

How Basic are Behavioral Biases?
Evidence from Capuchin Monkey Trading Behavior*
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Abstract

Behavioral economics has demonstrated systematic decision-making biases in both lab and field data. Do these biases extend across contexts, cultures, or even species? We investigate this question by introducing fiat currency and trade to a colony of capuchin monkeys, and recovering their preferences over a range of goods and gambles. We show that capuchins react rationally to both price and wealth shocks, but display several hallmark biases when faced with gambles, including reference-dependence and loss-aversion. Given our capuchins' inexperience with trade and gambles, these results suggest that loss-aversion extends beyond humans, and may be innate rather than learned.

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“Nobody ever saw a dog make a fair and deliberate exchange of one bone for another with another dog. Nobody ever saw one animal by its gestures and natural cries signify to another, this is mine, that yours; I am willing to give this for that.”

Adam Smith, Wealth of Nations

1 Introduction

Over the past few decades, behavioral economists have identified that human decision makers exhibit a number of systematic biases both in the lab and in the field. Two of these biases, reference-dependence and loss-aversion, have received a substantial amount of empirical attention, both from economics and neighboring disciplines such as psychology and sociology.¹ Evidence that agents treat losses differently than comparable gains has been found in: experimental markets as the endowment effect;² (Kahneman, Knetsch & Thaler 1980), in the trades of individual investors who are reluctant to realize losses; (Odean 1998), and in the behavior of house sellers who are unwilling to sell below buying price (Genesove & Mayer 2001).

Despite the mounting evidence of the importance of this behavior, less direct attention has been paid to understanding how basic or widespread these biases are. Are biases such as loss-aversion the result of social or cultural learning and specific environmental experiences? Or could they be more universal, perhaps resulting from mechanisms that arise regardless of context or experience? The root cause of a behavioral bias may effect how we think about both its potential scope, and the degree to which we believe market incentives will act to reduce its effects.

Traditionally, economists have remained agnostic as to the origins of human preferences, and usually assume their stability over both time and circumstance. For example, Becker (1976) writes, "generally (among economists)... preferences are assumed not to change substantially over time, nor to be very different between wealthy and poor persons, or even between persons in different societies and cultures."³ Indeed, coupled with maximizing behavior and market equilibrium, Becker asserts that the assumption of stable preferences

¹These biases, along with a probability-weighting function, make up "prospect theory," first introduced in Kahneman and Tversky (1979). For an excellent summary of the recent empirical work on prospect theory, see Camerer (2000).

²The endowment effect is the observation that minimum amount a subject is willing to accept to give up a randomly endowed good is often more than twice what they would have been willing to pay for and that good had they not been given it.

³It must be stressed that Becker was referring not to preferences over market goods, but to more primitive "underlying objects of choice" such as "health, prestige, sensual pleasure, benevolence or envy." (Becker 1976).

"forms the heart of the economic approach." If much of the fundamental structure of our preferences were so deep rooted as to extend to closely-related species, this would bolster the assumption of preference stability.

Indeed, early experimental work found support for the stability of economic choice theory far from its usual subjects; several studies have demonstrated that rat and pigeon behavior seems to obey the laws of demand (Kagel et al. 1975). Unfortunately, while rats and pigeons are easy subjects to work with, their limited cognitive abilities make it difficult to investigate more subtle aspects of economic choice, including many important and systematic human biases.

In this study we test for both adherence to the law of demand and the presence of reference-dependant and loss-adverse choice in a sophisticated and closely related primate, the tufted capuchin monkey (*Cebus apella*). To do this, we introduce a fiat currency to a colony of capuchin monkeys, teaching them that small coin-like disks can be traded with human experimenters for food rewards⁴, and are fungible across a variety of possible trades. Using this new ability, we are able to conduct a number of revealed-preference experiments analogous to canonical human choice experiments.

Our first set of experiments investigate capuchin purchasing behavior when they are asked to allocate a budget of tokens among a set of possible foods. In response to both price and wealth shocks, capuchins adjust their purchasing behavior in ways consistent with the Generalized Axiom of Revealed Preferences (GARP).⁵ In this way, capuchin choice closely mirrors our own, and admits the standard tools of utility analysis and price theory. This closely mirrors the early economic work on rats and pigeons, and provides a context in which to interpret the capuchins' latter departure from rational choice.

Our second set of experiments demonstrates that when faced with decisions involving simple gain-loss frames, capuchins demonstrate both reference-dependence and loss-aversion. In these experiments, a capuchin must choose between trades in which one amount of food is initially displayed (serving as a frame) but which may change in amount before being delivered. Specifically, in our main experiments capuchins express a strong preference for gambles in which good outcomes are framed as bonuses (the subject sometimes receives more than was initially displayed) rather than payoff-identical gambles in which bad outcomes are emphasized as losses. Furthermore, capuchins seem to and weigh those

⁴For similar trading methodologies with capuchins see Brosnan & de Waal, (2003, 2004); Liv et al., (1999); and Westergaard et al., (1998, 2004); for an very early example of the primate capacity to trade, see Wolfe (1936).

