The evolution of irrational decision-making: insights from non-human primates

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Abstract

Despite our species' impressive cognitive sophistication, adult humans are nevertheless notoriously bad at making normatively rational economic decisions. Much work has examined the nature of biased decisions such as framing effects, the endowment effect, and the peak-end principle in adult humans; however, research examining the origins of these biases is still in its infancy. This paper examines existing work on origins of economic biases – that is, whether these biases are shared with non-human primates. We survey recent work using a comparative approach to address the evolutionary origins of several classic biases, such as loss aversion, reference-dependence, the endowment effect and the peak-end principle. Novel evidence is provided that the peak-end principle – a bias involved in retrospective evaluations – is also found in capuchin monkeys. These studies suggest that such biases emerged long ago in our evolutionary history, and shed light on the psychological mechanisms behind biased decision-making.

Keywords: decision making, evolutionary psychology, experimental research with animals.

Introduction

In a variety of laboratory and real-world settings, people make decisions that conflict with what would maximize economic well-being. Although economists classically assume that we make decisions like rational optimizers – that is, by maximizing our utility in a mathematically axiomatic fashion -- social scientists have extensively documented that humans often make decisions that are at odds with this view.

Rather than treat consequentially-identical outcomes the same (i.e., exhibiting context invariance), decision-makers' choices depend heavily on the way outcomes are presented or framed and not on the absolute consequences of their decisions (a phenomenon termed reference dependence) (Kahneman & Tversky, 1979; Tversky & Kahneman, 1982, Tversky & Kahneman, 1992). Furthermore, people view losses as more consequential than equally-sized gains (Kahneman & Tversky, 1979).

Consequently, people require more resources to give up an object in their possession than they would spend to newly acquire that same object. Kahneman, Knetsch, and Thaler (1990) presented each participant with a new object (e.g. a box of pens) and then gave them the opportunity to exchange it for a second object of equal value (e.g. a mug). Surprisingly, participants consistently refused the opportunity to swap an endowed object for an equal valuable one and instead elected to hold on to the mug (or box of pens) that they were initially assigned. Moreover, they demanded nearly twice as much money to give up this object as buyers were willing to pay in order to acquire it. (Kahneman et al., 1990; Kahneman et al., 1991).

Similarly, loss-aversion also creates inconsistencies in when people are willing to take risks. When an outcome is framed as an opportunity to avoid a loss people are risk-seeking but, in contrast, people become risk-averse when the same outcome is phrased to emphasize gains rather than losses (Kahneman & Tversky, 1979). A simple demonstration of this phenomena (termed "the reflection effect") is that subjects reverse their preference to take a risk based on whether they're asked to make decisions about gains or losses, even though each case is simply an alternate formulation of the same outcome (since the gain and loss questions essentially present the same pair of choices: choosing between $1500, or a lottery with an expected value of $1500, Kahneman & Tversky 1979):

"Scenario 1: Gains
You have been given $1000. You are now asked to choose between:
(A) 50% chance to receive another $1000 and 50% chance to receive nothing [16%]
(B) receiving $500 with certainty [84%]

Scenario 2: Losses
You have been given $2000. You are now asked to choose between:
(A) 50% chance to lose $1000 and 50% chance to lose nothing [69%]
(B) losing $500 with certainty [31%]"
(Kahneman & Tversky, 1979, p. 273)

Finally, similar framing effects also have been found to impact peoples' subjective experiences of an past event. Kahneman and colleagues also observed that memories of pleasurable (and painful) experiences are also susceptible to systematic framing effects, which subsequently affect the choices people make.

Specifically, the remembered happiness of an entire episode is strongly influenced by its end point. In one study, patients receiving a colonoscopy were randomly assigned to one of two treatment groups: one group had a mildly painful procedure following the moderately painful colonoscopy, whereas the second group only received the colonoscopy. A prediction consistent with economic rationality would be that people would structure their choices to minimize the duration of pain. In contrast, subjects rated the sequence ending with mild pain as a less unpleasant episode than the colonoscopy alone (despite being in pain over a greater time span), and those receiving the compounded pain of the colonoscopy plus the mildly painful top-off procedure were actually more likely to return for a second colonoscopy (Redelmeier, Katz, and Kahneman, 2003). Crucially, these framing effects influence choices even when using pleasurable stimuli: when asked to judge the remembered pleasure of watching a sequence of (pleasant) movies of penguins at play, participants neglected the duration (that is, the overall amount of pleasant footage) and instead judged a shorter clip as more pleasurable (provided it was sequenced with the most pleasurable portion at the end) (Fredrickson and Kahneman 1993).

