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Learning From Mistakes: Decision-making Biases Within the Primate Lineage

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LEARNING FROM MISTAKES: DECISION-MAKING BIASES WITHIN THE PRIMATE LINEAGE

by

JULIA WATZEK

Under the Direction of Sarah F. Brosnan, PhD

ABSTRACT

Humans and animals alike make thousands of decisions each day, and good decision-making is crucial to survive and thrive in a competitive world. Much research has focused on how to make 'rational' decisions based on stable and absolute preferences. In reality, however, human and animal decisions are extremely context dependent. We show and act on relative rather than absolute preferences (e.g., relative to irrelevant options, previous choices, or what others receive), and these tendencies can lead to consistently ‘irrational’ behavior. Studying the flaws in our cognitive system can help us learn how it works. This dissertation explored the extent to which we share several such decision-making biases with other primates. In a series of manual and computerized tasks, capuchin monkeys’ and rhesus macaques’ choices shifted in response to theoretically irrelevant factors like the presence of unattainable options, inferior options, or social partners; how much work they had previously invested; and how frequently different stimuli were encountered. These findings suggest that evolutionary ancient mechanisms can underlie similar biases in humans, highlighting the need to evaluate the potential function of decision-making strategies in a species’ physical and social environment. However, seemingly minor aspects of the experimental paradigms, like monkeys’ baseline preferences or whether information about the reward contingencies was signaled, affected the magnitude of these biases. Such methodological details may contribute to mixed evidence for decision-making biases in animals and need to be assessed systematically for comparative research to make valid inferences. In doing so, studying whether species other than humans make similar mistakes allows us to better understand the underlying cognitive mechanisms and the evolutionary forces that shape them.

INDEX WORDS: Decision-making bias, Rationality, Comparative psychology, Capuchin monkey, Rhesus macaque

LEARNING FROM MISTAKES: DECISION-MAKING BIASES WITHIN THE PRIMATE LINEAGE

by

JULIA WATZEK

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To Ben,

the peanut butter to my jelly

& the best decision I have made

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DECISION-MAKING BIASES IN ANIMALS:
A CRITICAL REVIEW

A version of this manuscript has been submitted for publication. The preprint is available at https://doi.org/10.31219/osf.io/4gu2f

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Abstract

Humans make thousands of decisions every day, and in some situations, we make reliably bad ones. Much research has explored the circumstances in which such irrational decision-making occurs, but the underlying mechanisms are often unclear. One approach that has recently gained traction is to study other species' responses to similar scenarios to better understand our own decision-making strategies. Here we provide a critical discussion of experimental studies of decision-making biases in animals. We begin by demonstrating how comparative research can yield unique insights into our own decision-making that cannot be gained from studying humans alone. In particular, while comparative research helps us better understand how and why decision-making biases have evolved and which mechanisms underlie them, such studies often overlook how these behaviors vary, both within and between individuals. Methodological concerns and a lack in the diversity of species studied and the number of animals tested complicate this issue and can limit the inferences we can draw. We emphasize the need to study why and when some animals would be expected to show these biases while others would not. Further, rather than just assess whether a given bias is present, comparative research should measure the extent to which it is. We argue that studying how susceptibility to biases varies both within and between individuals is crucial to better understanding the nature of irrational decision-making. We suggest practical steps that open up exciting avenues for future comparative research in this area.

Keywords: decision-making, cognitive bias, rationality, comparative psychology

Introduction

Good decision-making is critical to the everyday lives of humans and animals alike. For animals, bad decisions can easily result in death or reproductive failure; for humans, in dire financial straits or toxic relationships. But what makes for a good decision? How can we evaluate decision-making objectively? Traditional economics provides benchmarks for optimal strategies in different situations (e.g., rational choice theory: von Neumann and Morgenstern 2007). Such theories typically assume that decision-makers have full information and the ability to use it. As a result, rational decision-makers should form stable and absolute preferences. However, we rarely do so in the real world. We are frequently influenced by factors that – according to such normative theories – should not matter (e.g., how a question is worded), and, as a result, we make consistently suboptimal decisions in certain situations. Our preferences can change based on how options are presented and which ones are available, on who else is watching or what they receive, or on what might have been (nudge theory: Thaler 1980, 1992, 2016; Kahneman et al. 1982; e.g., behavioral game theory: Camerer 2003; prospect theory: Kahneman 2011). Although it is now well known that we often do not behave rationally, there is no unified framework that explains when or how we fail to do so either. This issue is complicated because it is not always clear what behavior counts as irrational in the first place. For example, some perspectives define rationality in relation to a species' cognitive system and environmental conditions rather than in relation to traditional economic principles (Kacelnik 2006; e.g., bounded rationality: Camerer 1998; Gigerenzer and Brighton 2009; Gigerenzer and Goldstein 1996; Gigerenzer and Selten 2001; Gigerenzer and Todd 1999; ecological or biological rationality: De Petrillo and Rosati 2019; Stevens 2012; The Modelling Animal Decisions Group et al. 2014).

Irrational tendencies can lead to paradoxical behavior with real-world consequences. For example, we prefer a longer and more painful sequences if the pain tapers off, are less happy if we have more options, and reject free, no-strings-attached money if we see the situation as unfair (Camerer 2003; Redelmeier et al. 2003; Scheibehenne et al. 2010; Chernev et al. 2015). Of course, other people are not immune to these biases either, and their decisions can deeply impact our lives as well. For example, marketing strategies can affect how much money you spend on a travel package, and countries' policies can affect whether you become an organ donor or whether your child picks healthy foods in the cafeteria (Johnson and Goldstein 2004; Thaler and Sunstein 2009; Hanks et al. 2012; e.g., Cadario and Chandon 2019). Such irrational tendencies can also affect cornerstones of democracy and branches of government, e.g., when the wording on the ballot affects your votes, or when how well a judge slept or when they last ate affects your court case (Bütler and Maréchal 2007; Danziger et al. 2011; e.g., Burnett and Kogan 2015; Eren and Mocan 2016; Cho et al. 2017).

Given the wide-spread and dramatic consequences that decision-making biases can have on our lives, it is important to understand why we fall for them. If we want to make better decisions, we need to know why and under what circumstances we make bad ones. This is true for individual decision-makers, but it is particularly important for policymakers to recognize that humans are not always rational. From this knowledge, they should responsibly design decision contexts that elicit our inherent values and preferences without distorting them. However, because humans operate in complex physical and social environments in the real world, there are often multiple possible explanations for what causes our decision-making to go awry. For example, problem-solving skills and strategies may be rooted in biological predispositions *and* may be expressed differently depending on the cultural environment *and* may change over development. These influences are not mutually exclusive. Therefore, disentangling their role in bad decision-making is crucial because they have different implications for how to address them in order to lead to better choices. One approach to this problem is to study decision-making in other species, which not only gives us model systems free of many of these other influences but also helps clarify the evolutionary history of these decision-making behaviors, which can help us understand their potential function in solving problems we encounter in our environments. Incidentally, a better understanding of bad decision-making may also yield a better understanding of good decision-making, because the same psychological processes are likely involved.

In this paper, we demonstrate how studying decision-making biases in other species can help us better understand their evolutionary roots and their underlying mechanisms. We discuss several decision-making biases to demonstrate 1) what comparative studies can tell us, 2) what challenges comparative researchers face, and 3) where we can go from here.

Insights From Studies of Animal Decision-making Biases

The comparative approach

Comparing the behavior of multiple species, including humans, is the only way to systematically assess both similarities and differences in how we make decisions. Doing so is vital to understanding how these behaviors have evolved, which mechanisms are at work, and under which circumstances they might have been adaptive. This is important not just for good decisions that we make but particularly for bad ones, because they can be costly both for the individual and for society as a whole. Understanding such decision-making biases from an evolutionary perspective is advantageous if we want to predict when they occur and learn how to overcome them.

Similarities in the behavior of different species can result from two processes – homology and convergent evolution (Lorenz 1958; Rendall and Di Fiore 2007; Ereshefsky 2007). Behavior is homologous if it occurs in species that share a common ancestor who behaved in the same way. As a result, phylogenetically closely related species may behave more similarly than more distantly related species. For example, dominance patterns may be homologous among primates (Rajecki and Flanery 2013), suggesting that dominance may have been adaptive for the primate common ancestor, for example, as a response to social conflict. However, through convergent evolution, similar behavior can also arise in distantly related species, not due to common descent, but in response to the same selection pressure. Such cases can be particularly informative because the similarities in the ecologies of the species that show a given behavior can help generate hypotheses about its function and adaptive value. For example, inhibitory skills in primate species covary with the degree of fission-fusion dynamics (a form of social complexity in which primate groups split into and merge from variable subgroups) rather than with phylogenetic history. Specifically, apes do not categorically perform better than monkeys, suggesting that inhibitory control may have conferred an evolutionary advantage in potentially risky social interactions (Amici et al. 2008).

Importantly, although multiple species may show similar outcomes and a behavior can even serve the same function, it may arise from different psychological processes. For example, in a two-player coordination game, humans and rhesus macaques adopted a reward-maximizing strategy that led to nearly identical overall payouts, but people did so by matching their (simulated) partners whereas the monkeys developed a preference for the option that paid well most of the time (Brosnan et al. 2012b; Parrish et al. 2014). Comparative studies provide a unique way to constrain hypotheses about these underlying mechanisms. If other animals show similar behavior to humans, we can conclude that psychological processes unique to humans, such as human language, culture, or experience with financial institutions are not necessary for it to arise or may not affect how the behavior is expressed. Conversely, if we see a given behavior only in a specific species or group of species (e.g., only in humans or only in cetaceans), we can focus on the cognitive processes that may be specific to those organisms. Thus, although each species and population is subject to unique ecological influences, we can hone in on what causes a given behavior by examining the pattern across species through convergent research.

In this way, much comparative research has established areas in which we are indeed unique as well as areas in which we are not (Fig. 1.1). For example, humans are unrivaled in our ability to innovate by transmitting and building on the knowledge of previous generations, to work with others in teams comprising thousands of people spanning the globe, and to use these abilities to go to space and uncover the mysteries of the universe. But animals other than humans certainly also use tools (Sanz et al.

2013), cooperate at sometimes large scales (Dugatkin 1997), and show some forms of culture (Laland and Galef 2009). Thus, comparative research often shows that the difference between us and other animals may be one of degree rather than kind. Of course, different species often express behaviors differently (e.g., behaviors that involve extensive use of language in humans), but the degree to which we share them with other species provides distinct insights into how and why they evolved and helps us better understand the mechanisms that lead us to make both good and bad decisions.

Humans are uniquely smart	Humans are not uniquely smart
Humans are uniquely daft	Humans are not uniquely daft

Figure 1.1 A simple 2x2 classification for human decision-making phenomena in comparison to animals.

Distinguishing between abilities that we share with other animals and those we do not also provides a unique perspective into how to improve our decision-making approaches. For example, if ant colonies can find the optimal strategy in complex problems through simple individual-level heuristics, then humans may not need computationally intensive algorithms to solve similar problems either. Ants effectively and efficiently self-organize along lanes on their trails to adjust to heavier traffic, avoiding traffic jams but actually achieving greater speeds at higher traffic densities (Hönicke et al. 2015). These findings may help us develop improved traffic control measures that do not necessarily require complicated equipment and flow algorithms. Other endeavors, like colonizing the solar system, of course, rely to a large extent on human-unique abilities (e.g., human language), technologies (e.g., computers), and institutions (e.g., markets), and will need to optimize these aspects in order to succeed.

Mechanisms underlying decision-making biases

Using the comparative approach to study biases in decision-making can tell us whether humans are also uniquely daft in some situations or whether we share some of these irrational tendencies with other animals (Fig. 1.1). Similar to drawing this distinction for exceptional abilities, thinking about bad decision-making in comparison to other animals can lead to different implications for how to fix it. If only humans show a given bias, we may focus on tweaking human-unique features, such as aspects of digital communication, our financial institutions, or our education systems to elicit better decision-making. On the other hand, if other species show similar behavior, we know that it does not require human-unique mechanisms and can instead consider the role of more widely shared processes.

This rationale has been used to demonstrate, for example, that other animals like birds (Marsh and Kacelnik 2002) and monkeys (Lakshminarayanan et al. 2011) show framing effects – accepting more risk when outcomes are presented as losses than when the same outcomes are presented as gains. Similarly, comparative research found that apes and monkeys show the endowment effect – the tendency to overvalue items we own – in some situations (Brosnan et al. 2007, 2012a; Lakshminaryanan et al. 2008; Kanngiesser et al. 2011; Flemming et al. 2012; Drayton et al. 2013). These results challenge the idea that these hallmark economic decision-making biases (Kahneman and Tversky 1979; Kahneman et al. 1991, 2008; Knetsch 2000) are unique to humans and have to rely on, for example, interactions with formal economic markets. Consequently, both good and bad decisions may often result from simpler cognitive rules than previously recognized.

Of course, that does not necessarily mean that human-unique mechanisms play no role at all, both because several mechanisms may be involved and because the same outcomes may arise from different mechanisms. For example, the endowment effect in animals seems to be limited to food or tools that can be used immediately to obtain it (Brosnan et al. 2007, 2012a). Thus, human psychological processes are not necessary for endowment effects to arise, but they may explain why humans show it in broader contexts. Importantly, these differences in how widely the effect is expressed has prompted new inquiries into whether the "evolutionary salience" of the item may explain the variation we see in humans as well (Jones and Brosnan 2008), highlighting that comparative research can yield unique perspectives and testable predictions about human decision-making behavior.

One key feature of most decision-making biases that is obscured in all of these discussions (and our inferential statistics) is the often significant variability seen across individuals within species. Addressing this issue is important to assessing the stability of decision-making biases. Most basically, understanding this variability will help to clarify how different contexts influence decision-making, particularly if the same individuals respond differently across contexts. Moreover, different individuals may respond differently to the same context, suggesting that personality or preference may influence decisions. Here we discuss new research on the sunk cost effect and cognitive set bias and highlight that the extent to which animals show a given bias may vary not just across species but also across individuals or within individuals across trials or sessions. For further demonstrations of the comparative approach in the study of other decision-making phenomena, see reviews by Rosati and Stevens (2009), Santos and Chen (2009), Santos and Rosati (2015), Zentall (2016, 2019), and Williamson et al. (2019).

Sunk cost effect

Humans frequently take prior investments into account when making decisions. This susceptibility to irrecoverable sunk costs is irrational because we should only consider the future expected costs and benefits when making a decision. If you get more from selling your car than not selling it (e.g., because of running costs), you should sell it, regardless of how much you bought it for. People and organizations alike tend to persist in an endeavor to a greater extent the more resources (e.g., time, money, or energy) we have already invested (Arkes and Blumer 1985; Arkes and Ayton 1999), and this can lead to bad decisions. For example, the sunk cost effect may exacerbate a country's economic losses, cause a scientist to waste time on a doomed project, or make you finish (and later regret) a meal when you are already full. Indeed, this bias is sometimes called the Concorde fallacy, after the Concorde airplane project that wasted millions in funding even after it had become clear that it was a "commercial disaster" (Central Policy Review Staff 1971).

There are several possible explanations for this phenomenon, none of which are mutually exclusive, making it even trickier to tease them apart. People may rationalize their earlier decisions as sound rather than mistaken in order to justify continued investment (Staw and Fox 1977; Staw and Ross 1989; Staw and Hoàng 1995), may strive to avoid waste (Arkes and Blumer 1985; Arkes 1996; Arkes and Ayton 1999; Arkes and Hutzel 2000), may persevere until they are more certain of the outcome (Bragger et al. 1998; Navarro and Fantino 2005), or may shun a definite large loss (if they cut their losses) when a small additional investment may – but may not! – turn things around with a large gain (Kahneman and Tversky 1979; Thaler 1980; Tversky and Kahneman

1981). However, disentangling these theories empirically has been difficult because they make similar predictions – that the sunk cost effect increases with the size of the sunk cost.

The comparative approach presents one way to address this issue and to better understand the cognitive mechanisms underlying the sunk-cost effect. To the extent that human language and culture underlies tendencies such as self-justification and waste avoidance, these explanations would not predict a susceptibility to sunk costs in animals. On the other hand, if, for example, a more universal response to resource scarcity underlies waste avoidance in humans, then we would expect to find some evidence of the sunk cost effect in other animals as well. Similarly, uncertainty reduction and loss aversion, which do not rely on such human-unique factors, could account for sunk cost effects in animals. In fact, testing the effect in multiple animal species may help disentangle these possibilities even further if species differ in whether or how they express these behaviors. For example, to date, only starlings and capuchin monkeys have shown a human-like reflection effect by becoming more risk prone when prospects were framed as losses compared to the same prospects framed as gains (Marsh and Kacelnik 2002; Lakshminarayanan et al. 2011), although, to our knowledge, no other species have been tested in these paradigms. To the extent that the sunk cost effect arises as a result of loss aversion, we would expect it to emerge in species that overvalue losses in this way. Conversely, if loss aversion does not covary with the sunk cost effect, this suggests that it is not a major factor in making the bias emerge, including in humans.

Several animal species have now shown sunk cost effects both in the field and in the laboratory (Magalhães and White 2016). Ecological studies have mainly focused on parental investment in birds to assess whether sunk costs affect at what point parents stop raising the current offspring and start investing in the next. In line with the sunk cost effect, parents' nest defense behavior increases the more they have already invested (Weatherhead 1979; Dawkins and Brockmann 1980). However, because parental investments are often indicative of brood value, it is unclear to what extent the future costs and benefits – which should be taken into account – rather than sunk costs – which should not be taking into account – can explain these findings.