⁵Early papers by Samuelson (1938), Houthakker (1950), and Afriat (1967) established the revealed preference approach to evaluating whether any given set of choices is consistent with rational behavior. Varian (1982) generalized this approach, and showed that the Generalized Axiom of Revealed Preference (GARP), is a necessary and sufficient condition for any set of choices to arise from the maximization of a continuous, concave, weakly monotonic, and locally non-satiated utility function.

losses more heavily than comparable gains, displaying not just reference-dependence, but loss-aversion. These experiments also allow us to reject most competing models of naïve or unsophisticated choice. In particular, several of our results require a capuchin to overcome the impulse to try and obtain an initially larger food reward, and instead to trade with an experimenter who initially displays a smaller food reward. Numerous studies have shown that this type of inhibition problem is difficult for both monkeys and even great apes.⁶

Arguing that loss-aversion is not an acquired characteristic of capuchin preferences is the novelty of the situation. Abstract gambles were first introduced to these capuchins by our experiments and subjects encountered them alone, away from others; subjects had no prior trading experience that could have led to the development of these biases. As such, our results suggest that loss-averse behavior is a very general feature of economic choice, and extends to some of our closely related neighbors. Borrowing from a large body of research in biology, these results may further suggest an early-evolutionary origin for loss-averse behavior in humans, since the close kinship between humans and capuchins suggests common cognitive systems are likely to have a common origin. That is, our results may suggest that loss-aversion is an innate and evolutionarily prefigured feature of human preferences, a function of decision-making systems which evolved before the common ancestors of capuchins and humans diverged.

The remainder of the paper is organized as follows. Section II reviews the set of papers in behavioral economics which speak to the origin and scope of behavioral biases. Section III describes capuchins both as a species and as our test subjects, and lays out some of the tradeoffs inherent in experimenting on non-human primates. Section IV provides details on our laboratory setup and our method for eliciting preferences from capuchin trading behavior. Section V describes our initial compensated price-shift experiments, and before presenting those results. Section VI describes our method for inducing gain / loss frames and the setup of our loss-aversion experiments. Section VII presents the results of these experiments, which we discuss before concluding in in section VIII.

⁶Both new-world monkeys and great apes fail to solve reverse-contingency tasks (games in which an experimenter presents a large reward whenever the agent reaches for a smaller treat, and presents a small reward whenever the agent reaches for the larger treat)(Boysen et al., 1995; Kralik, et al., 2001). However, when the game is modified such that the large reward is presented whenever the agent reaches for a *symbol* of the small reward (and the small reward is presented whenever the agent reaches for a symbol of the large reward) many primates succeed (e.g., Boysen et al., 1999). A contribution of our work to the psychology literature is that we report the surprising result that capuchins have no trouble solving a reverse-contingency task when treats are obtained by exchanging fiat currency for the rewards, rather than simply reaching for them. That is, token-mediated exchange allows primates to overcome the impulse to simply reach for the greater reward – just as symbol-mediated choice does.

2 Related Literature

Several recent papers have shed light on the foundations of behavioral biases. A growing literature in the field of neuroeconomics has attempted to use imaging technology to map brain activity as subjects make economic decisions, and correlates these measures of brain activity to subjects' decisions. For example McClure, Laibson, Lowenstein, & Cohen (2004) show the spatial distribution of brain activity is correlated with decisions involving intertemporal choice. While this approach is extremely useful in shedding light on the mechanisms of decision making, the ability of this approach to address questions of universality and stability is limited by the scope of activities that can be scanned (subjects must be securely restrained inside a large magnet) and by the difficulty of translating neural correlates of behavior into causal statements.

A few theory papers have also tried to understand what types of evolutionary forces might have selected for preferences that display behavioral qualities. These papers typically model preferences as a means by which nature incentivizes an organism to maximize its evolutionary fitness; various constraints on nature's ability to achieve first-best incentives give rise to behavioral biases. Most notably, Rayo & Becker 2005 explore what types of evolutionary pressures would have produced both past-payoff and social reference-point effects, and Samuelson & Swinkels 2005 explore under what conditions choice-set effects might be evolutionarily optimal.

More similar in goals to our approach, Henrich et al. (2001) perform behavioral experiments in fifteen small-scale societies, all of which are relatively isolated and have had relatively limited market contact. Essentially, their approach exploits the extreme cultural variation between these societies and finds large differences in how they play an ultimatum game. We also hope to shed light on the origins of human economic behavior and the role of environmental experience, but exploit a very different source of variation than Henrich and colleagues. Our experiments can be seen as exploring which aspects of our behavior are not confined to the heavily socialized human species, but extend to primates that lack any previous market experience. Specifically, if loss-aversion emerged in our evolutionary past we would expect that closely related species would exhibit analogous behavior – and may better understand the origins of our biases by understanding their expression in our close evolutionary neighbors.

2.1 Economic Experiments with Children and Animals

Harbaugh, Krause and Berry also conduct experiments with similar goals to our own, exploiting age instead of cultural or species variation. Harbaugh et al. (2001a) conduct numerous simple budgeting experiments on children between the ages of seven and eleven,

and find that violations of GARP are relatively rare. Harbaugh et al. (2001b) in contrast, finds evidence of the endowment effect in children as young as five, and finds no evidence that the effect diminishes with age up through college.⁷ This suggests that the endowment effect is not reduced by market exposure, though leaves open the possibility that children learn this behavior through experience they receive before age five.