Thus, human behavior in a variety of contexts – from irrational reversals of risk preferences, sudden increases in an object's subjective value after becoming its owner, or paradoxically selecting more painful episodes over less painful ones – are puzzling from any perspective which assumes that decision makers have completely stable preferences and rationally ignore framing to concentrate on mathematical consistencies across contexts.

One possibility is that economic biases such as loss-aversion or the endowment effect are artifacts of the specific populations and cultures typically used as subjects. For example, researchers have suggested that the endowment effect is due to a rich sense of self – something that would only be found in human populations (Gawronski, Bodenhausen, & Becker, 2007). Alternatively, these biases might simply arise from the particular experimental procedures designed to elicit them – for example by verbal surveys, participants might be influenced by task demands or linguistic pragmatics.

However, another possibility is that these biases are fundamental aspects of decision-making. If this were the case, then we would expect biases such as framing effects or the endowment effect to exist in subjects who completely lack experience with humanlike educational or cultural contexts, and that these biases would exist even when nonverbal methods were employed. Under this view, even other species would exhibit the same decision-making biases previously thought to be unique to ours.

One way to test this final possibility is to determine whether these decision-making biases do, in fact, exist in non-human primates. Addressing this possibility, there is some evidence that certain biases emerge even without extensive experience or cultural learning and are shared with our closest living evolutionary relatives – non-human primates (for a review, please see Santos & Lakshminarayanan, 2008). The next section will survey previous work investigating economic biases present in capuchin monkeys (*Cebus apella*), an ancestrally-related New World monkey species (Santos & Lakshminarayanan, 2008; Chen, Lakshminarayanan, & Santos, 2006).

Evidence for Economic Biases in Monkeys

Here, we present prior research investigating whether capuchin monkeys' decision strategies were similar to those of humans in economic contexts. To design a monkey marketplace analogous to situations in which humans receive monetary payoffs, we developed a 'fiat currency' that our monkeys could spend on food (or, depending on the study, on gambles involving food). Essentially, we taught our capuchin monkey subjects that they could exchange small metal tokens with human experimenters for food rewards (e.g. Westergaard et al., 1998; Brosnan & de Waal 2003). Our monkeys developed this token-trading ability with relatively little training.

Once they had acquired the necessary trading skills, we then placed our capuchins in an economic market in which subjects could choose between different experimenters providing different goods at different prices. Each monkey subject began each session with a small 'wallet' of tokens and entered the market where two different experimenters offered different goods at different prices. The monkey could then choose to trade with whomever it most desired. We could then measure each monkey's preferences in terms of the percentage of tokens they traded with each of the experimenters (Santos & Lakshminarayanan, 2008; Chen, Lakshminarayanan, & Santos, 2006).

To ensure that the monkeys could understand which trader delivered each food reward, we distinguished the traders based on their clothing (e.g. a trader in blue scrubs versus one in red scrubs). Additionally, we gave each capuchin subject several training trials in which they were required to trade an equal number of times with each trader individually so they could learn the available choices. Finally, each test session began with two familiarization trades with each trader individually before both choices became simultaneously available to the subject. Therefore, the capuchin subjects were making an informed choice between the two traders.

We first used this token-trading set-up to explore whether capuchins exhibit the rudimentary principles of rational utility-maximization in this new economic market. To do this, we presented monkeys with a

choice between traders who offered two different kinds of food that the monkeys liked equally, e.g. apple slices and grapes. When presented with this choice, our capuchins subjects spent about half of their tokens on apples and half on grapes. We then introduced a compensated price shift, basically putting one of the goods -- say apples -- on sale by providing double the quantity provided for a single token (thus cutting the price of apples in half). Our monkeys bought more of the cheaper (half-priced) food when it went on sale, behaving rationally as a human consumer would to this shift in the prices (Chen et al. 2006).

We then examined whether the capuchins prefer a trading option that weakly dominates, or more specifically, one that provides the most food overall. We presented the monkeys with a choice between one experimenter who always offered (and gave) one piece of apple, and a second experimenter who always offered two pieces of apple but half the time gave one piece, and half the time gave two. When faced with this choice, the capuchins preferred to trade with the second experimenter, again choosing the option that allowed them to make the most of their token budget (Chen et al. 2006).