In the laboratory, where these factors are more easily controlled, pigeons and rats also show consistent sunk cost effects. They are more likely to complete a reinforcement schedule (rather than abandon it) the more pecks or lever presses they have already completed (Navarro and Fantino 2005; Macaskill and Hackenberg 2012; Magalhães et al. 2012). For example, pigeons completed one of four random fixed ratio schedules, where the schedule that required the fewest pecks was the most common (Navarro and Fantino 2005). Importantly, pigeons could opt out and skip to the next trial at any point by pecking the escape key. In this situation, you should peck for the minimum number of times and escape if that does not yield a reward, i.e., when one of the three longer schedules is in effect. This is the optimal response because, on average, completing the longer trials takes more pecks than starting a new, most likely short trial. However, three out of four pigeons persisted in almost all trials and failed to use the escape key. This effect disappeared when the cost of persisting was increased (i.e., when the longer schedules required many more additional pecks) and when the change in reward schedule was signaled (i.e., when the key changed color when the minimum number of pecks was completed). These results suggest that continued investment may, in part, arise from uncertainty about when it becomes more beneficial to quit than to continue, particularly if the cost to continue is small.

More recently, rats and mice have also shown sunk cost effects when they needed to wait rather than act repeatedly in order to persist (Sweis et al. 2018). In this clever design, the rodents foraged for four different reward options by moving around a testing area with separate compartments. In each room, they could choose whether to move to the next room or whether to accept a waiting time for a reward (the duration was signaled through sounds of varying pitch to remove uncertainty). If they accepted an offer by entering the wait zone of the room, the countdown began, and the rodents received a food pellet if they waited until the end of the countdown. Once again, they could leave at any time during the waiting period but would forfeit the reward and the work (waiting) that they had already committed. Optimally, you should finish all trials that you are willing to commit to; otherwise, you should simply opt out and consider a different offer. Consequently, if you commit to a waiting time, then the time that you have already spent waiting (i.e., sunk costs) should not affect whether you will wait until the end. That is, if you commit to waiting for 10 seconds, you should be just as likely to finish the trial when the wait time just started and when you have waited 9 seconds and only have 1 second left. However, in line with the sunk cost effect, rats and mice were more likely to finish a trial the longer they had already waited (Sweis et al. 2018).

Unexpectedly, this effect did not depend on the time that rodents spent making their initial choice about whether or not to commit, even though it also detracted from the rodents' total time budget. Thus, decisions about continued investment may arise from two different evaluation processes – an initial one involved in opting in or out of an investment and a secondary one involved in whether to continue investing. Only the latter process may be susceptible to sunk costs. Not only does this study demonstrate that animals can show sunk cost effects even when information uncertainty and the need for automated motor responses (such as pecking or lever pressing) are removed, but it highlights how studies of animal decision-making can generate novel hypotheses about human behavior as well. Indeed, the authors tested human participants using a similar procedure, in which they "foraged" for four categories of video clips and were shown a "download bar" that indicated the wait times. Humans showed the same pattern of results; they were more likely to wait until the end the longer they had already waited, but this was unaffected by how long they initially took to decide whether to “download” the video (Sweis et al. 2018).

These findings suggest that very distantly related species share our susceptibility to sunk costs in some situations. This bias therefore does not require tendencies to self-justify or to avoid waste, which are arguably unique to humans. Uncertainty about the remaining effort also cannot explain this behavior, because the wait times were signaled (through sounds) both in the offer and wait zones. While several cognitive mechanisms may be at play, it is informative that widely shared and likely evolutionarily ancient processes can be sufficient. One possibility is that animals rely on heuristics that use past investments as a proxy for future benefits or that increase the perceived value of the reward with increased effort and therefore increased energetic depletion. In other words, the cupcake seems better (and worth waiting longer for) the hungrier you get. In this way, comparative research can constrain our hypotheses about the cognitive mechanisms that underlie decision-making biases in cases in which humans are not uniquely daft (Fig. 1.1).

Cognitive set bias

One way we navigate complex environments with limited and imperfect information is by taking past investments into account, as illustrated by sunk cost effects. Another way we deal with this problem is by relying on learned rules, which often save us time and cognitive resources because we know what has worked in the past. This strategy is particularly useful if we are likely to encounter the same problem again. Of course, humans and animals alike make decisions in many different situations and those situations change over time. When the context for a decision changes, our learned rules of thumb can become inefficient or altogether ineffective. It is important for us to recognize when familiar rules may no longer work and to adopt alternative strategies that are more beneficial in these situations. However, if we are too receptive to new possibilities, we risk making bad decisions because we get distracted by irrelevant information. For example, a foraging animal may starve if it is unable to adapt to shifting environments; yet if foraging habits are too flexible, it may frequently consume novel and potentially poisonous food items. Thus, optimal behavior requires a balance between exploiting known solutions and exploring alternatives.

Humans are creatures of habit in this respect. For example, in the classic water jar task, participants had to measure out specific amounts of water using three water jars of different sizes (Luchins 1942). Participants had to complete practice problems in which they were "given" three water jars that could each hold a fixed amount of water and had to fill and empty them to measure out a target quantity (Fig. 1.2). After completing several problems that could be solved by a single, multi-step rule (fill Jar B, then pour water from it to fill Jar A once and Jar C twice), people were given critical problems that could also be solved using a simpler rule (fill Jar A and pour water into

Jar C once). Participants overwhelmingly persisted in using the longer solution. Humans have since shown this cognitive set, or Einstellung, bias – the tendency for a learned approach to block the use of a better alternative – in a variety of task designs (Duncker 1945; Luchins and Luchins 1950; Aftanas and Koppenaal 1962; Sweller et al. 1982; Ruscio and Amabile 1999; Arrington and Logan 2004; Chrysikou and Weisberg 2005; Bilalić et al. 2008b, a; Crooks and McNeil 2009; ErEl and Meiran 2011; Thomas and Didierjean 2016).

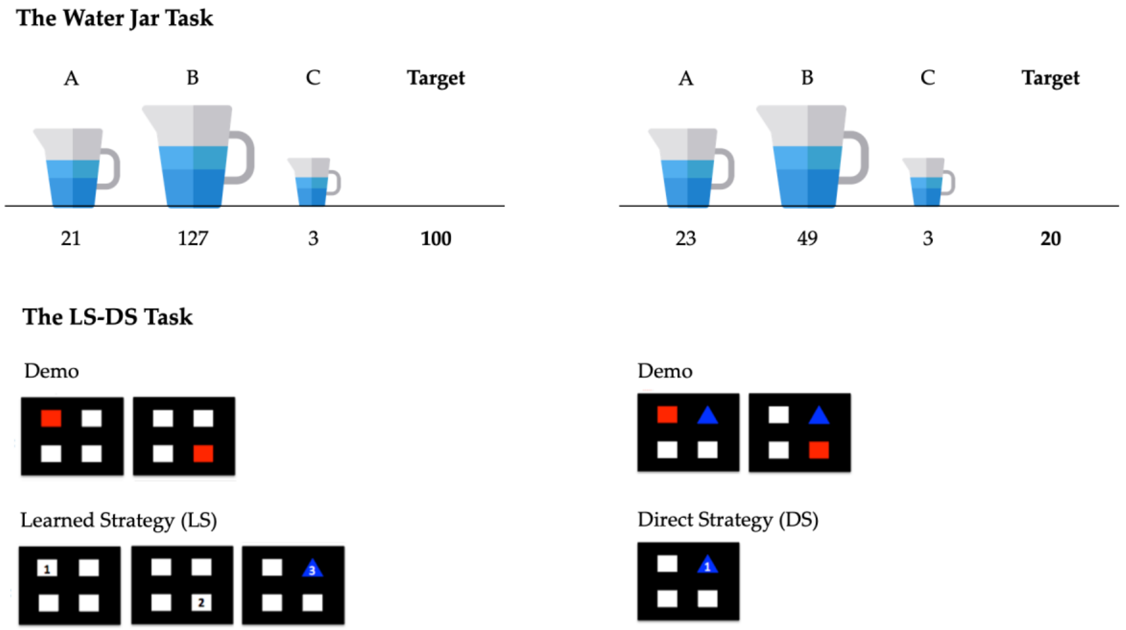

Figure 1.2 Schematics of the water jar problem (Luchins 1942) and the LS-DS task (Pope et al. 2015). In practice problems (left), participants learn to reach the target through a multi-step sequence. In probe trials (right), they can still use the familiar strategy, but could instead also use a more efficient shortcut.

Interestingly, other primates do not seem to share this cognitive inflexibility. In one nonverbal adaptation using a computer task (Fig. 1.2; Pope et al. 2015), participants are trained to select three shapes in sequence (Square 1, Square 2, Triangle). Once they are proficient at this learned strategy, they encounter probe trials in which the final shape is present from trial start. Participants can use this more efficient shortcut, but, similar to the water jar problem, the familiar three-step strategy can also be used. In this task, most humans once again stick with the learned strategy, whereas all monkey and ape species tested to date readily abandon the familiar strategy in favor of the shortcut (Pope et al. 2015, 2019; Watzek et al. 2019). These findings narrow down the possible mechanisms underlying cognitive set bias. The humans may have perceived the stimuli and the sequence globally, whereas the apes and monkeys perceived them locally (Fagot and Tomonaga 1999; Spinozzi et al. 2003; De Lillo et al. 2005). However, in a cross-cultural study testing the seminomadic Himba of Namibia with the same nonverbal paradigm, local and global processers within the same population did not differ in their shortcut use (Pope et al. 2018).

The Himba used the shortcut more than the Westerners, however, suggesting that cultural influences may shape how people conceptualize a problem and how flexibly they try to solve it. For example, formal schooling in Western cultures may encourage blind repetition and build an expectation that each problem has a single correct solution (Star and Seifert 2006). Indeed, when Westerners were prompted to "try something new," they did just as well as the Himba (Pope et al. 2018; see also Luchins 1942) and Western children used the shortcut more than Western adults (Pope et al. 2015). Thus, differences in how people conceptualize the problem and in what they think they "should do" likely play a role, but this does not explain everything. More than half the adults from both cultures still failed to use the shortcut, whereas none of the baboons or chimpanzees kept using the familiar strategy.

One possibility for why other primates use the more efficient shortcut more than humans is that it requires less working memory. If following the learned strategy is difficult, there is more benefit in seeking out a less effortful alternative (Beilock and DeCaro 2007). Thus, ironically, because the learned rule is easier for humans to learn (as indicated by the lower amount of training) and apply (as indicated by their higher accuracy), we might stick with it more even when a shortcut becomes available. In support of this point, other primates show somewhat more habitual strategy use (by starting with the first step in the sequence but taking the shortcut before completing the full sequence) among a primate species with reportedly high working memory capacity (Pope et al. 2019) and when the learned rule requires less working memory (Watzek et al. 2019). But having fewer cognitive constraints does not explain well why humans show such limited flexibility in this task. The ease with which humans learn and apply the learned strategy hints at yet another candidate explanation – because we can verbally encode the rule, we learn it quickly and it may become more firmly rooted.

This allows us to use the rule with high accuracy but may require more cognitive effort to switch to alternative strategies. Indeed, when humans did use the shortcut, they made more mistakes when they had to switch between strategies, whereas monkeys showed no such switch costs (Watzek et al. 2019).

However, while the difference between humans and other primates is stark and robust, there are also differences within each population. Some humans did use the shortcut in all of these studies, some monkeys and apes used the switch strategy, and individuals varied in the extent to which they showed either of the possible strategies. What underlies these interindividual differences in habitual rule use and their willingness to explore alternative strategies is an open question. Further, children used the shortcut more than adults, suggesting that we sometimes become less, not more, rational with experience (see also Williamson et al. 2019). And when humans were given additional test trials, more participants eventually started using the shortcut (Watzek et al. 2019). These results highlight both that individual participants may not show the population's average behavior and that a given participant's behavior may not reflect how they behave at all times. Although this point is hardly world-shattering, we argue that comparative research should study this variability explicitly and develop theories about its roots rather than simply treat it as noise.

This research on cognitive set bias provides a nice illustration of how comparative, developmental, and cross-cultural studies can triangulate the psychological mechanisms that underlie decision-making biases – here in an area in which humans seem to be uniquely daft. We showed how testing different species can tell us more than studying humans alone, in the same way that testing children can tell us more than studying adults alone and testing people with a different cultural background can tell us more than studying Westerners alone (e.g., Nielsen and Haun 2016). By comparing these different populations that vary in unique ways, e.g., in their perceptual processing, their cognitive abilities and constraints, their educational history and how they conceptualize problems, and their encoding modes, we can disentangle the role of these different factors in explaining our susceptibility to decision-making biases.

Evolution of decision-making biases

More than just eliminating or highlighting human-unique mechanisms that may underlie a given bias, the pattern of species that do or do not show it can tell us about its evolutionary history. Biases that are shared widely across the animal kingdom suggest that the proximate cause is evolutionarily ancient. Biases that are shared narrowly across one phylogenetic branch suggest a mechanism common to that group alone (e.g., primates only), and biases found sporadically across different branches suggest a stronger impact of species’ ecologies than shared evolutionary history.

To give an example of how this works, humans will routinely forgo or reject rewards if they are distributed unequally among people. Although cultures vary in their aversion to inequity (Henrich et al. 2001), this behavior is often seen as an indicator of the human sense of fairness. A wide array of animal taxa also respond negatively to unequal outcomes, although responding when one gets *more* than a partner is far less common, both within and among species, than responding when one gets *less* than the partner (for reviews, see Brosnan and de Waal 2014; Oberliessen and Kalenscher 2019). Interestingly, species that cooperate even outside of mating and kinship bonds typically exhibit inequity aversion, whereas related species that do not cooperate (or not as widely) typically do not. Phylogenetic relatedness alone cannot account for this pattern. One proposed explanation is that inequity aversion evolved to maintain equitable cooperative partnerships and to prevent exploitation in these species (Brosnan and de Waal 2014). Of course, there are likely both phylogenetic and ecological factors at play. For example, one form of inequity aversion – responding negatively to receiving more than another – has only been reported in any form in chimpanzees (Brosnan et al. 2010; Proctor et al. 2013), and is by no means ubiquitous (Jensen et al. 2007; Kaiser et al. 2012). Thus, cognitive processes that may only be shared with humans' closest living relatives, such as perhaps greater levels of self-control or anticipatory abilities, may be required to object not just to getting less, but also to getting more than others.

An evolutionary perspective also highlights the importance of considering both the social and physical environments that decision rules have evolved in. A strategy can be adaptive in one context but maladaptive in another, and even closely related species might have social or feeding ecologies that present them with different selection pressures that may, in turn, give rise to different behavioral strategies to cope with them. For example, highly social corvid and lemur species, who may need specific cognitive abilities to navigate more complex social environments, show greater reasoning skills than closely related but less social species (Bond et al. 2003; MacLean et al. 2008).

Differences in feeding ecology can result in similar patterns, for instance in the discounting behavior and risk preferences of primate species. Marmosets are willing to wait for a large reward longer than tamarins, but tamarins are willing to travel farther for it than marmosets (Stevens et al. 2005a, b). Although the two species are closely related, this difference in temporal versus spatial discounting makes sense given the marmosets' reliance on gum and sap, which requires self-control (i.e., waiting for the sap to ooze from a cut in the tree), and the tamarins' reliance on insects, which are ephemeral and require more travel. Similarly, among our two closest living relatives, bonobos, who rely on relatively consistent food sources, are more risk averse whereas chimpanzees, who feed on ephemeral and more highly contested food sources, are more risk prone (Heilbronner et al. 2008).

Such comparative research may further challenge assumptions of a scala naturae. Not only are humans not at "the top," neither are primates, mammals in general, or, for that matter, anyone. For example, when presented with an ephemeral food source that goes away and a permanent one that is always available, cleaner fish optimize by eating the ephemeral first and then the permanent one, much like they service visiting client reef fish before resident fish in the wild (Bshary and Grutter 2002; Salwiczek et al. 2012). Primates, rats, and pigeons, however, fail to follow this strategy that yields twice as much food in this simple task (grey parrots succeed; for a detailed review, see Zentall 2019), although highlighting cues relevant to primates leads to them demonstrating the same behavioral outcomes as the fish (Prétôt et al. 2016a, b). These results emphasize that animal decision-making needs to be evaluated against species' natural environments. We need to discard the notion that some animals are generally smarter than others because we may not always test them in species-appropriate ways and because, ultimately, the best decision-makers are the ones who solve problems that they actually encounter.

Even within a given species, the context therefore often matters (Rosati and Stevens 2009). For example, chimpanzees show endowment effects for food but not objects (toys; Brosnan et al. 2007), unless the objects are immediately useful to obtain food (Brosnan et al. 2012a), suggesting that the tendency to overvalue objects in one's possession may have evolved for salient items, like food, that have significant effects on fitness. Indeed, in the absence of formalized rules for trade, exchanges are risky, and thus a bird in the hand may well be worth two in the bush. That is, you should value important items that you already have more than those you might get – but might not! Moreover, this tendency may generalize to situations when the risk from exchanges is minimized or removed, as in these experimental tasks. Similarly, organisms may change their risk preferences based on their energetic state, taking on more risks to avoid starvation even if it theoretically pays less in the long run (e.g., Caraco 1981; Dener et al. 2016). Such results can highlight contexts in which irrational behavior might be adaptive and therefore how it may have evolved. Humans, too, may be particularly tuned into specific problems we encounter in everyday life, such as social interactions. For example, people have a hard time with a classic logic puzzle when it is presented in abstract terms but tend to solve it when it is presented as a social exchange (Cosmides and Tooby 1992).

Importantly, when we consider the environments in which decision rules have evolved, seemingly irrational behavior may not look so bad after all. In addition, situations in which we violate economic principles of rationality in the laboratory might happen only rarely in the real world. Nonsocial birds do not need to reason about transitive dominance hierarchies and tamarins do not need self-control to wait for sap to exude. If our irrational tendencies rarely lead to errors and are of little consequence when they do, then they cost us very little. But then why follow strategies that are sometimes irrational at all? In some cases, a short-term loss might yield a long-term gain, e.g., if forgoing an unequal reward now results in a more equitable cooperative partnership overall. In other cases, we benefit from following rules of thumb because they save us the time and effort that would be required to always find optimal solutions, especially if there is little to gain from doing so (e.g., Watzek and Brosnan 2018). Such heuristics are useful because our brains' computational power is limited, and if these heuristics fit our environment well enough, they lead to good decision-making most of the time. Thus, decision-making strategies that seem economically irrational may make more sense in the context of our cognitive constraints (bounded rationality: e.g., Camerer 1998; Gigerenzer and Brighton 2009; Gigerenzer and Goldstein 1996; Gigerenzer and Selten 2001; Gigerenzer and Todd 1999) and features of our internal and external environments (ecological or biological rationality: e.g., Kacelnik 2006; Stevens 2012; The Modelling Animal Decisions Group et al. 2014; De Petrillo and Rosati 2019).