While the use of animal subjects is widespread in psychology, their use as subjects in economics is relatively scarce. A notable exception is the work of Kagel, Battalio, Green, and colleagues (Battalio et al. 1981, Battalio et al. 1985, Kagel et al. 1975, Kagel et al. 1981, Kagel et al. 1990, Kagel et al. 1995). These researchers systematically explored a variety of economic decisions (e.g., consumer demand, labor supply, risk aversion, and intertemporal choice) in two classic exemplars of associative learning: rats and pigeons. Having been trained that different levers each delivered a unique reward at an experimentally-variable rate, subjects signaled preferences via their lever choices. Kagel and colleagues then employed a simple revealed preference method in which they examined their subjects' choices when presented with a "budget" of limited lever presses.

Most applicable to our work, Kagel et al. (1975) explores how rats and pigeons respond to a compensated price shift. They find that subjects' choices during such a shift largely respected GARP; in fact, utility maximization does a much better job of explaining their data than any other available choice theory (including the canonical non-human psychological choice model, the matching law).⁸ In later experiments involving gambles, Kagel and colleagues observed that on balance rats and pigeons obeyed expected-utility theory, but do display some systematic biases. However, unlike results on human (and our capuchin) subjects, Kagel and colleagues find that prospect theory does not explain the deviations from expected-utility theory that are present in rats and pigeons.⁹

We depart from the important work of Kagel and coauthors in two key ways. First, since rats and pigeons are very distantly related to humans, experiments on them are of limited use in answering questions about high-level human decision making, since most of the relevant neural architecture presumably emerged after our common evolution. The contribution of Kagel and coauthors is more closely akin to that of Becker (1962), demonstrating the robustness of price theory to large variation in the sophistication of agents.

⁷Closely related to loss-aversion, the endowment effect is the observation that consumers often seem to value goods more after possessing them than they do when they do not have them. This is often characterized by a set of people randomly endowed with an object exhibiting a higher willingness to accept (price for selling the good) than the control group's willingness to pay. For a good overview of this bias and its connection to loss-aversion, see Kahneman, Knetsch & Thaler (1991).

⁸For a good summary of the psychological literature on the matching law and its relationship to more modern theories of choice see Herrnstein and Prelec (1991).

⁹Instead, they find evidence of non-standard probability weighting that is best represented by some mix of fanning out and fanning in (see Kagel, MacDonald & Battalio 1990).

Second, since rats and pigeons lack the cognitive sophistication of humans, researchers working with these species can only carry out relatively simple choice experiments (i.e., choice between trained levers). These tasks seem unlikely to lead to the classic biases observed in humans, such as framing or reference-point effects. Capuchin monkeys on the other hand, are socially sophisticated organisms whose native ecology requires successful management of scarce resources and risky trade-offs. This sophistication and their evolutionary proximity to humans make capuchins far better-suited subjects with which to study the mechanisms that enable economic decision making; yet, since our subjects have all been raised in captivity we can limit the possibility that behavior analogous to human behavior developed in response to similar environments.

3 Subjects: The Tufted Capuchin

The tufted (or brown) capuchin is a new-world monkey native to tropical climates within South America. A cohabiting capuchin breeding group is usually characterized by a male-dominance hierarchy. A single alpha-male and several sub-alpha males and females normally live together, with the alpha-male holding sexual monopoly over the females within the group. Capuchins are often referred to as "extractive foragers"; they prefer easy to eat fruit but when pressed are capable of pounding apart hard nuts, stripping tree bark, raiding bee hives and even killing small vertebrates. For an excellent survey of the species covering all aspects of their native ecology see Fragaszy, Visalberghi & Fedigan (2004).

As a species, the tufted capuchin monkey (*Cebus apella*) has been widely studied in psychology and anthropology. They make excellent subjects since they are relatively quick and adept problem solvers, skilled tool users, and a close evolutionary neighbor to humans.¹⁰ Despite this history, conducting economic experiments with capuchins carries with it several trade-offs compared to conventional human subjects. Experiments with human subjects must inevitably assume some independence between the effect being studied in the laboratory and such things as subjects' selection into the subject pool, as well as pre- and post-experimental conditions outside the laboratory. With non-human subjects, we can control selection and directly manipulate various features of their daily environment and social interactions. However, because of the difficulties involved in housing and maintaining a rewarding environment for capuchin subjects, it is prohibitively costly to achieve sample

¹⁰Within the set of primates though, capuchins are actually very distantly related to humans. Capuchins diverged from our common ancestral line in what biologists call the new-world primate radiation. This is when all the primates who inhabit the new world split off from the old-world primates, the line humans emerged from. While the exact date of this split is not known, molecular-clock estimates suggest capuchins split off as a genus around 23 million years ago. Estimates of our latest common ancestor date around 40 million years (Schneider et al., 2001).

sizes to which economists are accustomed in testing humans. As such, we have chosen a sample size typical for comparative cognition studies with primates (e.g., Brosnan & de Waal 2003, Brosnan & de Waal 2004).

3.1 The Experimental Subjects

Our test subjects were all born in captivity and live in a single social group. Six adult capuchins, two male [AG, FL, NN] and three female [MD, HG, JM] ranging from seven to eight years old, participated in this experiment. All were genetically unrelated with the exception of JM [mother of MD]. Individuals were isolated from the rest of the group during each trial in order to minimize the effects of social interaction on experimental performance.