These results demonstrate a few important features of our capuchin market. First and most importantly, the capuchins seem to use the market we have created for them to select more desirable options over less desirable ones; with little training, our capuchins were able to pick up information about each trader's past behavior and use that information to make informed choices in the market. Second, our monkeys appear to behave rationally in the market, selectively trading with experimenters who offer them a better deal (Chen et al. 2006).

Having established that capuchins behave broadly rationally in some aspects of this market, we then examined whether capuchins display the heuristics that humans do—namely, reference dependence and loss aversion. In our first study, capuchins were presented with a choice between two traders who gave the same amount of food, either one or two pieces of apple. The first trader, however, gave food by way of a perceived gain. This trader started out by showing the monkey only one piece of apple but when paid gave an additional second piece of apple half the time. The second trader offered the same amount of food by way of a perceived loss. This second trader started out by displaying two pieces of apple but when paid took one of the pieces of apple away half the time. Although the two traders offered the same amount of food on average, our capuchin subjects did not treat them equally. Note that both experimenters stochastically altered their payoffs, thus any preference between the two would be due to framing (rather than a preference for consistency over risk). Furthermore, since both traders offered (on average) the same reward, if subjects associatively learned to choose the larger reward option then they would fail to exhibit a preference between the two traders. In contrast, the monkeys significantly preferred to trade with the trader who gave a perceived gain over the one who gave a perceived loss (Chen et al. 2006).

To rule out the possibility that these results were based on a lack of knowledge about the outcomes available to the subject, we once again ran each subject in a thorough familiarization and shaping procedure which required them to gain extensive experience with the food rewards available from each trader. Additionally, in this experiment the traders were different individuals than those used in previous experiments and were also clothed in different color scrubs that were novel to the subjects. We thus eliminated the possibility that their choices were based on previous associations between experimenter or scrub color with "good" outcomes.

To summarize, monkeys behaved much like human participants in classic studies (e.g. Tversky & Kahneman, 1992)—they evaluate their choices in terms of an arbitrary reference point, namely the initial amount of food that they were shown. We then went on to examine whether capuchins showed this pattern because they were seeking out perceived gains or whether they were instead avoiding perceived losses. Monkeys were given a choice between one trader who always showed one piece of apple and delivered that piece and second trader who always showed two pieces of apple but delivered only a single piece. Again, even though both experimenters gave the same pay-off (making it impossible to account for their preferences with a simple association between an experimenter and a greater reward) capuchins reliably avoided the experimenter who gave less than what he initially offered, suggesting that capuchins, like humans, are averse to losses (Chen et al. 2006).

In addition to loss-aversion and reference-dependence, we explored whether capuchins also exhibit a reflection effect – namely, whether they are risk-seeking over choices framed as losses but risk-averse when the same choices are framed as gains. Using a similar token-trading task, we gave capuchins a choice to trade with an experimenter who initially offered three chunks of apple but only delivered two chunks of apple (thus representing a certain loss) – or, instead, an experimenter who offered three chunks but either delivered one or three (thus representing a risky loss). In this experiment capuchins were risk seeking over losses; however, in the next experiment we observed that the same outcomes were treated very differently when framed as opportunities to secure gains. We modified our market so that now the capuchin subjects chose between one experimenter who initially offered one chunk of apple but always added a second chunk (thus promising a sure gain) – or instead,

an experimenter who offered one chunk but either added two chunks or nothing (thus representing a risky gain). Note that the outcomes were identical to the prior experiment involving risky choice (in which they chose between a safe and risky loss). However, when the same outcomes were framed as gains, capuchins were risk-averse and chose to trade for the sure gain. Thus they exhibited an analogous reversal of risk-preferences depending on whether outcomes were framed as gains or losses (Lakshminarayanan, Chen, & Santos, in press). Crucially, the expected value was identical across all four traders. Since all four traders offered (on average) equal rewards, if subjects simply associatively learned to choose the more rewarding option then they would fail to exhibit a preference between any pair of traders. In contrast they exhibited the humanlike pattern of being risk seeking when outcomes were framed as losses and risk averse when the same outcomes were framed as gains.

Finally, we investigated whether capuchin monkeys exhibit an analogous tendency to overvalue what they possess. That is, do they exhibit a humanlike unwillingness to trade away possessions for equivalently valued items in much the same way that humans do in demonstrations of the endowment effect?