Challenges for Studies of Animal Decision-making Biases

The importance of truly comparative methodologies

Although studying decision-making biases in other animals offers unique insights, comparative studies also present unique problems. If we want to draw valid inferences by comparing different species (or different populations within a species), we need valid comparisons. Otherwise, it is unclear whether mixed results within the same species reflect a failure to replicate or simply differences in methodologies (Tomasello and Call 2011; Smith et al. 2018). For example, comparative studies of the peak-end effect – the tendency to overvalue sequences with higher peak values and more positive events at the end – in rhesus macaques find opposite results. Three macaques consistently preferred to receive a higher valued food first and a lower valued food last (contrary to the peak-end effect) in a manual task (Xu et al. 2011), but three macaques from a different laboratory did prefer to "save the best for last" in a computer task in which they chose sequences of juice servings (Blanchard et al. 2014).

There are many methodological differences between the two studies that may have affected the monkeys' responses. The manual task involved fewer trials (30 test trials per session) than the computer task (thousands of training and test trials), used sequences of two rewards that differed in quality (e.g., a grape and half a green bean) rather than quantity, and were much larger than the sequences of five juice rewards (identical, but ranged in quantity from 0.08 to just 0.2 ml for the entire sequence). In addition, the time between items in the manual sequence was longer (several seconds) than in the computer task (always half a second). And while both tasks used two-choice paradigms, the manual task had monkeys choose between a decreasing and an increasing order for the same rewards, which also remained the same throughout testing. The computer task gave monkeys a probe sequence and had them choose whether to repeat it or receive one of several pre-trained comparator sequences, and both sequences varied across trials. Consequently, some possibilities for why the peak-end effect emerged in the computer but not in the manual task are that it might develop through repeated experience, only arises when rewards are small or vary in quantity but not quality, only arises when sequences are almost continuous rather than discrete, or perhaps only comes into effect when limited working memory or other cognitive constraints require the use of a shortcut (for example when comparing sequences of five rewards each that differ only by small amounts). Further, it is not clear how robust these findings are, given that both studies only tested three monkeys (and they did not always show consistent behavior in the manual task, Xu et al., 2011; though there was no statistical effect of monkey identity in the computer task on overall performance, Blanchard et al., 2014).

A study on capuchin monkeys' susceptibility to the peak-end effect (Egan Brad et al. 2016) helps to disentangle these possibilities. In each trial of a manual task, capuchin monkeys chose to trade tokens in exchange for biscuit sticks that were partly covered in frosting (i.e., sections that were preferable to biscuit alone). The biscuit sticks were fed through a little hole, resulting in continuous eating episodes for the monkeys. Other aspects of the procedure similar to Xu and colleagues' manual task (e.g., fairly low trial numbers, large and qualitatively different rewards, rewards remained the same across trials). Two of four capuchins preferred to trade with the experimenter who fed them the frosted end last rather than first (in line with the peak-end effect). These results suggest that, in monkeys, the peak-end bias may only affect evaluations of near-continuous sequences of events. However, because each of the three studies used vastly different methods, direct comparisons are limited and future research is needed to determine the extent to which these results generalize.

Even within the same individuals, housing conditions or small adjustments, such as in the length of an inter-trial interval, can make a bias “disappear.” Species as distantly related as pigeons, dogs, monkeys, and apes all prefer a high value food by itself to the same food and a low value food, e.g., choosing “cheese alone” over “cheese plus carrot” (for a review, see Zentall 2019). However, this less-is-more or selective-value effect disappears when pigeons in the same laboratory were deprived of food (Zentall et al. 2014) or when the same chimpanzees had longer intervals between trials (Beran et al. 2009b), indicating that experimental factors affect choice behavior through food motivation and expectations about what food will be available in the future.

Of course, these issues make comparisons of decision-making biases *between* species especially problematic. This effect is compounded if the task itself must be adjusted to take into account differences between the species (e.g., monkeys can indicate a choice by grabbing objects with their hands, but birds might use their beaks, and spiders may choose where to walk their entire bodies, the latter of which functionally disallows attempts to get both objects at once, which may affect bimanual species' choices) or if the comparison is between humans and any other species (see below). If two species are tested on different paradigms and one species shows the effect but another does not, it is difficult, if not impossible, to tell whether this indicates true species differences. Was the task easier for one species due to innate differences in how they interacted with it? Was the adapted task easier, perhaps by providing more cues or additional pretraining? Did the humans get verbal instruction or was the task oversimplified for the other species in an effort to make it comprehensible? Similarly, if both species show the effect or both do not, it is unclear whether the difference in methodology masks species differences that are actually there. If these challenges sound familiar, they are the same ones faced by developmental scientists adapting their tasks for younger and younger children or cross-cultural researchers making sure that their tasks are interpreted in the same ways across many diverse perspectives. It may be even harder for comparative scientists (and infant researchers), however, because we cannot even ask the animals what they thought we were doing as a validation.

For example, some studies have found decoy effects in animals – a shift in the preferences between two options simply by adding a third, non-viable option – but findings and methodologies are extremely mixed. Bees show decoy effects when foraging from artificial flowers that vary in the effort they require, gray jays do so when foraging from feeding tubes with varying predation risks (Shafir et al. 2002), and rhesus macaques do when discriminating rectangles that differ in size and orientation (Parrish et al. 2015). However, the same rhesus macaques are unaffected by decoy options when choosing between tasks that vary in effort (Parrish et al. 2018) and two other primate studies do not find decoy effects in capuchins (Cohen and Santos 2016) or four great ape species tested with different food choice tasks (Sánchez-Amaro et al. 2019). Given these differences in paradigms, it is difficult to say what is signal and what is noise, making comparisons – and the conclusions we can draw from them – extremely limited.

Comparative researchers need to be particularly aware of this problem when adapting designs from human decision-making studies for use with animals. Whereas humans can provide one-shot decisions after verbal instructions, animals typically complete trials offering the same choice repeatedly and after sometimes extensive training. If animals show the phenomenon, is it equivalent to the humans' behavior? One way to explore this is to repeat the animal version of the task with human participants. For example, capuchin monkeys' risk preferences change depending on whether options are framed as gains or losses in a nonverbal paradigm (Lakshminarayanan et al. 2011). Though seemingly similar to the classic human findings (Kahneman and Tversky 1979), humans do not show this framing effect when tested with a similar procedure to the monkeys (Silberberg et al. 2013). Of course, this could also be because the tasks used with other species are simplistic and artificial, making them challenging to use with humans, who may not be motivated to do well in them. On the other hand, if animals do not show the phenomenon, does that absence indicate a true species difference or would humans also behave differently if tested with the animal paradigm? For example, chimpanzees, unlike humans, acted in a rational, self-interested way in a nonverbal version of the Ultimatum Game often used to assess fairness (Jensen et al. 2007; see also Kaiser et al. 2012). But when humans are tested in a similar paradigm, they maximize, too (Smith and Silberberg 2010). If we want to draw strong conclusions from comparative research, we need to test different species – humans included – using the same or equivalent procedures (although doing so comes with its own difficulties; see also Smith et al. 2018).

Even within the same species or the very same study population, researchers may vary seemingly small factors for practical reasons. For example, different animals may reasonably work for different food rewards because they show different preferences. Even if the same foods are used for all animals, different animals will value them differently. Although animals may show similar preferences (e.g., as indicated by the percentage chosen in two-choice trials), the difference in value between options may be quite different (Casey et al. 2013; Schwartz et al. 2016). Of course, this point is especially important when the difference in reward value can affect the behavior of interest (e.g., Beran et al. 2009a; Xu et al. 2011). In general, comparative researchers need to carefully consider whether the choices that animals make actually reveal their underlying preferences or may instead, for example, result from a lack of inhibition. Primates may "prefer" choosing less over more in the ephemeral reward task not because they actually prefer receiving less but because they are unable to inhibit the prepotent response of reaching for a visible food item or because they are averse to the option that sometimes disappears (Prétôt et al. 2016b). Conversely, capuchin monkeys choose to wait for a “larger, later” reward rather than obtain a “smaller, sooner” one in an intertemporal choice task, but may not actually be able to maintain the longer delay, suggesting that this does not truly reflect a choice to wait (Paglieri et al. 2013). Such seemingly minor changes to methodology can affect animals’ choices and lead us to conclude that a given decision-making bias is present when it is not or that it is not present when it actually is, which can further complicate comparisons across species.

The importance of inter- and intra-individual variability

Of course, carefully designing our studies with comparable methodologies is necessary but not sufficient if we want reliable, let alone valid results. Comparative research is notorious for small sample sizes and a limited range of species, and this presents a major obstacle to the comparative study of decision-making biases as well. For example, a recent review of primate cognition research published between 2014 and 2019 found that the median sample size across studies and species was 7 individuals and that fewer than 15% of primate species had been studied, which limits the generalizability of the results (ManyPrimates et al. 2019). One of the reasons why small samples are problematic is because they reduce our power to detect effects that really exist. If a species does not show a given bias or if a replication attempt fails, we do not know whether it is truly not present or whether we simply failed to detect it. Combined with the file-drawer problem – if null results are less likely to be published than statistically significant results – this can distort the literature and stifle scientific progress.

Oftentimes, we might find null results when there is a lot of individual variability relative to the effect (e.g., a change in mean preference, averaged over individuals). This pattern can make it hard to detect group-level effects and to generalize from the sample to the population. But this variability can be informative, and we lose a lot by averaging over individuals (and sometimes over species). Indeed, for certain effects we should even predict individuals to vary substantially, e.g. for biases that are hypothesized to rely on limited working memory ability or that vary with personality or with an individual's social relationships or their standing in the group. Rather than focusing just on whether a given bias is absent or present on a species level, we should strive to assess the extent to which it is, because individuals may vary in the strength of the effect or some individuals may be susceptible whereas others are not. For example, animals from a variety of species have shown negative responses to inequity (Brosnan and de Waal 2014; Oberliessen and Kalenscher 2019), including chimpanzees. However, in no study to date has this been the case for every single chimpanzee, and factors such as personality and the length of the relationship between partners have been suggested to affect the inequity response (Brosnan et al. 2005, 2010, 2015; Bräuer et al. 2006).

Assessing biases on a continuum rather than on a binary also opens up opportunities to further understand the underlying mechanisms and to assess the effect of different methodologies. For example, whether animals with a certain rank, sex, age, or cognitive skill are more susceptible to a bias helps us tease apart the effect of cognitive constraints, social relationships, and hormonal factors. This is particularly true in situations in which an individual's outcomes depend on what others do, e.g., in tests of cooperation or competition (see, e.g., Watzek et al. 2018). For example, if experimental tests of cooperation in the laboratory rely solely on pairs of animals who are, at a minimum, willing to be in proximity of each other, they likely result in a distorted picture of cooperative behavior because we know that it varies depending on who the partner is and how many animals are involved (e.g., in chimpanzees: Melis et al. 2006a, b; Suchak et al. 2014, 2017). Similarly, if those animals who show an effect in one paradigm also do so in another, then we can be more confident that both paradigms tap into the same underlying concept. Ideally, we can even extend this approach to testing whether different decision-making biases tend to co-occur, to assess the extent to which individual factors play a role.

Another source of variation that is often masked by averaging comes from changes over time, e.g., over the course of trials or sessions. This can be problematic because decision-making strategies can change also over time, e.g., due to learning effects, order effects, or satiation effects as an animal's energetic state changes with rewards from earlier trials. For example, primates' previous choices can affect their valuation of current options (Egan et al. 2007, 2010; West et al. 2010), and food deprivation might lead animals to make more rational, reward maximizing choices (Zentall et al. 2014) or to take risks they prefer to avoid when satiated (Caraco 1981). Therefore, the assumption that animals' choices in repeated trials are independent may rarely hold true, and we need to systematically assess changes over time. Finally, to our knowledge there are no studies of decision-making biases that assess the stability of these effects over longer time periods. Such studies may be more feasible when working with animals in the laboratory because the same animals can be tested repeatedly.

Future Directions for Studies of Animal Decision-making Biases

Comparative research into how animals make good or bad decisions promises unique insights into our own behavior. By assessing how a phenomenon is distributed across multiple species that vary in their cognitive abilities, constraints, and experiences, we can constrain our hypotheses for the psychological processes that give rise to it. For example, sunk cost effects can clearly arise in the absence of formal economic markets or arguably human-unique tendencies such as waste avoidance, and may rely on more wide-spread cognitive mechanisms. On the other hand, cognitive set bias may be unique to humans and arise from verbal encoding, greater working memory availability, and cultural or educational expectations about how to solve problems.

Further, the patterns in how closely or distantly related the species that share a given effect are can reveal at which points in the phylogenetic tree it evolved. Knowing to what extent behaviors are homologous or convergent, in turn, lets us generate hypotheses about why they may have evolved. Do these decision strategies solve a problem that is commonly encountered in these species' environments? Inequity aversion, for instance, may lead to a short-term loss but ensure better cooperation in the long run. Or are biases simply by-products of otherwise adaptive strategies that fail in certain circumstances? If so, how often do animals actually encounter situations in which such irrational behavior would emerge and how costly is it? Studying decision-making biases in species other than our own lets us answer these questions. Importantly, this research can yield insights and new testable predictions that can help better explain human behavior as well. For example, the findings that the strength of endowment effects may vary with the evolutionary salience of the object, and that sunk cost effects may not accrue while weighing whether to invest but only for ongoing investments arose from comparative research but have implications for human decision-making.

However, in order to draw valid evolutionary inferences from cross-species comparisons, we need a reliable and valid body of empirical work. Methodological differences both within and across species, small sample sizes, and limited diversity in the kinds of species that have been tested are major challenges to the comparative study of decision-making biases. If we are not sure whether a given bias is present or not in a specific species, let alone whether the "same" bias was assessed in another species, any inferences that rely on how the phenomenon is distributed across species are severely limited. To complicate this issue, by simply assessing presence or absence, we may miss out on important variability in how strongly an effect manifests and whether it is affected by changes over time (e.g., learning through experience) or reliably predicted by individual differences.

Of course, no single researcher can address all of these issues and gaps in the comparative study of decision-making biases, but neither can they only be solved by top-down changes to the field at large. Practices that individual researchers can adopt range from minimal changes to current procedures to literal and figurative paradigm shifts. Of course, some of these measures will not be possible in every case, e.g., for practical or ethical reasons. Nonetheless, here we list some ideas that individual researcher can adopt themselves in their role as study authors or can encourage others to adopt in their role as reviewers and editors:

1. Conducting direct replications of previous studies in the same species.
2. Testing other populations and study species with the same paradigm used with other species in previous studies.

3. Testing the same study population with several paradigms for the same concept.

4. Collaborating with others to increase sample sizes and ensure direct comparability.

5. Reporting data for individuals and considering potential sources of variability. If possible, sharing raw data on a more detailed level to improve peer review and allow for secondary analyses.

6. Reporting the extent of biases as dependent variables and design experimental measures to capture a continuum rather than a binary.

7. Publishing results regardless of outcome. Preregistrations and article formats such as registered reports are two recent developments that can help in combatting the file-drawer problem from the researcher side. Of course, increased willingness to recommend and accept "negative" or mixed results by journals is necessary on the reviewer and publisher side.

We believe that the field stands to benefit immensely if comparative researchers adopt even just some of these practices. Doing so helps us build a robust body of scientific literature on both good and bad decision-making in animals. This allows us to more deeply understand how, when, and why we make these decisions than we could by studying humans alone, revealing the cognitive processes and evolutionary forces that give rise to irrational behavior. Combined with insights from developmental and cross-cultural perspectives, such an understanding is crucial to disentangling the factors that influence our own behavior, which, ultimately, will help us make better decisions.

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2

CAPUCHIN MONKEYS (*SAPAJUS [CEBUS] APELLA*) ARE MORE SUSCEPTIBLE TO CONTRAST THAN TO DECOY AND SOCIAL CONTEXT EFFECTS

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Abstract

Theories of optimal decision-making typically assume that animals have consistent preferences among options. In reality, economic behaviour in humans and foraging behaviour in some animals is often susceptible to choice-irrelevant factors such as inferior options or conspecifics' outcomes, but the evidence for primate decision-making is mixed. Unlike previous experiments, we assessed the relative magnitude of three context effects. Using a food preference paradigm, we varied the number of cereal pieces to determine how much a piece of food A was "worth" (50% choice) to each of 13 capuchins. We predicted that monkeys would devalue A in the contrast condition (when a higher-quality but unattainable food was present) and overvalue it in the decoy condition (when a smaller version of A was a third option) and social condition (when A, if unchosen, was given to a partner). Capuchins were 4 times less likely to choose A in the contrast condition, but 2 to 3 times more likely to choose it in the decoy and social conditions. When carefully accounting for initial preferences, we found that these primates, like humans, are sensitive to context effects. This suggests that these biases are evolved and impacts how we think about them in humans.