All subjects had previously participated in experiments concerning visual cognition, social cognition, and tool use, but had never before participated in a study involving trade. In all of our experiments we used sweet foods, which are highly valued by capuchins, as food rewards. Outside our experiments all subjects have ample access to water and calories (in the form of fruits and monkey chow); what motivate our capuchins are payments of desirable foods, not hunger per-se.

4 Methods: Setting and Apparatus

In all the following experiments subjects were allowed to trade tokens with one of two experimenters. Each experiment is composed of several sessions, each session constitutes twelve trials, and each trial is an opportunity to trade a token for one of two possible food rewards. Every capuchin was endowed with a budget of tokens at the beginning of each session and was allowed to allocate this budget however they saw fit; however, trades had to be conducted one at a time. Identical inch-wide aluminum discs were used as tokens in all exchanges.

Trading was conducted in a cubical testing chamber (28-inches wide) that was adjacent to the main cage, and into which subjects entered voluntarily. Two panels on opposite sides of the chamber allowed participants to interact with experimenters through rectangular openings, large enough for the capuchins to reach out of [and experimenters to reach into] the testing chamber (see figure one). In each trial, two potential trades were offered on opposite sides of the cube, and the subject made its choice between these two options by choosing which experimenter to exchange a token with. All sessions were videotaped in addition to an RA recording each actor's string of choices. The experimental trading protocol is pictured below.



Figure 1: *A capuchin decides which experimenter to trade with. The subject enters the testing chamber (A), takes a token from a tray (B), places it in the hand of an experimenter (C), and receives a food reward from a tray in his other hand (D). The film clip from which these are drawn is available from the corresponding author on request.*

4.1 General Methods

Before each session of twelve trials, two experimenters (E_1 and E_2 , wearing different colors)¹¹ arranged an endowment of tokens on a tray, which was in view but out of reach of the subject. To begin each session an experimenter pushed the tray within reach of the subjects through the front of the testing chamber. Then to begin each trial the two experimenters simultaneously positioned themselves in front of opposite side panels (panel A in figure 1). Each experimenter held a dish with a food reward (in clear view of the subjects) approximately six inches above the opening closest to the interior of the cage, and extended an empty hand into the other panel opening. If the capuchin took a token from the tray (panel B) and placed it in an experimenter's hand (panel C), then the experimenter would lower his food dish and present the capuchin with the food reward (panel D).

In later conditions the experimenters presented capuchins with risky choices; before lowering the food dish the experimenter would sometimes alter the amount of food, either taking away or adding to the amount of food in the dish. Between each trial the experi-

¹¹For expositional simplicity each experimenter is denoted by E_x where x is how many pieces of food the experimenter would initially display before possibly adding or taking away pieces.

menters swapped positions (replenishing the food in their dish if necessary), and resumed their initial stance, with the food reward held several inches above the opening closest to the main cage and an empty hand extended into the cube through the opening nearest the tokens. The session ended after the subject has exchanged all twelve of their budgeted tokens for food rewards. Non-standard trades (including those in which tokens were thrown from the enclosure or those in which multiple tokens were pressed into an experimenter's hand), were not rewarded and the subject was allowed to make that choice again. So as to minimize subject confusion, each experimenter represented a consistent choice for the capuchin throughout each experiment. No capuchin was allowed to participate in more than two experimental sessions on the same day, but could participate every day if they wished to.

Each subject participated in experiments one, two, and three in sequence, moving from one experiment to the next when their choices in the previous had stabilized. In each of our experiments this criterion was set as five consecutive sessions in which a capuchin allocated their tokens in near-constant proportion.¹² We took these final choices to express each actor's preferred split between the choices each experiment affords. In our data analysis we use only the last five sessions for each actor; each capuchin took between six to twelve sessions to stabilize. Once a subject was finished with an experiment, we transition them to the next by running several days worth of "forced trials." These trials were identical to the subject's next experiment, except that only one of his future choices (randomly selected each trial) was available at any given time. In this way the capuchin both became aware that the trading environment had changed, and was "forced" to become equally familiar with both of his new options.

5 Preliminary Experiments: Capuchins Obey Price Theory

Our preliminary experiments closely mirror those of Kagel and coauthors, and allow us to directly test that capuchin choice looks broadly rational and admits standard price theory. In order to do so we first found a set of two goods for each subject between which they were roughly indifferent, then elicited their choice over a simple budget set between these two goods. We then subjected each capuchin to a compensated price shift and examined how they respond.

¹²This meant their token allocations moved no more than one out of each session's twelve trials, for five consecutive sessions.

5.1 Methods: Identifying Preferences

Before beginning the pricing experiment, each participant was tested to identify two food rewards between which the subject was roughly indifferent. That is, starting with apples as the first good, we looked for another good such that when allocating a budget of twelve disks, the capuchin would reliably consume at least some of each good. Each experimenter was assigned a different good to display and exchange for a single token. When a subject reliably consumed a positive quantity of both apples and the other food over at least ten sessions, it was determined that the subject was roughly indifferent between the two goods offered (these foods ended up being either grapes or jello cubes). Until this combination was found, the non-apple experimenter changed the good they offered until this interior budgeting condition was satisfied.