To do this, we found treats (fruit discs versus cereal pieces) that the capuchins preferred equally. However, when endowed with one of these types of food and given the opportunity to trade it away in exchange for the equivalent treat, they chose instead to retain their endowed food. We established that this result was not due to issues related to trading food (since they were willing to trade for food of much greater value) and additionally show that these effects were not due to temporal or physical transaction costs (Lakshminarayanan, Chen, & Santos 2008).

Although prior research, as published in Chen et al. (2006), provides some evidence for decision-making biases in capuchin monkeys, the existing literature leaves open several important unanswered questions. Namely, do capuchins share other decision-making bias beyond reference-dependence and loss aversion, such as framing effects in their remembered happiness of previously experienced events – in which case they should be especially sensitive to the peak intensity and end-points of remembered events?

Retrospective Evaluation in Monkeys

People's memory of pleasurable and painful events are subject to framing effects in that they are not strictly related to the overall quality of an episode, but instead depend on the end-point and peak intensity of that experience. Human participants surprisingly rate highly painful experiences as more tolerable than less severe ones, simply based on whether the more painful experience concludes with a better end-point. Similarly, they choose to repeat episodes that conclude with highly pleasurable events rather than episodes that begin with the equally pleasurable events. Furthermore, the peak intensity of past experiences also influences how subjects remember the pleasure associated with those episodes. A pleasurable event spread out over a long duration is rated as less appealing than a comparable episode that is half as long but twice as pleasurable.

In our final two experiments, we show that capuchin monkeys make economic decisions (i.e., which experimenter to trade with) based on this "peak-end" principle.

Much like in previous studies, capuchin subjects are each given a budget of tradable tokens. Subjects then have a choice of two experimenters who each provide a reward for a token. These experimenters each displayed rewards that they would provide in exchange for tokens. When the monkey handed an experimenter a token, they then provided this food by holding it steady near the subject as the subject ate it. In the first experiment the choices provided the capuchin the chance to choose between a high end-point versus a low end-point, whereas in the second experiment they chose between a high peak versus a low peak.

Much like in previous experiments, we first began with a familiarization phase to allow the subjects to learn the consequences of trading with each experimenter. The experimenters wore different colored scrubs so that the capuchin subject would know which one delivered each reward (i.e., high versus low peak and high versus low end-point). Thus, we ensured that the capuchin was making an informed choice between the two experimenters. Just as in each previous experiment, the experimenters available to trade with the capuchin subject had not been involved in any other trading studies and were clothed in scrub colors that were distinct from previously used ones. However, in contrast to all of our previous trading studies, in these two experiments the traders concealed the food rewards until it was time to feed it to the capuchin subject. This ensured that the exchanges were conducted on the basis of the remembered pleasure from eating a food reward provided by a particular experimenter – therefore the experimenters held the rewards such that they were not visible to the subject. Therefore the basis of selection was not due to any visual differences between the two rewards but instead the remembered pleasure associated with trading with an experimenter for a high end-point (or high peak) reward versus the same reward re-sequenced for a low end-point (or low peak).

In our first experiment, the experimenters differed in that one of them treat with a high end-point whereas an alternative experimenter provided the same treat but sequenced so that it concluded with a low end-point. Specifically, the food reward in this study was a biscuit stick that was halfway coated with frosting resulting in

a reward with a highly-valued (frosted) half and a low-value (unfrosted) half. Thus, the high end-peak experimenter fed the food reward with the frosted half at the end whereas the low end-point experimenter fed the reward in the opposite configuration. In this experiment, capuchin monkeys preferred to trade tokens to receive a sequence of food rewards that provided the high point at the end of the feeding sequence rather than the beginning. That is, they preferred to trade with experimenter who sequenced the reward such that it started with the unfrosted half and concluded with the frosted half rather than vice versa. This preference was significant when pooled across subjects (63%, N=240, p = 0.00002, one-tailed binomial probability test). The results therefore supported the directional prediction that the capuchins preferred the reward with the high end-point.