Keywords: decision-making bias, context dependence, decoy effect, contrast effect, capuchin monkey, *Sapajus [Cebus] apella*

Introduction

Animals from a wide array of taxa change their preference depending on the context, such as what other options or social partners are present, how or in which sequence options are presented, what choices they previously made, or their current energetic state [for example, see 1,2]. Such aspects should be irrelevant if animals form stable preferences and use them to make consistent decisions, but responding to these factors can make more sense when viewed in the context of an individual's environment, which has been hypothesized to shift preferences in consistent ways [3–6]. For example, to be a successful member of the group, social animals *should* consider the effect of their actions on their relationships with others and modify their behaviour accordingly. If an animal is on the brink of starvation, it *should* take on more risk than it usually would. In the real world, making decisions contingent on these factors often makes sense, and indeed, our brains seem wired to do so [7–9]. Further, if an individual has limited cognitive resources, it seems reasonable to follow easier strategies if they work well most of the time, even if they fail in some situations [10–12]. However, comparative studies of context-dependent choice to date have typically emphasised only whether or not a given effect is present, but not to what extent it is or how its magnitude compares to other context effects. In this study, we quantified the relative importance of two non-social (decoy and contrast) and one social context effect on reward valuation in capuchin monkeys, who have shown human-like decision-making biases in some contexts [2,13–17] though not others [18–23].

The decoy effect – in which one option increases in value when an inferior one is added – has been found in some animal species but not others, but these studies have used vastly different methodologies, making it difficult to compare across studies, much less species. This limits the evolutionary inferences we can draw. For example, bees and grey jays show decoy effects when choosing among artificial flowers and tubes holding raisins, respectively [24]. But in primates, the only study that has found a decoy effect used a perceptual discrimination task [25], but the same monkeys do not show the effect when choosing among tasks that vary in effort required [26]. Further, two studies using food choice tasks, which are arguably most similar to the foraging experiments used with bees and grey jays, found no evidence of this bias [19,27]. One possibility for these results is that the primates' preferences between the initial options were too strong for the decoys to change their behavioural choices, even though they might have changed the perceived value of the options. For example, if you typically prefer a grape 80% of the time over a piece of banana, then the presence of a smaller grape might raise the value of the whole grape, but not enough to actually choose it statistically significantly more often, especially if they easily substitute for each other [28,29]. Here we test the possibility that primates' decoy effects in food choice experiments depends on the strength of their initial preference by assessing preference changes relative to both low and high baseline comparisons. Critically, we established baselines specific to each monkey to better compare shifts in preferences across individuals.

Contrasting the inconsistent evidence surrounding decoy effects, evidence for contrast effects – in which an option decreases in value when a superior one is present, but unattainable – is quite consistent. Indeed, operant conditioning relies on animals' expectations for specific outcomes (such as rewards) after specific actions and changing their behaviour if that outcome changes (i.e., learning) [30,31]. Presenting a reward presumably prompts an expectation to receive it and violating this expectation can result in a negative emotional response. Simply put, the animal may get frustrated [30,32–35]. Such frustration effects have been proposed to play a role in why animals may respond negatively to inequity, that is, when they receive less than a partner for the same work [15,36].

Here we used an identical paradigm to quantify and compare the extent to which these three context effects change how a food item is valued. We used a food preference paradigm typical for both decoy and contrast effects, although our social condition differs from typical studies on inequity aversion. Typically, the partner receives a food item that is assigned by the experimenter and is independent of what the participant does, whereas in our paradigm, whether the partner received a food item was explicitly linked to the participant's choice. We predicted that the monkeys would devalue a food item (e.g., a piece of apple) if there was a better, though unattainable option present (contrast condition), and overvalue the food if there was a worse option present (decoy condition) or when the food went to a social partner if the participant did not choose it (social condition). For a rational decision-maker, of course, there should be no differences between these conditions, as they should be unaffected by these choice-irrelevant factors.

Methods

Participants

We tested 13 capuchin monkeys (*Sapajus [Cebus] apella*, 10 female, 3 male, age $M \pm SD$ = 15.31±5.57, range: 7-23 years). These capuchins are socially housed in three mixed-sex groups, each with their own indoor/outdoor enclosures with a variety of climbing structures, visual barriers, and regularly provided enrichment devices. Capuchins routinely separate voluntarily into testing boxes attached to their enclosures for cognitive and behavioural studies. They were never required to come in for testing and could choose not to participate at any time without consequences. Monkeys always had access to water, including during testing, and were never food deprived (except for medical reasons unrelated to research studies). All testing food was given in addition to their daily diet of vegetables, fruit, and primate chow.

Procedure

We administered a series of food preference tests to determine how much a specific food item was valued in units of another food. We considered indifference (50% choice) between two options to indicate equivalence. Each trial began by placing two or three food items (depending on the condition, see below) on a board out of the monkey's reach. The board was pushed within the monkey's reach and the monkey made a choice by reaching for one of the available options. The experimenter covered the unchosen options with her hands and removed them while the monkey ate the food. The next trial began immediately. Options were counterbalanced so that they appeared in each of the locations on the board in an equal number of trials, but no more than twice in a row in the same location. Each session took place on a different day.

Test conditions

For each monkey separately, we identified food items A and B such that they reliably preferred food A over ½ a cereal piece and a smaller version of itself (decoy food A), but also reliably preferred 5 cereal pieces and contrast food B over food A (see ESM and Table S2.1).

Monkeys completed 6 sessions with 18 trials for the baseline condition. Monkeys then completed 2 sessions with 18 trials each of the decoy, contrast, and social conditions (Fig. 2.1) in a randomly assigned order.

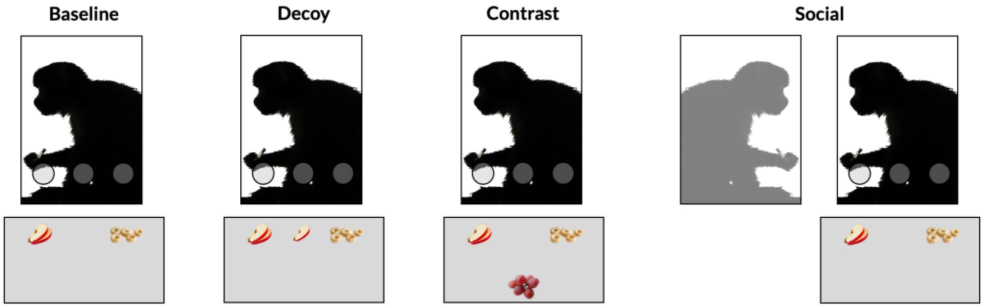

Figure 2.1 Test setup and test conditions. During test conditions, monkeys always chose between food A and ½ to 5 pieces of cereal (baseline). In the decoy condition, a smaller piece of food A was available as a third option. In the contrast condition, a better food item was present, but out of reach. In the social condition, a partner monkey (sitting in an adjacent test box) received food A if the participant monkey did not choose it.

In the *baseline* condition, monkeys chose between food A and X cereal. The number of cereal pieces, X, was the same within a session but varied across sessions. Monkeys completed one session each for X equal to ½, 1, 2, 3, 4, and 5 pieces of cereal in a random order. We then used this preference data to determine two "medium" amounts of cereal for each monkey (Table S3.1). Amount L (lower bound) was the largest number of cereal that the monkey chose less than 50% of the time compared to food A. Amount U (upper bound) was the smallest number of cereal pieces that the monkey chose more than 50% of the time compared to food B (Fig. S2.1).

The *decoy* condition was identical to the baseline condition except that the decoy food A was available as an option in addition to food A and X cereal (Fig. 2.1). Monkeys completed one session each for X equal to L and U in a random order (e.g., food A vs. 2 cereal and food A vs. 3 cereal).

The *contrast* condition was identical to the baseline condition except that the contrast food B was present in addition to the two food options (food A and X cereal). The contrast food was located in the middle of the board but remained out of the monkey's reach throughout the trial (Fig. 2.1). Monkeys completed one session each for X equal to L and U in a random order.

The *social* condition was identical to the baseline condition with one exception. If the monkey chose the cereal pieces, then food A was given to the partner monkey in a neighbouring test box (Fig. 2.1). If the participant monkey chose food A, the partner did not receive any food (see Table S2.1 for partner assignments). Monkeys completed one session each for X equal to L and U in a random order.

Results

To compare the effect of the different non-social and social contexts on monkeys' valuations of the food at the group level, we fit a mixed effects logistic regression model with choice as the binomial outcome variable. We included individual identity as a random effect to account for individual variability in baseline food preferences. We found a significant interaction effect of condition and number of cheerios on capuchin monkeys' food preferences (Fig. 2.2), $\chi^2(3)= 26.984$, $p<.001$.

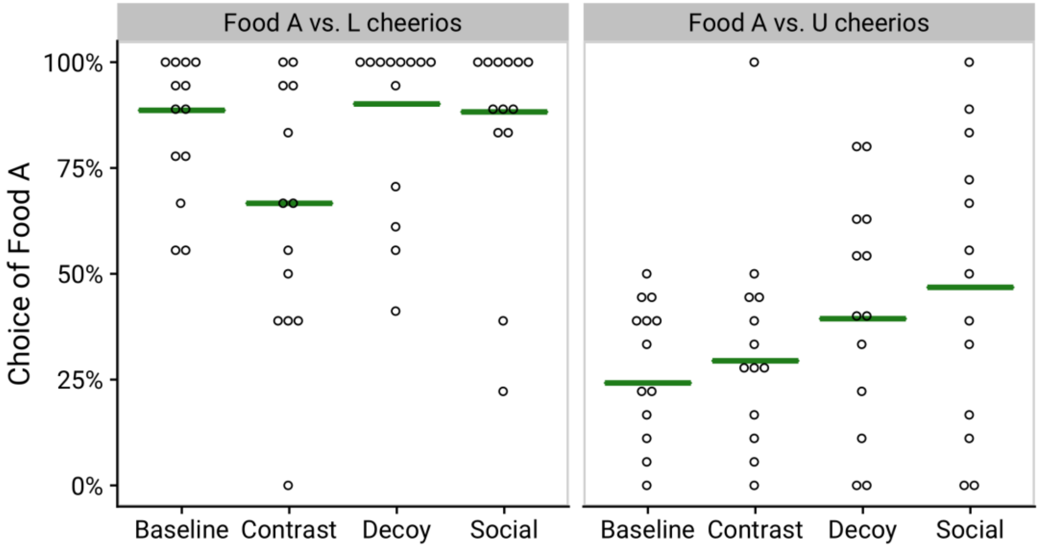

Figure 2.2. Food preference by condition and number of cheerios. Percentage of trials in which each capuchin monkey chose food A over L cheerios (left panel) or U cheerios (right panel). Horizontal lines indicate estimated marginal means.

Capuchins' choices for food A over L cheerios became 3.9 times less likely in the contrast condition (odds ratio [*OR*]=$^1/_{3.9}$, *SE*=0.06, *p*<.001), but did not change significantly in the decoy and social conditions compared to baseline (*p*s>.05). Conversely, capuchins' choices for food A over U cheerios became twice as likely in the decoy condition[1] (*OR*=2.04, *SE*=0.44, *p*=.003) and 2.8 times more likely in the social condition (*OR*=2.76, *SE*=0.60, *p*=.003), but did not change significantly in the contrast condition compared to baseline (*p*s>.05).

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[1] Decoy food A, intended as a non-viable option, was indeed chosen in only 2% of trials.

Discussion

Capuchin monkeys showed all three context effects in the predicted direction. They devalued a food item when a higher-quality but unattainable option was present (contrast effect) but overvalued it when an inferior option was available (decoy effect) or when it was given to a partner if the monkey did not choose it (social context effect).

These results held across different food items but depended on monkeys' initial preferences. Only relatively strong preferences for the target food were susceptible to being suppressed by contrast. Conversely, only relatively low preferences were susceptible to being boosted by the decoy or partner outcomes. This dependence on baseline preferences may, in part, explain why previous studies using food preference paradigms with primates [19,27] have found mixed results, because they used the same food items and quantities for each individual. In this study, we carefully calibrated monkeys' initial preferences 1) by changing the food items and sizes and 2) by using a countable food item that does not easily substitute for fruit and vegetable pieces. The latter is important because food preferences may not only reflect differences in value but also the degree of substitutability [28,29], because, for example, one type of nut can replace another but neither can replace water.

To our knowledge, this study is also the first to directly compare the magnitude of different context effects using the same paradigm to assess them. The contrast condition had almost twice as big of an effect as the decoy and social conditions, suggesting that devaluing food items in the presence of better ones potentially has a higher impact on fitness. Interestingly, capuchin monkeys' responses to the decoy and social conditions were similar. Note that in the social condition with relatively few cereal pieces (amount L), capuchins did not experience the social outcome (the partner receiving food A) very often because they typically chose food A themselves. However, preferences for food A were also predicted to increase, suggesting a possible ceiling effect. The fact that our paradigm can detect such sensitivity opens up exciting possibilities for future comparative research to systematically assess how differences in species' feeding and social ecologies may shape their relative susceptibility to different biases.

In this study, we found that capuchin monkeys, like humans, are susceptible to a range of context effects. These results support the hypothesis that these decision-making biases are evolved and has implications for how we address them in humans. Our paradigm allows researchers to test a wide range of taxa and to directly compare the magnitude, rather than just the presence or absence, of these effects. In particular, studying which aspects of animals' physical and social environments may have shaped the evolution of these biases lets us better understand why we show them and, ultimately, helps us make better decisions.

Ethics This study was purely behavioural, non-invasive, and was carried out in accordance with all applicable international, national, and institutional ethical guidelines and legal requirements. All procedures were approved by the Georgia State University Institutional Animal Care and Use Committee (IACUC A19028 and A20018). Georgia State University is fully accredited by the Association for Assessment and Accreditation of Laboratory Animal Care (AALAC).

Data accessibility The design and analyses for this study were preregistered at the Open Science Framework prior to data collection (osf.io/yx2pz). The data generated and analysed during this study are publicly available at the Harvard Dataverse (doi:10.7910/DVN/FDX7SC).

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Electronic Supplementary Material

Pretest conditions

During *pretest 1* sessions, monkeys completed 9 trials each for two comparisons presented in random order: food A vs. ½ a cereal piece and food A vs. 5 cereal. Monkeys advanced to *pretest 2* when they completed two consecutive sessions in which they chose food A over ½ cereal in 7 out of 9 trials and chose 5 cereal over food A in 7 out of 9 trials (i.e., 14 out of 18 total trials per comparison, a statistically significant preference in a binomial test).

During *pretest 2* sessions, monkeys completed 9 trials each for two comparisons presented in random order: food A vs. decoy food A and food A vs. contrast food B. Decoy food items were smaller versions of food A. Contrast food items were a qualitatively different food item, but identical in size to food A. For example, if food A was a 1g piece of apple, decoy food A was a 0.5g piece of apple, and contrast food B was a 1g piece of grape. Monkeys advanced to testing when they completed two consecutive sessions in which they chose food A over decoy food A in 7 out of 9 trials and chose contrast food B over food A in 7 out of 9 trials.

We changed the food items and their sizes to find a suitable combination for each monkey (Table S2.1).

Table S2.1. Partner assignments and test foods. * indicates males. In the pretest conditions, we identified food items for each monkey such that food A was reliably preferred over ½ cereal and a smaller version of itself (decoy food A), but such that 5 cereal and contrast food B were reliably preferred over food A. In the baseline condition, we identified two "medium" cereal amounts that the monkey preferred just less than (amount L) or just more than (amount U) food A (see main text and Fig. S2.1).

Group	Monkey	Partner	Food A	Decoy Food A	Food B	L	U
1	Logan*	Ingrid	Cucumber 1.5g	Cucumber 0.75g	Apple 1.5g	1	2
1	Ira	Irene	Cucumber 2g	Cucumber 1g	Apple 2g	0.5	1
1	Paddy	Ira	Cucumber 1g	Cucumber 0.5g	Apple 1g	2	3
1	Irene	Ingrid	Cucumber 2.5g	Cucumber 1.25g	Apple 2.5g	2	3
1	Ingrid	Ira	Apple 1g	Apple 0.5g	Grape 1g	1	2
2a	Griffin*	Wren	Apple 1g	Apple 0.5g	Grape 1g	2	3
2a	Lily	Griffin*	Cucumber 1g	Cucumber 0.5g	Apple 1g	0.5	1
2a	Wren	Lily	Cucumber 2g	Cucumber 0.5g	Apple 2g	0.5	1
2a	Widget	Wren	Cucumber 2.5g	Cucumber 1.25g	Apple 2.5g	0.5	1
2b	Nkima*	Gambit	Apple 1g	Apple 0.5g	Grape 1g	1	2
2b	Nala	Nkima*	Apple 1g	Apple 0.5g	Grape 1g	0.5	1
2b	Gambit	Lychee	Apple 1.2g	Apple 0.6g	Grape 1.2g	1	2
2b	Lychee	Nkima*	Apple 2g	Apple 1g	Grape 2g	2	3

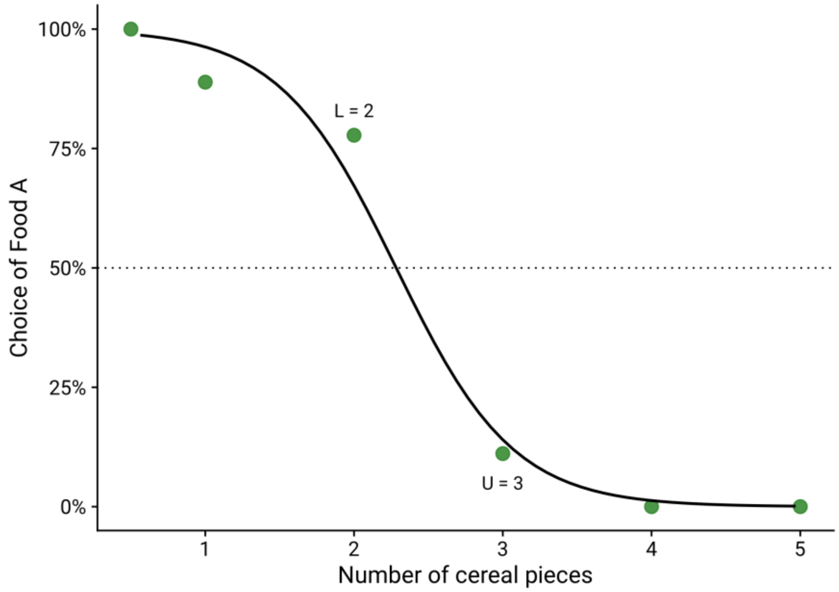

Figure S2.1. **Example of a monkey's preference data in the baseline condition.** Solid line indicates logistic curve fit. Amounts L and U indicate the lower and upper bound of how many pieces of cereal food A is "worth" (equivalent to).