5.1.1 Baseline and Compensated Price Shift

Once an appropriate good was found, the next steps of our price shift experiment are very straightforward. To establish a baseline measurement, each one of three subjects were repeatedly asked to allocate a budget of twelve disks between food one (apples) and food two (either grapes or jello). This was done exactly as described in the general methods above, with each experimenter trading one token for one piece of their respective food reward.

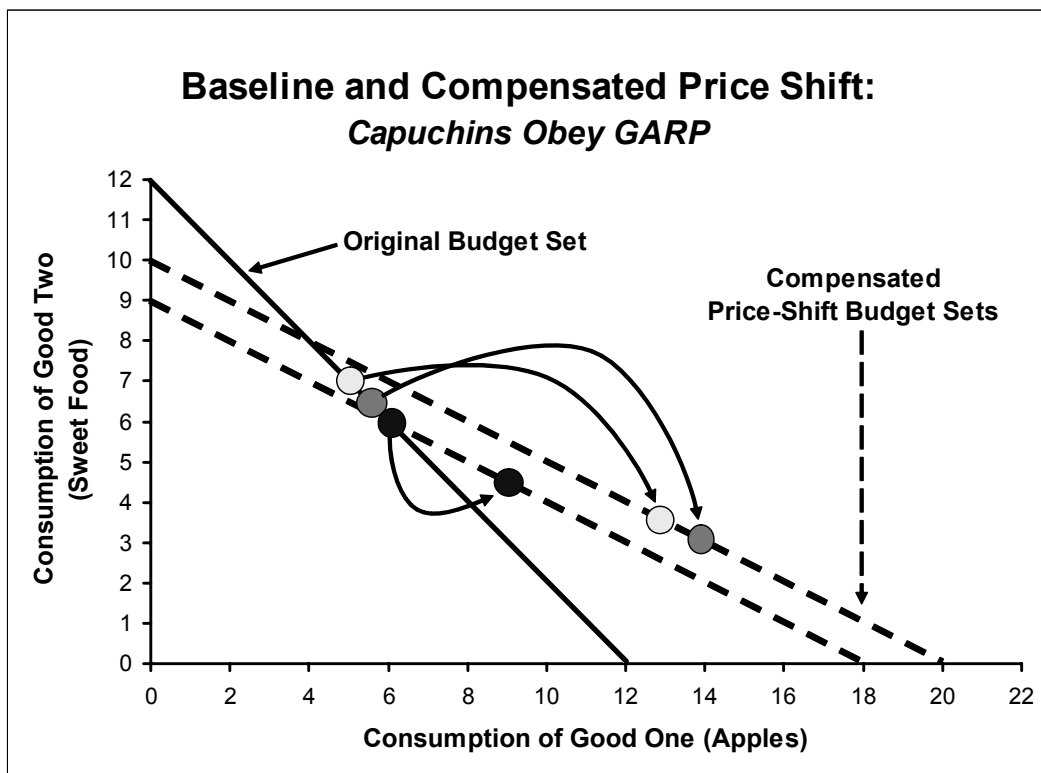
Each capuchin was run on this baseline condition until their choices stabilized; that is, until their choices didn't change by more than one token for a span of five sessions. Once an actor had stabilized, their behavior over the next week was averaged into a representative consumption bundle (see the solid budget line in graph one). Using this bundle, a new budget of disks was assigned to each actor for use in a compensated price shift.

This compensated price shift took the form of the experimenter who trades for apple changing the amount they were willing to trade for a token. Instead of trading a token for one piece of apple, the experimenter would now always display and trade two pieces of apple for each token. This represented a fall in the price of apples by a half, and in order to compensate for this each subject's budget was reduced. This reduction was from twelve to either nine or ten tokens, depending on which most closely shifted back the new budget set such that the bundle the subject originally consumed was close to still lying on the new budget line (see the dotted budget lines in graph one). Each subject's preferences were again allowed to stabilize, then another week's worth of sessions were elicited under this new price régime.

5.2 Results: Preliminary Price Theory Experiments

The results of the preliminary pricing experiment are summarized in table and graph one. In graph one, the solid line represents the initial budget set each actor was presented in the baseline condition, while the dotted line represents each actor's compensated budget after the price of apples falls in half. In order to satisfy GARP, an actor must consume (weakly) more apples after the shift than before. All subjects' choices are aggregated over at least ten sessions, and every actor's choices easily satisfies GARP at the 1% level.

Graph One: *Budget Sets and Subject Choices*



Each point represents the purchasing behavior of a subject after their choices had stabilized, averaged over a week.

Table One: *Price Theory and Compensated Price Shifts*

| Baseline Experiment: Subjects given a budget of 12 disks, both goods have price 1. | | | |
|--|------------------------|------------------------|-----------------------|
| | Actor 1 (FL) | Actor 2 (NN) | Actor 3 (AG) |
| Food used for good one: | Apples | Apples | Apples |
| Food used for good two: | Jello | Grapes | Jello |
| Percent of budget spent on good one: | 47% | 42% | 51% |
| Number of trials: | 132 | 72 | 144 |
| <i>Compensated Price Shift Experiment:</i> | | | |
| Good one's price falls from 1 to $\frac{1}{2}$, good two's price stays 1, and the budget shrinks. | | | |
| New budget of disks: | 10 | 10 | 9 |
| Percent of budget spent on good one: | 69% | 64% | 50% |
| Good one consumed before \rightarrow after shift: | 5.6 \rightarrow 13.8 | 5.0 \rightarrow 12.8 | 6.1 \rightarrow 9.0 |
| Number of trials: | 140 | 100 | 216 |
| Change in choice satisfies GARP: ¹³ | 0.001 | 0.001 | 0.001 |
| Choice % responds to price shift: ¹⁴ | 0.001 | 0.004 | 0.966 |

Tests of significance reported as p-values of a two-sided test.