In our second study, capuchins preferred to trade tokens for a food reward with a brief but high-quality peak rather than for an alternative food reward with a longer but lower-quality peak. The food reward, just as in the previous study, was a biscuit stick that was partially covered in high-value frosting. However, the biscuit sticks were modified by partially shaving off the frosting: the frosting was shaved off of the food rewards such that the subjects had a choice between a short but highly enjoyable reward or a longer but less enjoyable one. Specifically, an experimenter offering a food reward with a short but fully frosted section (followed by an unfrosted section) was preferred to an experimenter offering an alternative that was twice as long but only halfway frosted (ending in a much shorter unfrosted section). The amount of frosting was identical across both experimenters, however, one provided the frosted portion in a short high peak whereas the other provided a low peak. This preference was significant when pooled across subjects (59%, N=480, p = 0.00003, one-tailed binomial probability test).

Critically, just as in previous studies, a subject who merely forms an association between a trading partner and a greater quantity of food would not express a preference in either of the last two experiments. In the experiment concerning end-point sensitivity both experimenters delivered exactly the same food object (except rotated so that the frosting would come either first or last). In the second experiment both experimenters offered identical amounts of frosting except spread over a long or a short biscuit section. In contrast the capuchin subjects expressed a preference for a high end point and for a high peak – a preference that could not be explained by a mere association between a trading partner and a greater reward.

These results therefore suggest that monkeys, like humans, exhibit both end-point and peak sensitivity when evaluating the quality of remembered experiences. Accordingly, humans and capuchins may both judge past experiences similarly and prefer events with high peaks and end points. This suggests that this bias, much like other framing effects, did not necessarily emerge as a result of specific economic experiences and market disciplining. Instead, evaluating past experiences using a peak-end rule might be the result of cognitive strategies which evolved long ago in the primate lineage.

Conclusions and Discussion

The data presented here suggest that economic biases are present in an ancestrally-related species. Monkeys, like us, take into account subjective features of prospects that are irrelevant to the consequences of their choices, as well as exhibit classic framing effects such as reference dependence, loss aversion, and the endowment effect. Therefore these biases might rely on cognitive systems that are more evolutionarily ancient than previously thought.

These data support the claim that the cognitive (and possibly neural) architecture giving rise to economic biases and framing effects was present in an evolutionarily-ancient relative of both humans and capuchin monkeys. In addition to showing that these biases are not uniquely human, these results results eliminate the possibility that these heuristics are artifacts of the particular methods (such as verbal questionnaires) or subject pools used in human studies.

Additionally, these results support the claim that behavioral biases do not necessarily emerge as a result of specific economic experiences —instead, our human systematic biases might be the result of evolved cognitive strategies, ones present in our primate lineage for considerable phylogenetic time. This work provides further constraints on the cognitive and neural mechanisms that may underlie these biases in the human species. Specifically, our findings suggest that these heuristics cannot rely on language or linguistic processing. In addition, our result hint that these biases cannot be due to complex or uniquely human cognitive capacities, such culture, learning, or market disciplining.

Second, and perhaps more importantly, these results provide the first demonstration that framing effects, the endowment effect, and reward sequencing elicit preference-reversals in a nonhuman animal. Therefore, these behavioral results provide a new avenue for neurophysiological investigations of subjective and contextual aspects of decision-making. Non-human primates are frequently used as neural models for exploring the anatomical basis of decision-making under uncertainty (Glimcher, 2003; Platt & Glimcher 1999) but much of this work has focused on simpler types of decisions (such as determining the direction of a saccade). Accordingly, a sharp disconnect exists in the methodologies employed in these studies and those

used in neuroimaging work concerning complex decisions undertaken by humans (see Camerer, Lowenstein & Prelec, 2004) for review). The proposed work provides novel behavioral evidence that measures of preference, such as purchasing behavior when provided with a scarce budget of tokens, can also be used to test the predictions of prospect theory in a non-human primate model.

To summarize, finding these biased tendencies in capuchin monkeys impacts our understanding of human decision-making in three key ways. First, the fact that seemingly "irrational" tendencies may actually have been around for over 35 million years would suggest that classical economic decision-making biases may possibly be well-adapted to ancient rather than modern decision-making environments. Second, the observation that capuchins and humans reason about economic decisions in the same way would suggest that decisions involving framing and risk-taking operate in a fast-and-frugal way, meaning that they don't require computationally-intensive, uniquely human processing. Finally, the hypothesized findings would also the point that throughout evolutionary history, strategies like framing effects may have played a role in our economic decision-making, thus allowing these traits to be passed along from ancestral species to humans (Lakshminarayanan, Santos, & Chen, in press).

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