3

CAPUCHIN AND RHESUS MONKEYS SHOW SUNK COST EFFECTS IN A PSYCHOMOTOR TASK

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Abstract

Human decision-making is often swayed by irrecoverable investments even though it should only be based on future – and not past – costs and benefits. Although this sunk cost effect is widely documented and can lead to devastating losses, the underlying psychological mechanisms are unclear. To tease apart possible explanations through a comparative approach, we assessed capuchin and rhesus monkeys' susceptibility to sunk costs in a psychomotor task. Monkeys needed to track a moving target with a joystick-controlled cursor for variable durations. They could stop at any time, ending the trial without reward. To minimize the work required for a reward, monkeys should have always persisted for at least 1 second, but should have abandoned the trial if that did not yield a reward. Capuchin monkeys and especially rhesus macaques persisted to trial completion even when it was suboptimal, and were more likely to complete the trial the longer they had already tracked the target. These effects were less pronounced, although still present, when the change in expected tracking duration was signalled visually. These results show that sunk cost effects can arise in the absence of human-unique factors and may emerge, in part, because persisting can resolve uncertainty.

Keywords: decision-making bias, sunk cost, rhesus macaque, capuchin monkey, *Macaca mulatta*, *Sapajus [Cebus] apella*

Introduction

We routinely consider sunk costs (irrecoverable prior investments of e.g., money, time, or effort) when making decisions that should only be based on the future costs and benefits. For example, if your benefit from selling your car is bigger than from keeping it (e.g., due to lack of use or maintenance and repair costs), then you should sell it, regardless of what you initially paid for it. However, humans tend to persist in an endeavour the more resources we have already invested into it[1,2]. This susceptibility to sunk costs can lead to bad decision-making for individuals, organizations, and even societies as a whole, for example, if people spend time, money, and effort on doomed projects or policy initiatives. In one notable example, the Concorde airplane project wasted millions in funding even after decision-makers realised that it had become a "commercial disaster[3];" in fact, this bias is sometimes called the Concorde fallacy. Here we assess capuchin monkeys' and rhesus macaques' susceptibility to sunk costs to better understand the mechanisms that underlie this phenomenon.

Such a comparative approach is particularly useful in this case because there are several psychological explanations for why this effect may arise that we can discriminate among by examining other species' choice patterns. For example, people may justify continued investments because they have publicly committed to doing so, because they rationalize their previous decisions as sound rather than mistaken, because they want to avoid being wasteful, because they are uncertain about their prospects, or because they eschew a definite loss (if they sell lower than they bought) in case a small additional investment turns things around for a gain[1,2,4–13]. Disentangling which processes contribute to sunk cost effects empirically is difficult because multiple may play a role and because they make similar predictions – that people consider sunk costs when it is suboptimal to do so and that the effect increases with the size of the sunk cost (i.e., irrecoverable prior investment).

Assessing susceptibility to sunk costs in species other than humans can help us narrow down the possible explanations because other animals differ in some of these psychological mechanisms. If the sunk cost effect relies on human-unique factors, such as self-rationalization or public commitment, we would not predict other animals to show the sunk cost effect. On the other hand, if widespread responses to uncertainty or resource scarcity underlie the sunk cost effect, we would expect other animals to also be susceptible to sunk costs. We can further disentangle possible explanations by systematically studying the effect in species that vary in the behaviour of interest. For example, only starlings and capuchin monkeys have shown human-like loss aversion under risk[14,15], becoming more risk prone when options were framed as losses than when the same options were framed as gains. To the extent that loss aversion contributes to the sunk cost effect, we would expect it to emerge in these species, but not in others that do not respond to losses in this way (although this has not been widely studied in animals). Conversely, if susceptibility to sunk costs does not covary with differences in how a proposed mechanism is expressed across species, this suggests that this mechanism does not contribute to the emergence of the sunk cost effect in these species or in humans. Such a comparative approach can be particularly insightful if several mechanisms may contribute to the sunk cost effect in humans, because understanding the pattern of responses lets us assess their relative contributions.

Indeed, humans are not the only species that shows sunk costs effects[16], suggesting that human-unique factors such as human language, culture, or formal economic markets are not required for this bias to arise. For example, in experiments in which pigeons and rats needed to complete a repetitive action (such as pecks or lever presses), both species showed sunk cost effects, persisting with the action even when it became optimal to abandon the reinforcement schedule by selecting an opt-out option that skipped to the next trial[8,17–20] (but see ref. [21]). However, this effect disappeared when uncertainty about the remaining investment (required pecks or lever presses) was removed by signalling, via colour change, that a specific number of actions had been completed[8,17] or when persisting required many more responses to reward[8,17,18,22]. These results suggest that the sunk cost effect emerges, in part, when we are uncertain about when it becomes beneficial to opt out rather than to continue investing, especially if there is little cost to persisting. In a foraging task that required waiting (i.e., inaction rather than action), rats, mice, and humans also showed sunk costs effects, becoming more likely to complete a trial (i.e., to continue waiting rather than to opt out) the longer they had already waited[23]. Here, however, information about the remaining investment was always signalled via sound, suggesting that uncertainty reduction does not explain susceptibility to sunk costs in all contexts.

In this study, we tested capuchin and rhesus monkeys using a computer task to assess the sunk cost effect in nonhuman primates for the first time. These species make economically suboptimal choices similar to humans' in some situations[24,25] (e.g., framing effects[26] and loss aversion[14], endowment effects[27], peak-end effects[28,29] [but see ref. [30]], sensitivity to counterfactual outcomes[31–33]). In other contexts, however, capuchin and rhesus monkeys are more likely than humans to abandon a learned strategy in favour of a more efficient one in others (e.g., switching to an optional shortcut[34] or violating transitivity when it is optimal to do so[34,35]), suggesting that they may not be as susceptible to sunk costs as people are. Our psychomotor task required continued action to persist (similar, in some aspects, to the repetitive-action paradigms used with pigeons and rats[8,17,18,21]), but unlike previous work, it required a continuous action (maintaining pressure on a joystick to keep a cursor moving) rather than a discrete response (pecking or lever pressing). We implemented this change to encourage monkeys to perceive and assess the investment in its entirety and not potentially as a series of seemingly unconnected actions, only some of which were rewarded.

If monkeys are susceptible to sunk costs, we predicted that they would persist in tracking a target even when opting out was optimal, and that they would be more likely to persist the longer they had already persisted. Further, we explicitly tested the extent to which the sunk cost effect in primates may arise due to uncertainty about the required additional effort by signalling effort visually. Based on previous work in pigeons and rats, we expected monkeys to show smaller sunk cost effects in the signalled condition, when this uncertainty is removed, than in the unsignalled condition, when there is uncertainty.

Methods

Participants

We tested 26 capuchin monkeys (18 female, 8 male, age: *M* ± *SD* = 17.65 ± 8.06, range: 7 to ca. 45 years) and 7 rhesus macaques (all male, age: *M* ± *SD* = 23.57 ± 7.35, range: 16-37 years) at the Language Research Center of Georgia State University.

Capuchin monkeys were socially housed in mixed-sex groups, each with their own indoor/outdoor enclosures with a variety of climbing structures, visual barriers, and regularly provided enrichment devices (e.g., foraging boards and puzzle boxes). Capuchins had been trained to separate voluntarily into testing boxes attached to their indoor enclosures for cognitive and behavioural studies. They were never required to come into the test boxes for testing and they could choose not to participate at any time without consequences. Rhesus macaques were individually housed with continuous auditory and visual access to other monkeys and, when possible, regular social periods with compatible partners. Their enclosures doubled as testing boxes, but they too could choose not to participate at any time without consequences.

All monkeys had access to water at all times, including during testing, and were never food deprived (except for medical reasons unrelated to research studies). All testing food was given in addition to their daily diet of vegetables, fruit, and primate chow.

Task

Monkeys were tested on individual computer testing systems (for details, see ref. [36]). In this study, they needed to track a moving target with a cursor that they controlled with a joystick. After maintaining contact with the target for a specified duration, monkeys received a reward. If monkeys lost contact with the target, they did not receive a reward and the next trial began immediately.

All trials began with the target, a purple circle with a 150-pixel diameter, placed at a random location on an 800 × 600-pixel screen and a red cursor placed directly under the target at a distance of 85 pixels (Fig. 3.1). While the cursor was outside the target, the target only moved when the cursor moved and stopped moving when the cursor stopped moving. The target moved in a straight line, starting with a random direction.

When it reached the edge of the screen at a given angle, it reflected at the same angle, like a billiard ball bounces off a rail.

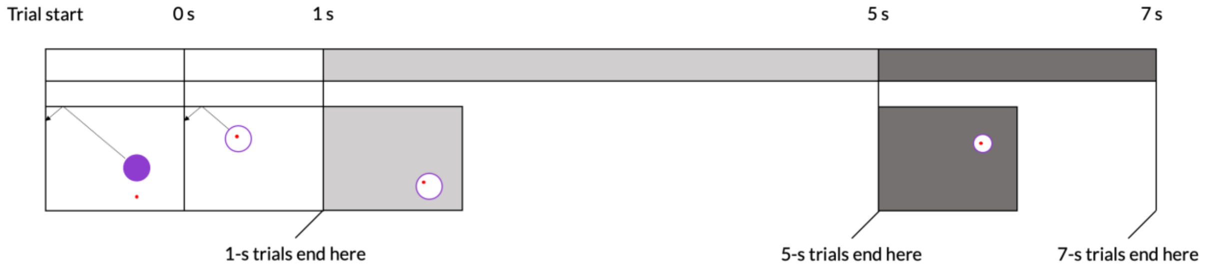

Figure 3.1. Schematic trial progression. Dotted line and arrow show an example trajectory of the target (not present on actual trials). The tracking duration started when the cursor entered the target and lasted 1, 5, or 7 seconds. If the target was tracked for the entire duration, the monkey was rewarded; if they lost contact with the target, the trial ended without reward. In the unsignalled condition, the background colour remained white throughout the trial. In the signalled condition (shown here), the background colour changed to light grey after 1 second and to dark grey after 5 seconds (if applicable).

When the cursor entered the target, the target changed colour to white and now kept moving even when the cursor stopped. If the cursor lost contact, the trial ended without reward. If monkeys maintained the cursor within the target for a specified duration, they received positive auditory feedback (*whoop*) and a banana-flavoured food pellet. The next trial began immediately. Monkeys completed blocks of 24 trials.

During *training*, monkeys learned to track the target for variable durations, including but not limited to the tracking durations used during testing. The tracking duration required to receive a reward was a randomly determined number between 0 and X seconds for each trial (drawn from a uniform distribution and rounded to milliseconds, i.e., three decimal places). The maximum tracking duration possible (X) increased as monkeys proceeded through training; monkeys automatically proceeded to next phase when they successfully earned the reward in at least 80% of trials in two separate trial blocks (Table 3.1).

Table 3.1. Training phases. Maximum tracking duration required and monkeys' training performance (number of blocks required to meet criterion and number of monkeys who did and did not meet the criterion) for each phase.

Phase	Maximum Duration	Species	Blocks to Meet Criterion			N_{passed}	N_{failed}
			Mdn	*IQR*	Range		
1	1 s	Capuchin	3	2-7	2-35	24	2
2	3 s	Capuchin	20	10.5-105.5	3-204	20	4
3	6 s	Capuchin	71	35-219.25	3-292	16	4
4	8 s	Capuchin	21	15-51	2-100	13	3
1	1 s	Rhesus	2	2-2	2-19	7	0
2	3 s	Rhesus	2	2-2.75	2-11	6	1
3	6 s	Rhesus	2.5	2-8.25	2-36	6	0
4	8 s	Rhesus	5	2.25-11.5	2-20	6	0

During *testing*, each block consisted of 12 baseline trials and 12 probe trials for all species. Baseline trials had a tracking duration of one second; probe trials had a tracking duration of either five (6 trials) or seven seconds (6 trials).

At the beginning of each trial, the expected value for the tracking duration was 3.5 seconds (1/2 chance of 1 s + 1/4 chance of 5 s + 1/4 chance of 7 s). The measure of interest was monkeys' behaviour in probe trials after they had tracked the target for one second. At this point, they could have realized that it was not a baseline trial and that the expected additional tracking duration had changed (Table 3.2). Monkeys would now need to track the target another four or six seconds to receive the reward. But if they stopped moving the cursor to let the target lose contact ("opting out"), a new trial would begin that required only one second of tracking in most trials (and 3.5 seconds on average). Thus, opting out was optimal if there had not been a reward after one second of tracking. However, if monkeys persisted and tracked the target for a total of five seconds, they either received the reward at that time (in a five-second trial) or should have persisted for another two seconds (in a seven-second trial), which was less additional tracking time than a new trial required on average (3.5 seconds).

Table 3.2. Expectations for tracking durations. Expected values for additional tracking required to receive the reward depended on the duration already spent tracking and the likelihood for which trial duration was in effect.

Duration spent tracking target	Expected additional duration required	Calculation
0 s	3.5 s	½ × 1s + ¼ × 5s + ¼ × 7s
1 s	5 s	½ × 4s + ½ × 6s
5 s	2 s	2s

In the *unsignalled* condition, the background colour remained white throughout the trial. In the *signalled* condition, the background colour changed when the expected duration changed (Fig. 3.1). In five- and seven-second trials, the background colour changed to light grey after the target had been tracked for one second. In seven-second trials, the background changed to dark grey after the target had been tracked for five seconds.

Design

We used a within-groups design; each monkey completed both the unsignalled and the signalled condition. Half of the monkeys were assigned to complete the unsignalled condition first and half were assigned to complete the signalled condition first. Monkeys who passed all training phases completed 40 blocks per condition, resulting in a total of 1920 trials (960 × 1 s, 480 × 5 s, and 480 × 7 s). Monkeys could complete as many trials per session as they wanted and completed testing over several test days (capuchin *Mdn* = 6 days, *IQR* = 3-9 days, range = 2-11 days; rhesus *Mdn* = 2.5 days, *IQR* = 2-3 days, range = 1-3 days).

Data Analysis

To assess monkeys' susceptibility to sunk costs, we fit mixed effects logistic regression models with trial completion as the binomial outcome variable (did or did not track the target for the entire duration; i.e., did or did not earn the reward). We included individual identity as a random effect to account for individual variability in persistence. We included required tracking duration (1, 5, and 7 s), condition (unsignalled and signalled), species (capuchin and rhesus), block bin (each bin comprised 4 blocks, i.e., 96 trials; thus, monkeys' first condition comprised bins 1-10 and the second comprised bins 11-20, centred to $M = 0$), and training duration (total number of blocks required to pass criterion, standardized to $M = 0$ and $SD = 1$) as fixed effects. We further included trial duration × condition × species and trial duration × condition × block bin interaction terms. We computed pairwise contrasts for significant model terms. We used likelihood ratio tests using single-term deletions to assess each factor's importance with respect to model fit.

To assess monkeys' susceptibility to sunk costs depending on how long they had already tracked the target, we first organized the data into seven non-exclusive subsets for sunk costs of 0, 1, 2, 3, 4, 5, and 6 s. That is, each subset contained data for trials at the points when monkeys had already tracked the target for at least 1 to 6 s, respectively. For example, sunk cost 0 s applied to all trials, and sunk cost 6 s applied to all trials for which monkeys had already tracked the target for at least 6 s (by definition, this subset could not include trials with tracking durations of 1 or 5 s). We then calculated the time remaining for the trial by subtracting the sunk cost from the required tracking duration. For example, if a monkey had already tracked the target for 3 s in a 5-second trial, the time remaining was 2 s. However, for a monkey to have 2 s remaining in a 7-second trial, they would have already tracked the target for 5 s. That is, 7-second trials had higher sunk costs than 5-second trials when the same amount of time was remaining. We excluded 1-second trials for this analysis because sunk costs were always at least 0 but never more than 1 s (i.e., there was no variability in sunk costs for these trials).

For the combined data, we then fit a mixed effects logistic regression model with trial completion as the binomial outcome variable (did or did not track the target for the entire duration; i.e., did or did not earn the reward). We included the trial duration × time remaining interaction as a fixed effect. We again included individual identity as a random effect to account for individual variability in baseline persistence and included the trial duration (5 and 7 s) × condition (unsignalled and signalled) × species (capuchin and rhesus) interaction as a covariate. We used likelihood ratio tests using single-term deletions to assess each factor's importance with respect to model fit. We computed a pairwise contrast to compare the regression coefficients for 5- and 7-second trials. If monkeys were more likely to finish tracking the target the longer they had already tracked it, then the probability to complete the trial should be higher for higher sunk costs (i.e., higher in 7- than 5-second trials if the same time was remaining), and it should be less affected by the time still remaining. That is, the slope for 7-second trials should be shallower than for 5-second trials.

Results

Effects of trial duration and signalling condition

We found a significant trial duration × condition × species interaction effect on monkeys' likelihood to track the target for the required duration, $\chi^2(2) = 17.22$, $p < .001$, suggesting that species differed in whether they completed trials depending on how long it took to do so and whether this duration was signalled or not. We dropped the trial duration × condition × block bin interaction term and fixed effect of training duration, as they did not significantly improve model fit, $\chi^2(3) = 3.87$, $p = .276$. However, we found significant two-way interaction effects of block bin with trial duration, $\chi^2(2) = 103.07$, $p < .001$, and condition, $\chi^2(1) = 15.14$, $p < .001$, indicating that monkeys' responses changed over time.