Note though that with only one compensated price shift, several naïve models of choice will satisfy GARP. Indeed as Becker (1962) points out, many forms of random behavior can satisfy GARP in response to compensated price changes. In this setting, note that since we have experimenters switch sides of the testing chamber after each trial (to eliminate side bias), constant budget-rationing could arise from complete inattention. To account for this we also test whether each subject's choices are inelastic enough to have arisen from random behavior, using as our null that neither price nor wealth shocks effect a capuchin's choices. Accordingly, in table one we also examine the percent of trials each capuchin spends trading for apples before and after the price shift, and test whether these percents differ. Two out of three subjects showed a significant response to this test at the 1% level. Note that our third subject, AG, does not pass this test, spending 50% of his time (and consequently, his budget) trading for apple both before and after the price shift. AG's behavior suggest that he is either maximizing Cobb-Douglas preferences (with a price elasticity of -1), or is inattentive to prices when choosing which experimenter to trade with.

¹³Our test of GARP is a two-sided p-test that the number of pieces of apple that the actor consumes weakly increases after the compensated price-shift.

¹⁴This is a two-sided p-test that the *fraction of trials* the subject chooses apples responds to the price shift; NN and FL change significantly while AG does not.

6 Main Experiments: Are Capuchins Reference-Dependant?

Once our original subjects completed these initial experiments an additional three subjects were recruited for our main set of experiments, while AG was dropped from the study for becoming unresponsive. In this set of experiments the same budgeting procedure was used to elicit choices, with each session composed of twelve opportunities to trade a token for one of two possible food rewards. Unlike the initial experiment though, only apples were used as food reward, and the experimenters no longer automatically presented the capuchin with the apples displayed in their tray when given a token. Now, experimenters sometime altered the food in the presentation tray before making that tray available to the subject. In this way, we were able to independently vary what the capuchin was initially shown and what the capuchin would receive in exchange for a token, with the latter sometimes consisting of a gamble.

6.1 Methods: Experiment One, Stochastic Dominance

In experiment one, a capuchin could trade their tokens with one of two experimenters. Experimenter E_2 represented a random payoff of one or two apple pieces each with equal probability, and experimenter E_1 represented a sure payoff of one piece. E_1 and E_2 also differed in how many pieces they initially showed the capuchin; E_2 displayed two squares of apple, while E_1 displayed only one square of apple. This experiment tests whether capuchin choice respects first-order stochastic dominance; that is if they prefer gambles that weakly dominate another option.

Specifically, after being given a token experimenter E_1 always lowered his dish to present the subject with one apple piece – exactly as many as he had displayed. In contrast E_2 started every trial displaying two apple pieces in her tray, but would only deliver both pieces half the time she was traded with. The other half of the time E_2 would remove one of her two apple pieces and deliver only the remaining piece to the subject. A random-number generator determined beforehand whether any given trade would result in a payoff of two or one; when a apple piece was removed it was placed into an opaque receptacle underneath the testing table that was both out-of-sight and out-of-reach of the subjects.

6.2 Methods: Experiment Two, Reference-Dependence

In experiment two, subjects chose between experimenters who both delivered identical gambles – differing only in whether they added to or subtracted from their initial displayed offering of one or two apple pieces. This was designed to test whether capuchins would respond to a simple framing manipulation, presenting some payoffs as gains and some as losses, while holding constant the underlying payoffs.

Specifically, E_1 and E_2 would stand on opposite sides of the testing chamber displaying one and two apple pieces, respectively. Upon being presented with a token, E_2 would present the subject with either the two apple pieces he had displayed, or would visibly remove one piece and deliver only the remaining apple piece to the subject. When an apple piece was removed, it was placed into an opaque receptacle underneath the testing table that was out of sight and out of reach of the subject.

When the subject traded with E_1 however, she would either present the single piece she displayed, or add one apple piece and deliver two pieces. When this bonus piece was added it was drawn from an identical receptacle.

Essentially then, both experimenters represented a fifty-fifty lottery of one or two apple pieces. They differed only in whether they initially had displayed one or two apples, framing for the marginal apple piece as either a gain or a loss. A random-number generator determined beforehand whether any given trade would result in a payoff of two or one; we call these the bonus vs. penalties conditions.

6.3 Methods: Experiment Three, Loss-Aversion

In experiment three, subjects chose between experimenters who both delivered a payoff of one apple piece – differing only in whether they initially displayed one or two pieces. This experiment was designed to test for the presence of reference-effects in riskless situations, and when combined with experiment two, allows us to measure loss-aversion.

Specifically, E_1 and E_2 would stand on opposite sides of the testing chamber, displaying one and two apple pieces, respectively. Upon being presented a token, E_2 always removed one apple piece and delivered the remaining piece to the subject. The removed square was placed into the opaque receptacle underneath the testing table. In contrast if the subject traded with E_1 , she always presented the single square she displayed.

