What have we learned in non-human primate behavioral economics?

Spring 2017

Cognitive Science

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Abstract:

Much work with nonhuman primates has been inspired by work from behavioral economics with humans. Topics studied include inequity aversion, prosociality, risk aversion, the framing effect, the endowment effect, and other so called cognitive biases. In this paper, I review the pre-existing literature, including, when relevant, active debates over the strength of evidence for particular cognitive biases in non-human primates. I conclude there is strong evidence that non-human primates have the framing effect and the endowment effect in common with humans, but that it is unlikely non-human primates are inequity averse or prosocial in the way we understand these terms with humans. I conclude by discussing future directions, including the possibility of studies designed to quantify the extent to which there are behavioral differences between individuals within nonhuman primate species. Based on recent discussions in human literature (e.g., regarding the replication crisis), I conclude that such advances likely will need larger sample sizes, and more standardized experimental protocols across research groups.

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Section 1
Introduction

In this first section, I introduce the paper's major concepts, which are behavioral economics, nonhuman primates (referred to in the paper as *primates*), and the utility of comparative research. I end this section with an outline of the rest of the paper.

Behavioral Economics

Behavioral economics is the study of the decisions agents make given particular payoffs and risks. The field was introduced by Daniel Kahneman and Tversky and their use of stylized economic games in a laboratory setting.[1] Games are usually played with money, or some item with similar characteristics as money, like tokens or food. They generally involve an exchange between a participant and an experimenter or an exchange between two participants. For example, in the Ultimatum Game (UG) an agent proposes an allocation of a resource to a second agent who can then either accept or decline the allocation. If the second agent declines the offer neither agent receives any payout.[2] If the second agent is motivated only by maximizing the payout from this specific interaction, then the best option is to accept any offer. But it is common for people to decline inequitable offers. Given this behavior, it can be wise for the first

[1] List, J. A. (2007). On the interpretation of giving in dictator games. Journal of Political Economy, 115(3), 482-493.
[2] Thaler, Richard H. "Anomalies: The ultimatum game." *The Journal of Economic Perspectives* 2.4
[2] Thaler, Richard H. "Anomalies: The ultimatum game." *The Journal of Economic Perspectives* 2.4
(1988): 195-206.

agent to offer either an even split or something approaching it, and indeed many people do exactly that.

A famous offshoot of the Ultimatum Game is the Dictator Game (DG). In a Dictator Game, an agent is given an endowment of resources and must decide how much of the resource to keep for himself and how much to give to his conspecific, who is unable to decline any offer. Thus, the first agent is free to offer any amount, including nothing. The Dictator Game is thus often used as a measure of prosocialty.

More general than the Ultimatum Game and Dictator Game, behavioral economics has shown that human choices are the product of *both* their subjective mental states and the payoffs they face. Behavioral economics has drawn its successes by showing that humans seem to behave in ways that contradict rational economic theory, which holds that there is a single optimal action given a known set of payoffs, and that individuals will approximate the optimal choice with their actions.[3]

Behavioral economics has brought into our lexicon terms such as hyperbolic discounting, risk aversion, framing, anchoring, and loss aversion. It has also provided insights into the nature of human altruism and other regard. For example, numerous behavioral economic studies have shown that humans tend to be hyperbolic discounters (discontinuity in the rate at which future utility is discounted).[4] In contrast, traditional

[3] List, J. A. (2007). On the interpretation of giving in dictator games. Journal of Political Economy, 115(3), 482-493.

[4] Laibson, David. "Golden eggs and hyperbolic discounting." *The Quarterly Journal of Economics* 112.2 (1997): 443-478.

economic models expect humans to discount exponentially, but with no discontinuities in the rate at which future utility is discounted.[5]

Behavioral economics has also shown that humans are not perfectly rational in their willingness to take bets. One manifestation of this tends to be referred to as risk aversion, which is a preference for avoiding risks when a payoff ratio isn't overwhelmingly favorable.

Other studies have shown that priming can change how we assess payoffs. As an example, one study found that priming participants to think of themselves as traders reduced their loss aversion.[6]

Additional studies have shown that humans, in experimental settings, are averse to unequal outcomes, which has been termed inequity aversion. These finding broadly fit into two categories: disadvantageous inequity aversion (DIA) and advantageous inequity aversion (AIA). The literature has shown that adults and children both have robust disadvantageous inequity aversion, or an aversion to receiving a lesser outcome than someone else. Further, both adults and children show advantageous inequity aversion, though to a lesser degree.[7]

[5] Kirby, Kris N., and Nino N. Maraković. "Delay-discounting probabilistic rewards: Rates decrease as amounts increase." *Psychonomic bulletin & review* 3.1 (1996): 100-104.
[6] Sokol-Hessner, Peter, et al. "Thinking like a trader selectively reduces individuals' loss aversion." *Proceedings of the National Academy of Sciences*106.13 (2009): 5035-5040.
[7] Blake, Peter R., and Katherine McAuliffe. ""I had so much it didn't seem fair": Eight-year-olds reject two forms of inequity." *Cognition* 120.2 (2011): 215-224.

Similar concepts have been studied on primates. In the next subsection I provide background information on evolutionary relatedness of primates and humans.