Overall, monkeys completed almost all 1-second trials but were 7 times less likely to complete 5-second trials and 10 times less likely to complete 7-second trials (Fig. 3.2), odds ratios (*OR*±*SE*) 5s: 6.88±0.26, 7s: 10.25±0.39, *p*s < .001. However, the magnitude of this effect depended on the species and the condition. Although capuchin monkeys and rhesus macaques completed 1-second trials at similar, high rates, capuchins became 11 and 19 times less likely to complete 5- and 7-second trials, respectively (*OR*±*SE* 5s: 11.45±0.45, 7s: 19.04±0.78, *p*s < .001). Rhesus macaques became only 4 times and 5.5 times less likely to do so (*OR*±*SE* 5s: 4.13±0.27, 7s: 5.52±0.36, *p*s < .001), suggesting that they suffered more from sunk cost effects than capuchins. Further, when the trial duration was signalled through a change in background colour, rhesus macaques (*OR*±*SE* 5s: 1.27±0.07, 7s: 1.50±0.06, *p*s < .001) and especially capuchin monkeys (*OR*±*SE* 5s: 2.37±0.02, 7s: 2.88±0.02, *p*s < .001) became even more likely to opt out of the trial.

Across conditions and species, we also found changes in trial completion over time suggestive of learning (Fig. 3.3). Specifically, as testing progressed, monkeys became more likely to opt out of 5-second and 7-second trials (*b*±*SE* 5s: -0.05±0.004, 7s: -0.06±0.004, *p*s < .001) but not 1-second trials (*b*±*SE* = -0.003±0.004, *p* = .460). This effect was more pronounced in the signalled than in the unsignalled condition (*b*±*SE* = -0.04±0.009, *p* < .001).

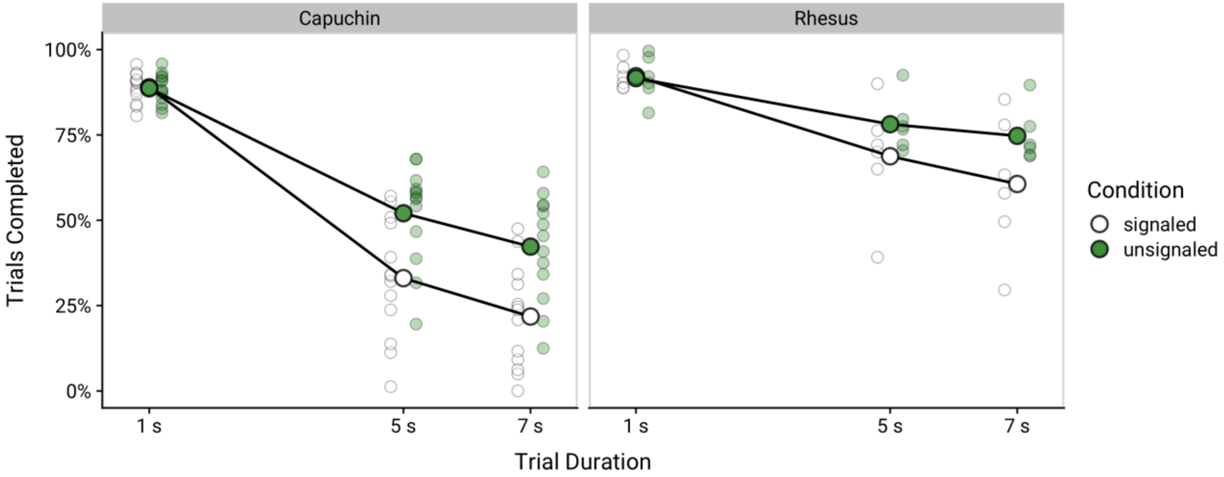

Figure 3.2. Mean trial completion by species, trial duration, and condition. Small transparent points indicate individual monkeys; large points connected by lines indicate group means.

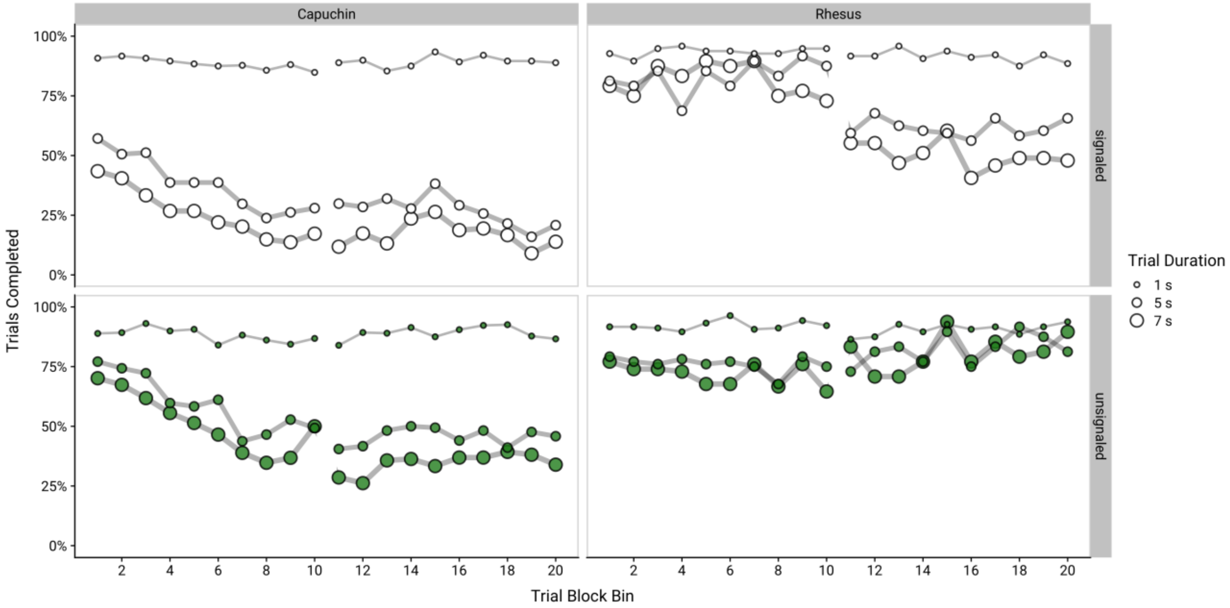

Figure 3.3. Mean trial completion by species, trial duration, condition, and trial block bin. Bins comprised 4 blocks (96 trials). Note that monkeys completed 10 bins of each condition, either the signalled condition first (bins 1-10) and then the unsignalled second (bins 11-20), or the unsignalled condition first (bins 1-10) and the signalled second (bins 11-20). Thus, each panel shows data from different monkeys in bins 1-10 and 11-20, depending on the order that they completed the conditions.

Effect of time already spent tracking

We found a significant trial duration × time remaining interaction effect on monkeys' likelihood to track the target for the required duration (Fig. 3.4), $\chi^2(1) = 95.92$, $p < .001$. Monkeys became more likely to complete the trial when less time was remaining, i.e., the longer they had already tracked the target. However, this effect was stronger in 5-second than in the 7-second trials ($b \pm SE$ 5s: -0.48±0.01 vs. 7s: -0.37±0.01, $p < .001$). That is, in 7-second trials, in which sunk costs were by definition higher than in 5-second trials if the same time was remaining, the likelihood to complete the trial was less affected by the time remaining. In other words, for a given remaining time, monkeys were also more likely to finish tracking the target if they had already tracked it for longer.

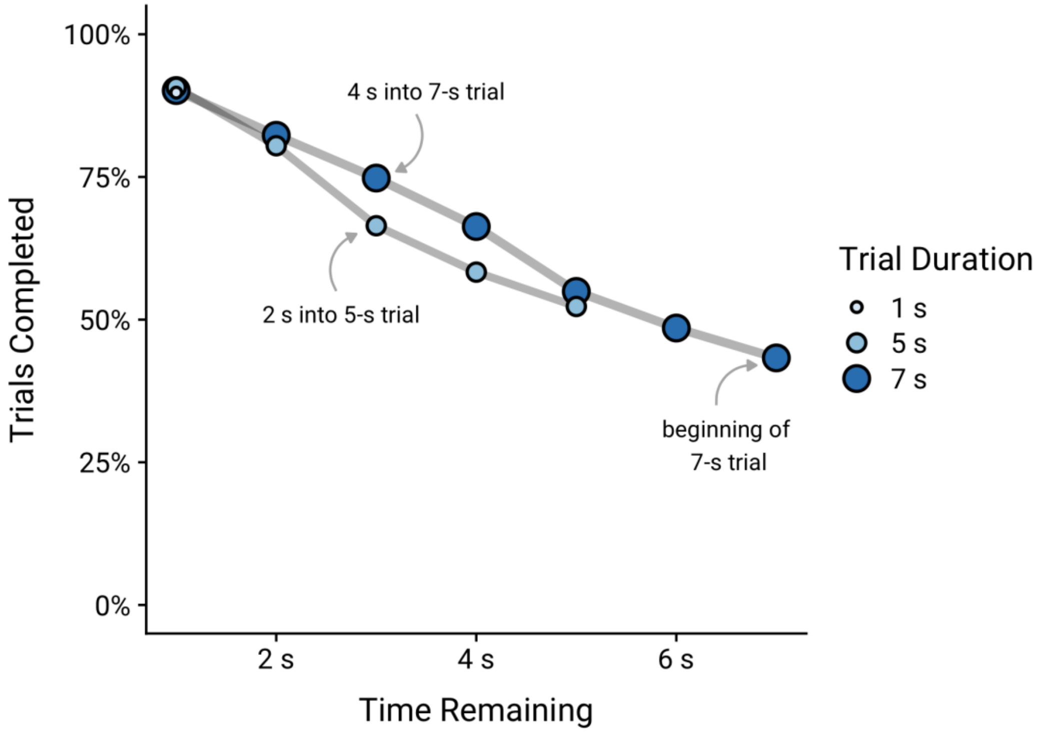

Figure 3.4. Mean trial completion by trial duration and time remaining. Time remaining refers to durations of *at most* X seconds, e.g., if a monkey had tracked the target for 3.2 seconds, the sunk cost (time already spent tracking) was considered to be 3 seconds and the time remaining either 2 seconds (in a 5-second trial) or 4 seconds (in a 7-second trial).

Discussion

Capuchin and rhesus monkeys showed pronounced sunk cost effects in this study. Instead of opting out and forfeiting their initial small investment, both species persisted 5 to 7 times longer than was optimal and were especially likely to complete a trial the longer they had already persisted. We found that rhesus macaques were more susceptible to the sunk costs than capuchin monkeys and that both species showed more pronounced sunk cost effects when changes in trial duration were not signalled. These findings suggest that uncertainty plays a part in the emergence of this bias and highlight that qualitatively similar responses can still vary in magnitude both across and within species.

To our knowledge, this is the first demonstration of the sunk cost effect in nonhuman primates. Together with previous evidence of the effect in more distantly related species like pigeons, rats, and mice[8,17–20,22,23], our results suggest that this bias can emerge as a result of evolved decision-making strategies that are widely shared across animal taxa and do not require human-unique processes, such as those underlying human language, formal economic markets, or self-rationalization. In particular, our finding that the sunk cost effect was more pronounced when changes in tracking duration were unsignalled indicates that the effect may arise because continued investment helps animals resolve uncertainty about future expected costs and benefits. Indeed, in pigeons, the sunk cost effect disappears completely when information about changes in the expected work requirement is provided[8]. However, in primates, lack of information about when exactly it becomes optimal to opt out does not explain everything, as both capuchin and rhesus monkeys still showed pronounced sunk cost effects in the signalled condition.

One possible explanation is that primates overly rely on heuristics that use their past investment as a proxy for future costs and benefits or adjust how much they value an expected outcome based on their past investment. Heuristics are computationally simple rules of thumb that are likely to evolve if they work well in most situations that animals encounter, but they can sometimes lead to consistently suboptimal choices[37]. The sunk cost effect may arise as a result of such heuristics, especially when the cost is low compared to the optimal response (see ref. [35]). Indeed, pigeons[8,17], rats[18], and humans in a similar paradigm[38] are less susceptible to sunk costs when persisting to trial completion requires much more work than opting out to begin a new, likely shorter trial. These results suggest that the sunk cost effect only arises when it is "mildly" suboptimal to show it. Unlike pigeons and rats, capuchin and rhesus monkeys show this behaviour even when changes in expected effort are signalled, suggesting that primates may be more reliant on heuristics. Future work should compare humans' responses to sunk costs in signalled versus unsignalled versions of the paradigm[8,38] to assess this possibility empirically.

This sensitivity in response to different task contingencies raises the question of how much animals understand about them and how they came to do so. Of course, they cannot be told the rules of the task ahead of time and need to learn over time through trial and error. Indeed, we found that monkeys' responses in the test condition changed over time. They initially completed trials of all durations at high levels, as they did in training, but opted out of more 5- and 7-second trials (but not 1-second trials) as testing progressed. That is, their responses became more optimal over time. One possibility is that monkeys who easily learned to track the target (as evidenced by fewer trials before they met the training criteria) simply continued tracking the target in the test condition, too. For example, rhesus monkeys met the training requirement sooner and also completed test trials (showing a stronger sunk cost effect) at higher rates than capuchins. However, we found no statistical effect of training trials required on trial completion, nor can this explanation account for why they did not continue tracking trials of all durations at high levels or for the differences in signalling conditions. Alternatively, fast learners might be expected to also learn the contingencies of suboptimal versus optimal opting out, but this would not explain why monkeys of both species plateaued to complete at least 25% of 5- or 7-second trials at all. Thus, although learning certainly occurred, monkeys' sunk cost effects in this study did not seem to arise from differences in learning.

Nonetheless, rhesus macaques showed a stronger sunk cost effect than capuchin monkeys in this study. In the unsignalled condition, all rhesus completed more 5- and 7-second trials than any of the capuchin monkeys, and they responded less to transitions in trial duration being signalled. Although the overall pattern of responses cannot be fully explained by training experiences, the training data may still provide insight into this species difference. That rhesus monkeys reached the training criteria in many fewer trials than capuchins suggests that completing the task was generally easier for them to do. Therefore, the additional effort of tracking to trial completion may have presented even less of a cost to rhesus than to capuchin monkeys, favouring the sunk cost effect in this situation. This fits evidence from prior research that nonhuman primates may be more likely than humans to take a more optimal shortcut because the familiar, trained strategy is harder for them to learn and execute than it is for humans[34,39]. If so, we would expect humans in a comparable task to show even stronger sunk cost effects and would expect that the benefit from opting out compared to persisting would need to be larger than for rhesus macaques (whose in turn should be larger than for capuchins) in order to for them to consistently opt out. Future comparative research should also extend this work to contexts other than continued motor action (for example, ref. [23]) to investigate how general these effects are.

In this study, we report the first evidence for sunk cost effects in primates other than humans. We found that monkeys were less susceptible to the bias when transitions in expected additional work were signalled, indicating that animals may suboptimally persist, in part, because doing so resolves uncertainty about future outcomes. However, sunk cost effects emerged even when this uncertainty was removed and after continued experience with the task contingencies. We suggest that the sunk cost effect, a hallmark of human economic decision-making, may arise from evolutionarily ancient mechanisms that function to balance the costs and benefits for a given species' cognitive abilities and environment.

Ethics This study was purely behavioural, non-invasive, and was carried out in accordance with all applicable international, national, and institutional ethical guidelines and legal requirements. All procedures were approved by the Georgia State University Institutional Animal Care and Use Committee (IACUC A19028 and A20018 for capuchins and A19029 for rhesus). Georgia State University is fully accredited by the Association for Assessment and Accreditation of Laboratory Animal Care (AALAC).

Data availability The data generated and analysed during this study are publicly available at the Harvard Dataverse (doi:10.7910/DVN/0YNZ0Q).

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4

CAPUCHIN AND RHESUS MONKEYS' SIZE JUDGMENTS SHIFT WHEN STIMULI CHANGE IN FREQUENCY

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Abstract

As humans, we often need to hold ourselves and others to objective, absolute standards when making decisions. Although our concepts can change in response to societal developments or additional information, our judgments should not be swayed by extraneous factors such as the sequence or frequency of events to be judged. Yet when items become less frequent, humans respond by expanding their concept of it to include more ambiguous stimuli. We assessed the origins of this bias by testing capuchin and rhesus monkeys in a computer task in which they had to classify circles of different sizes as either small or large. Small and large circles initially appeared with equal probability but, over time, either small or large circles became less frequent. In contrast to humans, capuchin and rhesus monkeys responded by contracting, rather than expanding, their concepts of the less frequent category. When large circles became rare, monkeys were more likely to judge intermediate sized circles as small, and when small circles became rare, monkeys were more likely to judge those same circles as large. These results suggest that difficulties in maintaining absolute standards are widely shared with other animals, but human-unique tendencies may lead us to overcorrect shifts in our responses, especially if feedback about the accuracy of our judgments is unavailable.

Keywords: decision-making bias, frequency effect, concept expansion, rhesus macaque, capuchin monkey, *Macaca mulatta*, *Sapajus [Cebus] apella*

Introduction

Humans in modern society frequently make judgments based on – ideally – objective standards, for example, when we judge what counts as a crime, a great manuscript, or a score in sports. However, some judgments (like verifying plagiarism or scoring a touchdown in American football) are easier to assess than others (like grading writing style or scoring a figure skating routine), and both more quantitative and more qualitative standards may change over time. For example, what we now consider sexist or racist behavior is vastly different compared to just a decade or two ago, illustrating that our concepts sometimes expand to include a broader set of situations. Such concept expansion (or contraction) sometimes arises from broader societal impacts, such as changes in cultural norms and laws or activist movements. However, lowering or raising our standards is not always desirable. For example, when we aim to reduce statistics such as scientific misconduct rates, we should not unintentionally adjust our definition of data fabrication to include honest mistakes in data entry. Here we investigate a cognitive quirk that may lead to such suboptimal changes in our standards: to some extent, we may expand our concepts of events simply because they become rarer, and contract them because they become more frequent.