Essentially then trading with either E_1 or E_2 delivered identically payoffs. However, on all trades E_1 gave exactly the quantity of apple he displayed, while E_2 displayed a quantity of apple that was always reduced from two to one before it was made available to the subject.

7 Results: Main Experiments

The results of all our experiments are reported below in tables two through four, broken down by subject. We will first discuss what can be learned from our results without imposing any significant parametric assumptions; in the next section we fit a simplified version of the standard prospect-theoretic utility function to our subjects which allows more precise analysis.

The results of experiment one are summarized below. Table two shows how each subject behaved over five sessions (60 trials), after an initial set of sessions in which their choices stabilized as they learned about the experimental choices.

Table Two: *Experiment One, Gambles and Stochastic Dominance*

| E_1 shows 1 and gives 1, E_2 shows 2, then gives 1 or 2 with prob. 1/2. | | | | | |
|---|--------|--------|--------|--------|--------|
| Subject (name): | 1 (FL) | 2 (HG) | 3 (JM) | 4 (MD) | 5 (NN) |
| Percent of trials E_1 chosen: [†] | 10% | 18% | 12% | 22% | 5% |
| Sessions till stable: | 7 | 6 | 7 | 6 | 11 |

[†] All subject's choices different from 50% at the 1% level in a two-sided p -test.

The capuchins express a clear preference (87% of trades) for E_2 , the experimenter who displays two apple pieces and delivers either one or two pieces with equal probability. This is of course not surprising; the second option stochastically dominates the first and gives on average a half-piece more of apple.

Given this result though, the results of experiment two are quite surprising. All subjects left experiment one conditioned to favor E_2 , the experimenter who displays two pieces of food. Despite this, in experiment two the capuchins quickly reverse this preference and trade much more with the experimenter who displays only one piece of food. Table three summarizes these results.

Table Three: *Experiment Two, Reference-Dependence in Gambles*

| E_1 shows 1 and E_2 shows 2, then both give 1 or 2 with prob. 1/2. | | | | | |
|--|--------|--------|--------|--------|--------|
| Subject (name): | 1 (FL) | 2 (HG) | 3 (JM) | 4 (MD) | 5 (NN) |
| Percent of trials E_1 chosen: [†] | 68% | 70% | 70% | 70% | 78% |
| Sessions till stable: | 11 | 9 | 9 | 9 | 13 |

[†] All subject's choices different from 50% at the 1% level in a two-sided p -test.

Contrary to both their conditioning and the intuition that naive subjects would favor greater initial displays of food (experimenter E_2), capuchins express a preference for E_1 , the experimenter who frames the gamble as a 50% chance of a bonus rather than a 50% chance of a loss. Pooled, subjects traded with E_1 in 71% of trials in their last five sessions (again, measured after each subject's choices stabilized). For all five subjects this change was significantly different not just from experiment one but from random (50-50) behavior.

Note that any theory of choice which does not take into account reference-dependence fails to predict this pattern of behavior. Indeed, since our experimenters switch sides of the testing chamber between each trial, in order to express a preference between E_1 and E_2 a

capuchin has to actively follow their preferred experimenter from side to side, expending both time and attention.

Experiment three shows this effect is not confined to risky choices, and when combined with experiment two suggest that capuchins are not just reference-dependant, but loss-averse. The results are summarized in table four below.

Table Four: *Experiment Three, Riskless Reference-Dependence*

| <i>E₁ shows 1 and E₂ shows 2, then both give 1.</i> | | | | | |
|---|--|--------|--------|--------|--------|
| Subject (name): | 1 (FL) | 2 (HG) | 3 (JM) | 4 (MD) | 5 (NN) |
| Percent of trials <i>E₁</i> chosen: [†] | 73% | 75% | 80% | 82% | 87% |
| Sessions till stable: | 9 | 10 | 10 | 8 | 10 |
| Choice % greater than in exp. 2, p-value: | 0.27 | 0.27 | 0.10 | 0.07 | 0.11 |
| Pooled, choice % greater than in exp. 2: | <i>p < 0.023, two-sided p-test.</i> | | | | |

[†] All subject's choices different from 50% at the 1% level in a two-sided p-test.

Subjects strongly preferred experimenter *E₁* over experimenter *E₂* (who initially displayed one and two pieces of apple, respectively), despite the fact that both always provide the same, sure payoff of one apple piece. For all subjects this preference (% of trials trading with *E₁*) was stronger than in experiment two, suggesting this was not due to conditioning from the previous experiment. Since the only difference between the two experimenters was that *E₂* showed more than he eventually gave, these results suggest our capuchins are reference-dependant even in riskless choice settings.

To investigate whether capuchins display loss-aversion, we now compare their behavior across experiments. Table five summarizes the aggregate behavior of our subjects in all three experiments, and summarizes what each available gamble represented with respect to expected gains, losses, and food rewards.

