://www.annualreviews.org/errata/psych

Annu. Rev. Psychol. 2015.66:321-347. Downloaded from www.annualreviews.org
Access provided by Harvard University on 01/06/15. For personal use only.

ANNUAL REVIEWS
It's about time. Your time. It's time well spent.

New From Annual Reviews:

Annual Review of Organizational Psychology and Organizational Behavior
Volume 1 • March 2014 • Online & In Print • http://orgpsych.annualreviews.org

Editor: **Frederick P. Morgeson,** *The Eli Broad College of Business, Michigan State University*

The *Annual Review of Organizational Psychology and Organizational Behavior* is devoted to publishing reviews of the industrial and organizational psychology, human resource management, and organizational behavior literature. Topics for review include motivation, selection, teams, training and development, leadership, job performance, strategic HR, cross-cultural issues, work attitudes, entrepreneurship, affect and emotion, organizational change and development, gender and diversity, statistics and research methodologies, and other emerging topics.

Complimentary online access to the first volume will be available until March 2015.

TABLE OF CONTENTS:
- *An Ounce of Prevention Is Worth a Pound of Cure: Improving Research Quality Before Data Collection,* Herman Aguinis, Robert J. Vandenberg
- *Burnout and Work Engagement: The JD-R Approach,* Arnold B. Bakker, Evangelia Demerouti, Ana Isabel Sanz-Vergel
- *Compassion at Work,* Jane E. Dutton, Kristina M. Workman, Ashley E. Hardin
- *Constructively Managing Conflict in Organizations,* Dean Tjosvold, Alfred S.H. Wong, Nancy Yi Feng Chen
- *Coworkers Behaving Badly: The Impact of Coworker Deviant Behavior upon Individual Employees,* Sandra L. Robinson, Wei Wang, Christian Kiewitz
- *Delineating and Reviewing the Role of Newcomer Capital in Organizational Socialization,* Talya N. Bauer, Berrin Erdogan
- *Emotional Intelligence in Organizations,* Stéphane Côté
- *Employee Voice and Silence,* Elizabeth W. Morrison
- *Intercultural Competence,* Kwok Leung, Soon Ang, Mei Ling Tan
- *Learning in the Twenty-First-Century Workplace,* Raymond A. Noe, Alena D.M. Clarke, Howard J. Klein
- *Pay Dispersion,* Jason D. Shaw
- *Personality and Cognitive Ability as Predictors of Effective Performance at Work,* Neal Schmitt
- *Perspectives on Power in Organizations,* Cameron Anderson, Sebastien Brion
- *Psychological Safety: The History, Renaissance, and Future of an Interpersonal Construct,* Amy C. Edmondson, Zhike Lei
- *Research on Workplace Creativity: A Review and Redirection,* Jing Zhou, Inga J. Hoever
- *Talent Management: Conceptual Approaches and Practical Challenges,* Peter Cappelli, JR Keller
- *The Contemporary Career: A Work–Home Perspective,* Jeffrey H. Greenhaus, Ellen Ernst Kossek
- *The Fascinating Psychological Microfoundations of Strategy and Competitive Advantage,* Robert E. Ployhart, Donald Hale, Jr.
- *The Psychology of Entrepreneurship,* Michael Frese, Michael M. Gielnik
- *The Story of Why We Stay: A Review of Job Embeddedness,* Thomas William Lee, Tyler C. Burch, Terence R. Mitchell
- *What Was, What Is, and What May Be in OP/OB,* Lyman W. Porter, Benjamin Schneider
- *Where Global and Virtual Meet: The Value of Examining the Intersection of These Elements in Twenty-First-Century Teams, Cristina B. Gibson, Laura Huang, Bradley L. Kirkman, Debra L. Shapiro*
- *Work–Family Boundary Dynamics,* Tammy D. Allen, Eunae Cho, Laurenz L. Meier

Access this and all other Annual Reviews journals via your institution at www.annualreviews.org.

ANNUAL REVIEWS | Connect With Our Experts
Tel: 800.523.8635 (US/CAN) | Tel: 650.493.4400 | Fax: 650.424.0910 | Email: service@annualreviews.org