In a recent study, people had to judge circles as blue or purple, faces as threatening or non-threatening, and research proposals as unethical or ethical (Levari et al., 2018). Initially, the two respective categories appeared on an equal number of trials, but as testing progressed, the frequency of blue, threatening, and unethical stimuli was gradually decreased to appearing in 50% of trials to just 6% of trials. When these categories became rarer, participants did classify fewer stimuli as blue, threatening, and unethical, but they included more ambiguous stimuli (purplish circles, neutral faces, and harmless proposals) in those categories than they had when these stimuli were more prevalent. This response held when participants were told about the phenomenon, or even when they were paid to resist it. This concept expansion is irrational because the frequency of an event or behavior should not be factored into our judgments. If the number of violent crimes decreases, we do not want to now include previously innocuous behavior in our definition of assault simply because this type of offense has become less common. This example illustrates that adjusting our standards in response to frequency alone would be particularly problematic in cases in which we strive for absolute standards in theory but that often require subjective judgement in practice, such as in assessing criminal or immoral intent.

This finding fits a growing literature showing that we make relative rather than absolute judgments in various contexts, which can systematically bias our decision-making (e.g., Camerer, 2003; Kahneman, 2011; Kahneman et al., 1982; Kahneman & Tversky, 1984; Thaler, 1980, 1992, 2016). Indeed, our brains seem wired to do so, as neuron responses adapt to reflect value information relative to previous outcomes rather than proportional to objective value (Khaw et al., 2017; Louie et al., 2013;

Parducci, 1968; Rangel & Clithero, 2012; Tymula & Plassmann, 2016), suggesting that this tendency is evolutionarily ancient. We need to better understand how and under which circumstances factors such as frequency or the sequence of events affect our judgments in order to make better decisions. Indeed, the finding that humans expand their concepts for items that become more frequent not only for social or moral situations (judging faces and research proposals) but also for perceptual judgments (judging circle color) suggest that this frequency effect does not arise solely in response to societal pressures. One way to study this is to test whether other animals, who are not subject to human culture and society, share this bias. Doing so allows us to assess how widely the underlying mechanisms may be shared and can provide insight into the evolutionary pressures that gave rise to them (e.g., Santos & Rosati, 2015; Watzek & Brosnan, 2020c).

In this study, we assessed whether capuchin and rhesus monkeys, like humans, would expand their concepts of items that became less frequent over time. Both species are susceptible to some of the same decision-making biases as humans in some contexts that favor relative rather than absolute judgments (Chen et al., 2006; Egan Brad et al., 2016; Lakshminarayanan et al., 2011; Lakshminaryanan et al., 2008; Watzek & Brosnan, 2020c, 2020a; see also Santos & Rosati, 2015; Watzek & Brosnan, 2020b), but not in others (Cohen & Santos, 2016; Watzek & Brosnan, 2018; Watzek et al., 2018, 2019; Xu et al., 2011). Further, there is some evidence that these monkeys expand their perceptual concepts in the context of visual illusions (Agrillo et al., 2014a, 2014b; Fujita, 1997; Parrish, Brosnan, et al., 2015; Parrish, Evans, et al., 2015) and change their valuation of a reward depending on the sequence of events (Blanchard et al., 2014; Egan Brad et al., 2016; but see Xu et al., 2011), suggesting that their concepts may be similarly susceptible to the frequency effect as humans.

In our task, loosely modeled after Levari et al. (2018), monkeys had to judge circles of varying sizes as large or small. Circles of any size were initially just as likely to appear as any other, but over time, either the small or the large circles became less frequent. We predicted that the monkeys, similar to humans, would respond by including more ambiguous circles of medium size in the category that became less frequent. In contrast to Levari and colleagues, the monkeys in our study received immediate feedback on their judgments after each trial. This was a practical necessity, as our monkeys are accustomed to participating in cognitive and behavioral testing that yields high-value food rewards in addition to their daily diet, but this methodological change also allowed us to assess the role of feedback. If this frequency effect emerges in humans simply because participants did not receive information about the 'objective truth' (which, indeed, is often not available in real-life scenarios, either), then we would not expect to see the effect when such feedback is provided. Testing this possibility is crucial to designing interventions for specific situations in which we want to ensure that we make decisions based on absolute and not relative standards.

Methods

Participants

We tested 25 capuchin monkeys (17 female, 8 male, age: *M* ± *SD* = 17.88 ± 8.19, range: 7 to ca. 45 years) and 7 rhesus macaques (all male, age: *M* ± *SD* = 23.57 ± 7.35, range: 16-37 years) at the Language Research Center at Georgia State University.

Capuchin monkeys were socially housed in mixed-sex groups, each with their own indoor/outdoor enclosures with a variety of climbing structures, visual barriers, and regularly provided enrichment devices (e.g., foraging boards and puzzle boxes). Capuchins had been trained to separate voluntarily into testing boxes attached to their indoor enclosures for cognitive and behavioral studies. They were never required to come into the test boxes for testing and they could choose not to participate at any time without consequences. Rhesus monkeys were individually housed with continuous auditory and visual access to other monkeys and, when possible, regular social periods with compatible partners. Their enclosures doubled as testing boxes, but they too could choose not to participate at any time without consequences.

All monkeys had access to water at all times, including during testing, and were never food deprived (except for medical reasons unrelated to research studies). All testing food was given in addition to their daily diet of vegetables, fruit, and primate chow.

Procedure

We generated 50 circles with different radii ranging from 32.8 to 110 pixels (displayed on an 800×600-pixel screen), with circle radii increasing by 2.5% from one circle to the next (Fig. 4.1). We refer to circles 1-25 as the "small spectrum," and to circles 26-50 as the "large spectrum."

Figure 4.1. Test stimuli from the small and large spectrums. Circles 1, 10, 20, 30, 40, and 50 from left to right.

Monkeys were tested in individual test boxes that connected to their indoor enclosures. They moved an onscreen cursor using a joystick that is part of their computer testing system (for details see Evans et al., 2008). Each trial, monkeys saw one of these circles at random and needed to classify it as "small" or "large" by selecting one of two arbitrary icons (Fig. 4.2). Icon assignment and placement (left or right) was counterbalanced across monkeys but remained the same for a given monkey throughout the experiment.

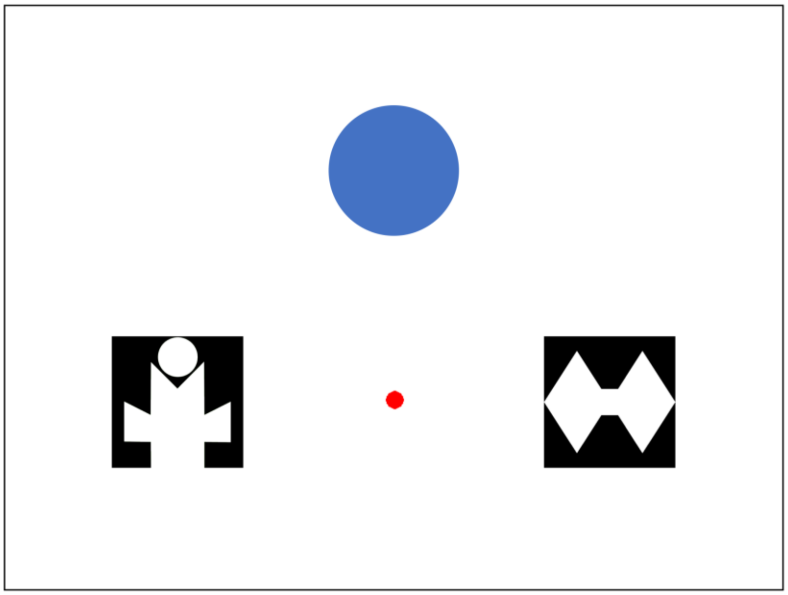

Figure 4.2. Trial screen. Monkeys saw circles one at a time and needed to classify them as “small” or “large” by selecting one of the two icons.

When the monkeys correctly classified circles from the small spectrum as “small” or circles from the large spectrum as “large,” they received positive auditory feedback (*whoop*) and a banana-flavored food pellet. When they incorrectly classified circles from the small spectrum as “large” or circles from the large spectrum as “small,” they received negative auditory feedback (*buzz*) and a 2.5-second timeout. Each trial was followed by a 1-second inter-trial interval (in addition to the timeout, if applicable) before the next trial began.

During *training*, monkeys were gradually introduced to circles from the different ends of the spectrum. Monkeys automatically advanced to the next phase when they reached 80% accuracy in two separate trial blocks (Table 4.1). In Training 1 and 2, monkeys completed blocks of 30 trials. In Training 1, each block consisted of 15 trials

Table 4.1. Training performance. Number of blocks required to meet criterion for the first time and number of monkeys who did and did not ever meet the criterion for each phase.

Phase	Circles Presented	Species	Blocks to Meet Criterion			N_{passed}	N_{failed}
			Mdn	*IQR*	Range		
1	1 & 50	Capuchin	80	20.5-145.5	4-652	18	7
2	1-15 & 36-50	Capuchin	12.5	3.5-20.75	2-57	16	2
3	1-25 & 26-50	Capuchin	4.5	4-10	2-25	14	2
1	1 & 50	Rhesus	56	18.75-91.75	10-188	6	1
2	1-15 & 36-50	Rhesus	27	7-67.25	6-129	6	0
3	1-25 & 26-50	Rhesus	15.5	3.25-31.5	2-42	6	0

with circle 1 (small) and 15 trials with circle 50 (large), presented in a random order. In Training 2, each block consisted of 15 trials with circles 1-15 (small) and 15 trials with circles 36-50 (large), each circle size presented once in a random order. In Training 3, monkeys completed blocks of 50 trials, 25 trials with circles 1-25 (small) and 25 trials with circles 26-50 (large), each circle size presented once in a random order. Classification for 16-35 (i.e., the more ambiguous, medium sized circles) was not considered relevant for the training criterion in this phase, because correct learning of the small/large distinction should result in (near) indifference for these circles. However, they still appeared in this training phase so that these trials were identical to the baseline testing trials, ensuring that transition to testing was imperceptible and nondisruptive to the participants. Thus, to meet criterion, monkeys had to reach 80% accuracy in the 30 trials presenting circles 1-15 and 36-50, just as in Training 2. Testing began immediately, with no indication to the monkeys that anything had changed.

During *testing*, monkeys completed 10 blocks of 50 trials. In the *control* condition, circles were sampled from the small and large spectrums with equal probability (identical to training). In the *fewer-large* condition, large circles were shown less frequently as testing progressed across blocks. Likewise, in the *fewer-small* condition, small circles were shown less frequently. Specifically, circles were sampled from the small (or large) spectrum in 50% of trials in test blocks 1-2, 40% in block 3, 28% in block 4, 16% in block 5, and 6% in blocks 6-10. These probabilities were chosen to compare the results to the progression used by Levari and colleagues (2018).

We used a within-groups design; monkeys each completed all three conditions (control, fewer-large, and fewer-small), with the order fully counterbalanced. Monkeys completed the training phase before each of the three conditions and did not begin a new condition on the same testing day that they had completed a previous one. If a monkey did not complete a condition on a given test day (e.g., because they did not meet the training criteria, lacked motivation, or because testing time was limited by the research schedule), the condition was repeated on the next testing day. Monkeys completed a total of up to 9 test sessions (three per condition). Eight capuchins and 6 rhesus monkeys completed all 9 test sessions. Six capuchins completed 1-6 test sessions during the limited time period available for testing. Inclusion of their data does not change the pattern of results and all data are provided in a publicly available repository (see data availability).

Results

To assess whether decreasing the frequency of small or large circles expanded participants' size concepts, we fit a mixed effects logistic regression model with choice as the binomial outcome variable ("small" or "large" judgements). We included individual identity as a random effect to account for individual variability in baseline size thresholds. We included circle size (1-50), block (1-10), condition (control, fewer-small, and fewer-large), species (capuchin and rhesus), session (1-9), and their interactions as fixed effects. To aid model conversion, we rescaled block by dividing by 10 (new range: 0.1-1), session by dividing by 9 (new range: 0.11-1), and circle size by dividing by 10 and subtracting 2.55 (new range: -2.45-2.45, with 0 indicating the midpoint between the small and large spectrums). We computed pairwise contrasts for significant model terms. We used likelihood ratio tests using single-term deletions to assess each factor's importance with respect to model fit.

We found a significant circle size × block × condition × species interaction effect on monkeys' likelihood to classify a circle as "large," $\chi^2(2) = 13.7$, $p = .001$. Objectively larger circles were more likely to be classified as "large," but whether the threshold for "large" judgments shifted over the course of the session depended on the condition and the species (Figs. 4.3 & 4.4). Specifically, in the control condition, classification for the same size circle did not change over time, (predicted slope for a hypothetical objectively medium circle of size 25.5: $b \pm SE = -0.01 \pm 0.06$, $p = .913$). In contrast, as testing progressed,

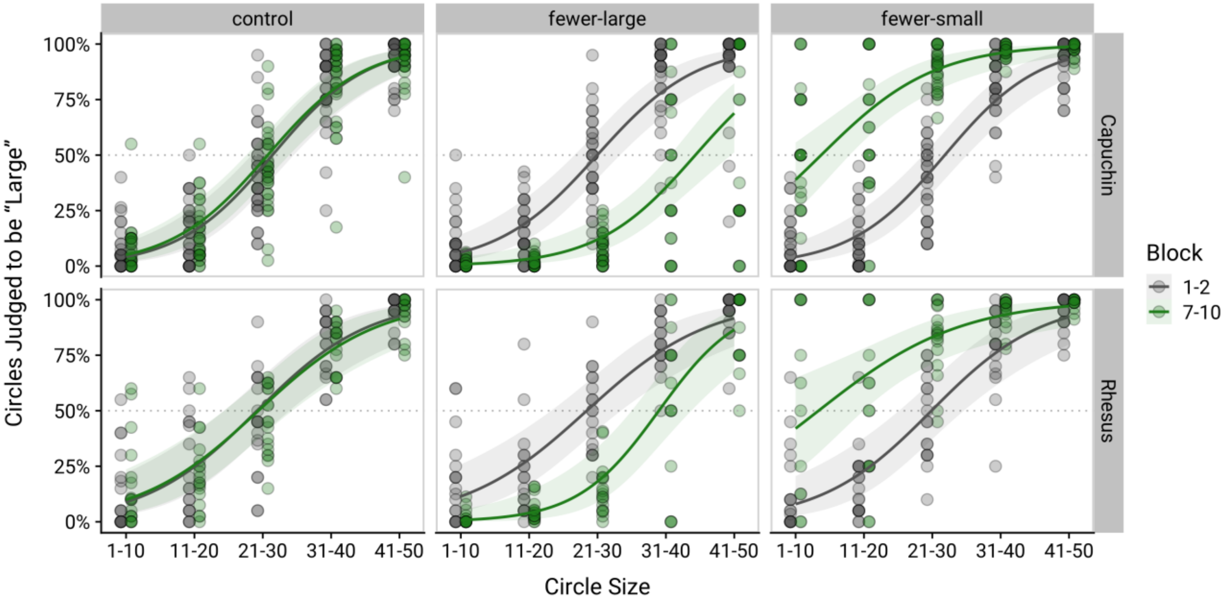

Figure 4.3. Size judgments early and late in the session by circle size, species, and condition. Small transparent points indicate individual monkeys; solid lines and transparent bands indicate logistic regression fit and 95% confidence interval. For visualization only, circles were binned and only data from blocks at the beginning (when small and large circles were equally likely) or at the end (when either small or large circles appeared in only 6% of trials in the fewer-small and fewer-large conditions, respectively) of the test sessions are shown.

monkeys became more likely to classify the same size circle as small when large circles became less frequent (in the fewer-large condition; $b \pm SE$ = -2.61±0.08, $p < .001$). Similarly, monkeys became more likely to classify the same size circle as large when smaller circles became less frequent (in the fewer-small condition, $b \pm SE$ = 2.80±0.08, $p < .001$). That is, monkeys' "large" judgments included fewer objectively large circles in the fewer-large condition and monkeys' "small" judgments included fewer objectively small circles in the fewer-small condition. Notably, monkeys did not only shift their size judgments for the ambiguous, intermediate-sized circles, but also for the objectively

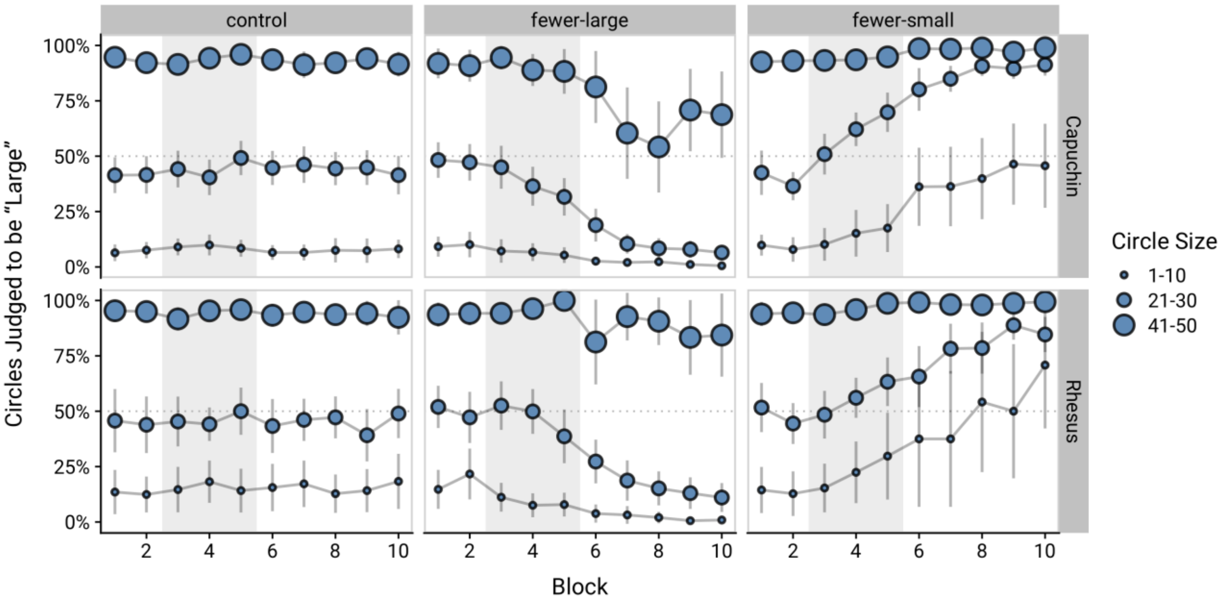

Figure 4.4. Size judgments for small, medium, and large circles by block, species, and condition. Point ranges indicate group means and 95% confidence intervals. For visualization, circle sizes were binned and only circles 1-10 (small), 21-30 (medium), and 41-50 (large) are shown. In blocks 1-2 of a test session, small and large circles were equally likely, but in the fewer-small and fewer-large conditions, either small or large circles (respectively) became less likely and appeared in only 6% of trials from blocks 6-10.

very large or very small circles that they had classified correctly in at least 80% of trials during training. For the half of the spectrum that became less common, monkeys now misclassified these circles in up to half the time. Another way of understanding this shift is by examining monkeys' indifference point – the circle size which they were equally likely to judge as small or large. In the fewer-large condition, the indifference point became a larger-than-medium circle; in the fewer-small condition, it became a smaller-than-medium circle.