Table Five: *Expected Gains, Losses, and Values for each Experimental Choice*

| Experiment: | One | | Two | | Three | |
|----------------------------|----------------------|----------------------|----------------------|----------------------|----------------------|----------------------|
| | E₁ | E₂ | E₁ | E₂ | E₁ | E₂ |
| Experimenter: | | | | | | |
| Gamble offered: | (1, 1, 1) | (2, 1, 2) | (1, 1, 2) | (2, 1, 2) | (1, 1, 1) | (2, 1, 1) |
| Gains: | 0 | 0 | $\frac{1}{2}$ | 0 | 0 | 0 |
| Losses: | 0 | $\frac{1}{2}$ | 0 | $\frac{1}{2}$ | 0 | 1 |
| Expected Value: | 1 | $1\frac{1}{2}$ | $1\frac{1}{2}$ | $1\frac{1}{2}$ | 1 | 1 |
| % of trials chosen: | 13% | 87% | 71% | 29% | 79% | 21% |

Table constructed pooling all subjects' last five sessions after choices stabilize (60 trials).

Looking at experiments two and three, note that in experiment two subjects chose between E_2 who gave a *half-chance of a loss* and E_1 who gave a *half-chance of a gain*, both of these forces pushing the subject to chose E_1 . In experiment three however, E_1 always gives exactly what they showed while E_2 delivers a *sure loss*. An interpretation of the fact that subjects show a stronger preference in experiment three than two (79% to 71%), is that a sure loss has a stronger effect than the combined effects of a half-loss and a half-gain, or that losses affect subject's choices more than gains. In other words:

$$|loss| > \frac{1}{2} |loss| + \frac{1}{2} |gain| \Leftrightarrow |loss| > |gain|$$

Thus, the pooled p-test of experiment three being stronger than experiment two ($p < 0.023$ in a two-sided p-test) can be taken to confirm the presence of loss-aversion in capuchin choice.

A similar intuition suggests that expected value calculations weigh more heavily than framing effects on capuchin choice. Comparing experiments one and two, note that in both choices, a half-chance of a loss push subject to prefer E_2 to E_1 . However, these experiments differ in what force would attract a subject to E_1 ; in experiment two it is the half-chance of a possible gain while in experiment one it is the expectation of an extra half-piece of apple. That the capuchins strongly prefer E_2 in experiment one and E_1 in experiment two suggest that increases in expected rewards greatly outweigh the effects of potential losses.

8 Discussion and Conclusion

Taken together our results suggest that capuchin choice is both very sensitive to changes in prices, budgets, and expected payoffs, and to a lesser degree displays both reference-dependence and loss-aversion. That expected rewards carry a much larger effect than gain / loss frames in our experiments is perhaps not surprising; our analysis only examines at the long-run behavior of our subjects after facing the same choice many times and our reference-point treatment is a relatively mild framing intervention.

It is tempting to ask whether capuchin loss-aversion resembles human aversion in magnitude; for example, in much of the work on human loss-aversion, the ratio of the coefficients on losses and gains is remarkably stable and is commonly used as a measure of loss-aversion, representing how "kinked" the utility function is at the reference point. Tversky & Kahneman (1991) summarize a large body of survey evidence on minimally acceptable gambles and find a ratio of roughly 2.5 to 1. Average ratios of willingness to pay to willingness to accept found in most endowment-effect experiments (see for example Kahneman, Knetsch, & Thaler 1990) yield a ratio of around 2.7 to 1. Benartzi and Thaler (1995) calibrates a ratio of approximately 2.3 from the aggregate risk preferences of stock investors. Although

the amount of price-variation we achieve with only three experiments is minimal, imposing additional structure on capuchin preferences allows the estimation of a comparable but extremely rough measure of a losses to gains measure for our capuchins.¹⁵

We have argued that finding behavioral biases in capuchin choice can suggest an early-evolutionary origin for these biases in humans. This relies heavily on the fact that on questions of origin, it is widely accepted in both cognitive science and evolutionary psychology that a mechanism is most likely evolutionarily ancient if it explains analogous behavior in both humans and primates. That is, since primates and humans are closely related, it is unlikely that a common trait evolved in parallel between our two species, and much more likely common traits evolved once during our common evolutionary heritage. While our results are by no means definitive proof that loss-aversion is innate in humans, to the degree that they make us more likely to believe that some amount of this behavior has a biological component, they may have implications for how we treat loss-averse tendencies in human behavior.

For example, if these biases are innate, we may be more inclined to believe they will persist in both common and novel settings, be stable across time and cultures, and may endure even in the face of large individual costs, ample feedback, or repeated market disciplining. This would greatly constrain both the potential for successful policy intervention, and the types of remedies available. In contrast, while a learned, non-innate heuristic may arise in many (if not all) cultures, we may not expect it to persist in settings in which it was highly sub-optimal, or in which market forces strongly discipline behavior. This would limit the potential scope and scale for welfare losses, and may suggest that policy interventions which increase feedback or learning may eliminate what losses do exist.

Short of this attributional leap however, that loss-averse behavior is not confined to humans can be seen as adding scope to the growing evidence of loss-averse behavior in many aspects of human economic behavior. Understanding how broadly these biases manifest themselves may influence how we should incorporate them into an adequate model of individual decision making. Hopefully, our paper also suggests the utility of methodological exchanges between economics and the closely related behavioral sciences. Bringing the analytic framework of revealed preference to bear on questions at the intersection of economics, biology and psychology carries the possibility of insights useful to each.

¹⁵In a preliminary analysis, we fit a simple linear utility specification to our capuchin's behavior. While parametric results are always to be taken with caution, the relative strength of losses to gains in capuchin decisions (the coefficient of loss-aversion) seems similar to human estimates. For details please see the working version of this paper on the first author's website.

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