Although capuchin monkeys and rhesus macaques classified circles of varying sizes as large at similar rates in the control condition (*b*±*SE* capuchin: 0.08±0.07 vs. rhesus: -0.10±0.09, $p = .103$), capuchins' size judgements shifted more than rhesus' in both the fewer-large (*b*±*SE* capuchin: -2.93±0.10 vs. rhesus: -2.28±0.13, $p < .001$) and fewer-small conditions (*b*±*SE* capuchin: 3.26±0.10 vs. rhesus: 2.34±0.13, $p < .001$), suggesting that they were more sensitive to changes in how frequently circles of different sizes were presented.

Discussion

Capuchin and rhesus monkeys in this study showed robust shifts in their size judgments when either small or large circles became less frequent. However, against our predictions, monkeys adjusted their size judgments in the opposite direction as humans did in a similar experiment (Levari et al., 2018). When large circles became rare, monkeys classified intermediate-sized (and even some large) circles as small; when small circles became rare, monkeys classified the same intermediate-sized (and some small) circles as large. That is, monkeys showed concept *contraction* rather than concept expansion for the (now) minority category. Humans, on the other hand, showed concept expansion, including more ambiguous stimuli in the category that became rare (Levari et al., 2018).

One possibility for this difference is that the monkeys in our study received immediate feedback for each of their judgments. When large circles became rare (in the fewer-large condition), monkeys encountered more small circles and were rewarded for judging them as small (and vice versa in the fewer-small condition). Thus, monkeys may have learned the most common response for each test session and, perhaps habitually, also made this judgment when more medium sized circles appeared. However, monkeys' responses were not indiscriminate (i.e., they did not simply always make the same judgment), as they still classified very large circles as large and very small circles as small even when they appeared only in a few trials. Lack of attention therefore does not seem to be a likely explanation. Instead, monkeys' indifference point – the size at which they were equally likely to judge a circle as small or large – became a larger-than-medium circle in the fewer-large condition (and a smaller-than-medium circle in the fewer-small condition).

Although information about the objective truth may not always be available in real-world scenarios, studying the extent to which humans would respond similarly to monkeys in response to trial-by-trial feedback is an open and highly necessary question for research. If humans continue to show this bias even when feedback is available, this would suggest that mechanisms unique to humans, such as those arising from human language, culture, or formal institutions like markets, underlie the effect. Perhaps humans implicitly expect a minimum number of items from both ends of a spectrum.

However, humans were susceptible to concept expansion even when they were told about the effect and were incentivized to resist it (Levari et al., 2018), suggesting that this bias may be difficult to combat through reasoned thinking. If, on the other hand, humans, like monkeys in our study, do not expand their concepts for rare stimuli when they receive feedback, this would suggest that cognitive mechanisms that we share with other animals give rise to the bias. For example, primates may not easily detect changes in stimuli frequencies without clear information about which category any given stimulus belongs to. In this scenario, we may therefore adjust our estimates too slowly (or not enough) and respond accordingly by sorting more stimuli into the minority category than there actually are. Future research is needed to explore these possibilities.

Notably, a shift away from the true medium in *either* direction was suboptimal. Monkeys still lost time (in the form of a timeout) and forfeited food rewards because any shift led to more misclassified circles (especially circles of the minority category). However, stimuli from that category only appeared in 6% of the trials in the second half of the test session, resulting in relatively few errors if monkeys adopted a “mostly choose small” (or large) strategy. It is possible that such a strategy, while not optimal, conferred enough of a benefit to offset this cost because such a heuristic strategy may be computationally easier to follow (see also Camerer, 1998; Gigerenzer & Todd, 1999; Stevens, 2012). Indeed, this strategy would become optimal if stimuli from the (now) less frequent category completely disappeared, that is, if the trend continued. It is possible that high sensitivity to the changing availability of options that an animal encounters and interacts with is adaptive. Quick adjustments in strategies, even if they overshoot, may be favored in such circumstances, especially if environments change over space and time (The Modelling Animal Decisions Group et al., 2014), for example, if an animal relies on ephemeral fruit patches.

In this study, we tested whether capuchin and rhesus monkeys, like humans, respond to events that decrease in frequency by expanding their concepts for them, that is, by including more ambiguous stimuli in the now less frequent category. We found that monkeys showed exactly the opposite pattern when they received feedback on their judgments, considering almost all stimuli to belong to the now more common category. Our findings support previous evidence that animals including humans make relative rather than absolute judgments. We suggest that such shifts in decision-making are adaptive in situations that animals may encounter in their environments. However, human-unique tendencies may lead us to overcorrect shifts in our responses, especially if information about the accuracy of our judgments is unavailable. Further research is needed to more fully assess the cognitive mechanisms that underlie this bias, which will help us combat it in situations when we do want to uphold absolute standards.

Ethics This study was purely behavioural, non-invasive, and was carried out in accordance with all applicable international, national, and institutional ethical guidelines and legal requirements. All procedures were approved by the Georgia State University Institutional Animal Care and Use Committee (IACUC A19028 and A20018 for capuchins and A19029 for rhesus). Georgia State University is fully accredited by the Association for Assessment and Accreditation of Laboratory Animal Care (AALAC).

Data availability The data generated and analysed during this study will be made publicly available at the Harvard Dataverse.

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5

CONCLUSIONS: LEARNING FROM MISTAKES

Humans and animals alike make thousands of decisions every day that affect our own lives as well as those of others. In doing so, however, we navigate complex environments in which we often have to rely on imperfect information and, even if we had perfect information, we may not have the cognitive abilities to derive the optimal strategy every time. As a result, we sometimes make bad decisions, and much research has explored under which circumstances such irrational decision-making occurs. Because these decision-making biases can have far-reaching consequences for our lives, it is important to understand why we fall for them. Unfortunately, the underlying mechanisms are often unclear. In this dissertation, I used a comparative approach to assess whether animals make similarly bad decisions. Doing so helps us learn about human decision-making and, potentially, develop interventions to improve decision-making in situations in which it is warranted, such as saving for the future. Moreover, these results have important implications for how we design comparative studies, as I found that seemingly minor factors, such as the presence of other food and the frequency with which stimuli are presented, can inadvertently affect animals' decisions.

In Chapter 1 (Watzek & Brosnan, 2020), I assessed the degree to which studying the extent to which other species respond in similar ways as we do yields unique insights into our own behavior, discuss challenges faced by studies of animal decision-making, and propose future directions for such comparative research. Based on this analysis, this dissertation expanded on this line of research through several studies in which I investigated decision-making biases in capuchin monkeys and rhesus macaques, two primate species that share a number of irrational behaviors with humans (see also Addessi et al., 2020; Santos & Rosati, 2015). In particular, I focused on better understanding the circumstances under which these biases emerge and carefully considered the, often underappreciated, role of methodology.

Summary of Findings

Across one manual and two computer tasks, I found that capuchin and rhesus monkeys' choices consistently shift in response to factors that should be irrelevant to maximizing the expected benefits and minimizing the expected costs, resulting in economically irrational responses. These results suggest that many decision-making biases do not rely solely on human-unique factors, such as language and culture, or formal institutions, such as economic markets or education systems. However, I also found important differences between monkey and human decision-making in these situations, providing further insight into the relative contribution of different cognitive mechanisms that may underlie these biases.

In Chapter 2, I demonstrated that capuchin monkeys, like humans, are susceptible to a range of context effects. Capuchins devalued a food item when a better one was present, but unavailable (contrast effect), but overvalued a food item when an inferior option was available (decoy effect) or when the food, if unchosen, was given to a conspecific (social context effect). The contrast effect was almost twice as large as the decoy and social context effect, suggesting that devaluing food items in the presence of better ones may be a more adaptive response in other contexts.

In Chapter 3, I reported the first evidence of sunk cost effects in primates other than humans. Capuchin and rhesus monkeys were more likely to persist in a psychomotor computer task the more time and effort they had already invested, even when doing so was suboptimal compared to opting out. I found that sunk cost effects emerge especially when information about future outcomes is uncertain. Persisting may therefore provide an opportunity to gain more information. The effect remains when such uncertainty is removed, however, suggesting that animals may broadly rely on heuristics that use prior effort as a proxy for future outcomes or to adjust their evaluation of eventual outcomes.

In contrast to the previous studies, in Chapter 4 I found that capuchin monkeys and rhesus macaques behave differently than humans in how they judge rare stimuli. Specifically, both monkey species shifted their judgments of stimuli that occur less often by contracting their concepts for them, i.e., by including previously ambiguous stimuli in the now more common category. When large circles became rare, monkeys judged intermediate (and even some large circles) as small. Conversely, when small circles became rare, monkeys judged those same intermediate circles (and even some small circles) as large. Like humans, monkeys were unable to maintain absolute standards when stimuli changed in prevalence, suggesting that such shifts in judgment may be adaptive in natural environments. However, unlike humans, monkeys adjusted their 'definitions' of the categories by contracting rather than expanding their concepts for the minority category. One possibility is that psychological mechanisms unique to humans lead us to overcorrect such shifts in the opposite direction. However, future research is needed to determine how humans respond in a similar procedure and to assess the role of information uncertainty in driving this response.

Implications

Evolutionary roots of bad decision-making

Overall, I found robust evidence that primates other than humans are also susceptible to (theoretically) choice-irrelevant factors such as the presence of a superior or inferior option, the outcomes of a group member, their prior investments, and the prevalence of stimuli in some situations. These findings show that biased decision-making does not arise simply as a result of abilities that are unique to humans, such as human language and culture, or environments that are built by humans, such as formal economic or political systems. Instead, irrational behavior is likely, at least in part, the result of evolved mechanisms.

This possibility raises the question of why strategies that lead to bad decision-making would evolve. If bad decisions lead to decreased survival or reproductive success, then behaviors that lead to them should die out. To better understand which circumstances might favor such strategies, then, we need to consider an organism's decision-making in the context of its environment, to see whether these decisions really do lead to decreased evolutionary fitness. In many cases, they do not (e.g., Watzek & Brosnan, 2018). Thus, I argue that the monkeys' irrational behavior in this dissertation can be understood quite well under the overarching frameworks of bounded and ecological rationality (Camerer, 1998; De Petrillo & Rosati, 2019; Gigerenzer & Brighton, 2009; Gigerenzer & Goldstein, 1996; Gigerenzer & Selten, 2001; Gigerenzer & Todd, 1999; Kacelnik, 2006; Stevens, 2012, p. 201; The Modelling Animal Decisions Group et al., 2014).

In this view, biased decision-making is the result of heuristics, or computationally simple rules of thumb, gone awry. Heuristics can be favored by evolution when they work well in most situations that an animal actually encounters, even if they occasionally lead to suboptimal choices. In these scenarios, the benefit from using a simpler strategy is greater than the infrequent cost of getting it wrong, especially if such errors are not particularly costly (e.g., Houston, 1997; Watzek & Brosnan, 2018). For example, considering the results of Chapter 4, the changing frequency of stimuli in a natural environment (e.g., patches of ripe fruit) may typically be predictive of those items disappearing soon. Thus, it would be adaptive for monkeys to change adjust their behavior accordingly. Similarly, considering sunk costs (Chapter 3), the time and effort that an animal has already spent may typically correlate with future benefits, such that further persistence does result in optimal outcomes. However, in an experimental context, when such spatial or temporal relationships are deliberately removed, this change in behavior results in suboptimal choices.

This dissertation illustrates how assessing differences and similarities in how multiple species respond to the same problem can help us tease apart potential explanations for a phenomenon, particularly because several of these (including human-unique ones) may play a role. For example, sunk cost effects in monkeys seem to emerge, in part but not entirely, because information about the future may be uncertain (Chapter 3). In pigeons, on the other hand, signaling changes in expected effort completely eliminated the sunk cost effect in most birds (Navarro & Fantino, 2005). This pattern suggests that monkeys employ additional mechanisms in this situation. Similarly, tendencies that are unique to humans may explain why we respond to changes in stimulus frequency in the opposite direction to monkeys (Chapter 4).

Importantly, not only is the comparative approach well-suited to assess the relative importance that different psychological processes play in giving rise to decision-making biases, but it can also help us understand our own behavior better than studying humans alone. For example, animals other than humans show the endowment effect – the tendency to overvalue items in our possession compared to the same items not in our possession – in some circumstances, but only for food or tools that can be used to obtain food (Brosnan et al., 2007, 2012; Drayton et al., 2013; Flemming et al., 2012; Kanngiesser et al., 2011; Lakshminaryanan et al., 2008). One of-debated aspect of the endowment effect in humans is its variability across studies and contexts, and the results in animals suggest the reason for this (Jones & Brosnan, 2008). Indeed, this research has spurred new investigations into the role of the "evolutionary salience" of the items, which explain much of the variation in humans' susceptibility to the effect (Jaeger et al., 2020; Jones & Brosnan, 2008). Similarly, an innovative study using a comparable paradigm to test rodents' and humans' susceptibility to the sunk cost effect recently found that the effect does not emerge when an individual first decides whether or not to invest, but instead arises only while the individual needs to maintain the investment (Sweis et al., 2018). These examples nicely illustrate how comparative research of decision-making biases can lead to novel insights and testable hypotheses about human behavior as well.

Methodological considerations for assessing bad decision-making

This series of experiments also highlights the importance of carefully considering methodological details when conducting experiments designed to compare the behavior across different studies or across multiple species. For example, seemingly minor methodological aspects such as changing the background color of the computer screen greatly reduced the magnitude of monkeys' sunk effect (Chapter 3). Similarly, although previous evidence for the decoy effect in primates was mixed, here I found that capuchins were susceptible to the effect (Chapter 2). However, monkeys only increased their preferences for the target food (which looked better in comparison to the smaller decoy) when their initial preferences for this food were weak, not when their initial preferences were strong. The opposite pattern emerged for contrast effects, in which monkeys' preference for the target food decreased when a better food was present, but only when initial preferences were relatively strong. These results suggest that floor and ceiling effects around variability in initial food preferences may have obscured context effects in previous studies. Here I carefully calibrated monkeys' baseline preferences by using different food items and sizes across monkeys and by using a countable food item as a ‘price unit.’ Such details are important to assess how broadly decision-making biases emerge.

Differences in methodology are particularly tricky when comparing different species. For example, monkeys show concept contraction in response to changes in stimuli prevalence – the opposite pattern to humans, who show concept expansion (Chapter 4). However, monkeys received immediate feedback on their size judgments, whereas humans received no feedback at all about how accurate their judgments were. This difference, while to some extent unavoidable when testing these monkeys, makes it difficult to assess whether this finding arises from a true species difference or results from objective information being made available or not. An obvious next step to differentiate between these possibilities is to test a human population with a comparable paradigm to the one I used with monkeys.

Research on decision-making biases in animals is itself affected by methodological choices, but the findings also have practical implications for studies of animal cognition that focus primarily on other topics. Because such research typically relies on animals’ behavior, it is important for researchers to carefully consider the presence of factors that are not of interest to the research question but that may nonetheless inadvertently bias animals’ choices (such as the presence of other food items or conspecifics, changes in the required effort, or the sequence of options), and ensure that they do not vary systematically across test conditions.

Future Directions: The Fun is in the Error Bars

Studying and comparing decision-making biases in species other than humans is a promising approach to better understanding why, how, and when they occur. Although such research has yielded valuable insights, and I hope that this dissertation contributes to this body of knowledge, there is still much that we do not know. As noted in Chapter 1, ideally, we would test large samples of a wide range of animal species, including humans, using several comparable paradigms. Of course, this is typically impossible for a single researcher or laboratory to accomplish; therefore, here I will focus on future work that can yield additional insights that does not require additional (nonhuman) animals.

The present research can be extended in several directions. First, if comparison to human decision-making is an explicit goal, then whenever possible, humans should be tested in a paradigm that is as comparable as possible to the one used with animals. More generally, if the behavior of any two or more different species is compared, inferences will be greatly improved if a comparable methodology is used (Smith et al., 2018; Tomasello & Call, 2011).

Second, I see the most promising opportunities to expand on our knowledge of decision-making biases in exploring what explains variability in how susceptible animals are to a given effect. Future work should assess the magnitude of a number of different biases in the same individuals and systematically 1) compare their relative importance on decision-making (as in Chapter 2) and 2) assess the extent to which they co-occur. Doing so helps us clarify the potential importance of different underlying mechanisms, the latter by highlighting the potential role of individual differences (such as those related to sex, age, social standing, specific cognitive ability) in the emergence of these biases. Further, comparing the behavior of the same individuals on different paradigms designed to test the same phenomenon can tell us to what extent they tap into the same concept. Similarly, comparing the behavior of the same individuals on the same paradigm, conducted after a hiatus, can tell us about the stability of the bias and the potential effect of experience on its emergence.

Systematically testing and comparing the decision-making behavior of multiple species, including humans, is crucial to understanding how our strategies have evolved, which mechanisms give rise to them, and in which situations and environments they may have been adaptive. This dissertation has expanded on this understanding and opens up exciting avenues for future research that will help us better predict and, ultimately, overcome bad decision-making.

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