Nonhuman Primates

Behavioral economics studied have been conducted with a number of non-human primate species of varying relation to humans. In all, primates share a common ancestor dating back perhaps more than 60 million years, but some species share much more recent ancestors with humans. Bonobos (*Pan paniscus)* and chimpanzees are our two closest living relatives, with whom we share a common relative dating back roughly 4.6 to 6.2 million years.[8]

Yet more distant are Gorillas (*Gorilla gorilla),* with whom we share a common relative dating back 6.2 to 8.4 million years, and Orangutans (*Pongo Pygmaeus),* with whom we share a common relative dating back 12-16 million years.[9] These relatives form the group we refer to as apes. The ape lineage and human lineage share a common ancestor with monkeys.

[8] Chen, Feng-Chi, and Wen-Hsiung Li. "Genomic divergences between humans and other hominoids and the effective population size of the common ancestor of humans and chimpanzees." *The American Journal of Human Genetics* 68.2 (2001): 444-456.
[9] Chen, Feng-Chi, and Wen-Hsiung Li. "Genomic divergences between humans and other hominoids and the effective population size of the common ancestor of humans and chimpanzees." *The American Journal of Human Genetics* 68.2 (2001): 444-456.

Capuchins (*Cebus apella)*, a type of monkey, share a common ancestor with humans dating back roughly 35 million years.[10] Other old world monkeys include baboons, langurs, colobuses, and macaques.

Yet more distant relatives are the new world monkeys. New world monkeys are those that made it from Africa to South America, and thus were separated from the rest of the primate lineage. New world monkeys include the marmoset (*Callithrix jacchus),* tamarin, and spider monkey. In the next subsection, I discuss the motivations for applying behavioral economic research techniques to primates.

The Utility of Comparative Cognition

Studying animals of varying genetic relation to humans, particularly when combined with our knowledge evolutionary history, might prove informative for several reasons.

For one, it could help gives us a picture of the sequence in which particular cognitive capacities evolved in the past. This could help us to parse which cognitive abilities are more likely to have distinct underlying mental structures, and which cognitive capacities are more likely to share the same underlying mental structures. For example, if we were to find that every animal within a lineage that shows loss aversion also shows an endowment effect, it could be suggestive of a common evolved trait that

[10] Visalberghi, Elisabetta, et al. "Selection of effective stone tools by wild bearded capuchin monkeys." *Current Biology* 19.3 (2009): 213-217.

enables both these behaviors. On the other hand, if we found that within the same lineage, some animal X shows no inequity aversion, some animal Y show disadvantageous inequity aversion, but not advantageous inequity aversion, and some other animal Z shows both disadvantageous inequity aversion and advantageous inequity aversion, it could be suggestive of at least two distinct traits. In this way, a more complete set of findings for the economic behavior of primates could ultimately help us pinpoint evolved traits that are associated with human behavioral biases.

As another example, comparative knowledge could give us insights into the selective pressures and evolutionary incentives behind the development of human cognitive traits that interest researchers. Other researchers may find the comparative literature helpful in forming models of the conditions in which human-like intelligence is most likely to emerge.

It is important to acknowledge that non-human behavioral economic studies are not limited to primates. The arguments above are relevant to comparative studies involving any sort of animal. Studies involving non-human primates are often more difficult to conduct than studies with human subjects. This is in contrast to studies on animals such as mice, which can be faster, more dangerous, more precise, and less expensive than studies with humans.

Primate behavioral economics research has tended to seek replications of what has been found in research with human participants. For an incomplete list, primate

researchers have tested for the endowment effect, framing effect, anchoring effect, and hyperbolic discounting. Researchers have also studied whether non-human primates show altruistic helping behaviors These studies have typically been done with economic trading games resembling what one finds in the human literature.

Goals of the Current Paper

In section 2, I will discuss the major findings and active debates within the field of primate behavioral economics. Subsections will include fairness, prosocial donation, the endowment effect, and the framing effect. In section 3, I will discuss the nuances in behavioral economics that have been studied with humans but not primates. In section 4, I will discuss the criticisms of behavioral economics and the extent to which they apply to the study of primates. Finally, in section 5, I will discuss the most useful methods and topics for researchers in the field of primate behavioral economics pursue to pursue in the future.

Section 2
The findings and open debates in primate behavioral economics

Fairness

A common measure of sensitivity to fairness is inequity aversion. Inequity aversion describes an agent's preference for receiving similar rewards as conspecifics or third parties. Researchers have found robust inequity aversion in humans, in particular

contexts. With children, advantageous inequity aversion[11] [12] and disadvantageous inequity aversion[13] [14] has been shown. Further, in infants, evidence for inequity aversion[15] [16] has been shown. Though, it has also been shown that human inequity aversion is not without exception, for an example consider the study "Anti-equality: Social Comparison in Young Children"[17], where a preference to inequity is observed in children.

Evidence has also been gathered for the neural mechanisms underlying inequity aversion[18]; inequity aversion in the context of team efforts[19] [20]; Children's gender differences in inequity aversion[21]; and differences in children's inequity aversion given in-group and out-group control conditions[22].

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[11] Shaw, Alex, and Kristina R. Olson. "Children discard a resource to avoid inequity." *Journal of Experimental Psychology: General* 141.2 (2012): 382.
[12] Blake, Peter R., and Katherine McAuliffe. "'I had so much it didn't seem fair": Eight-year-olds reject two forms of inequity." *Cognition* 120.2 (2011): 215-224.
[13] Fehr, Ernst, Helen Bernhard, and Bettina Rockenbach. "Egalitarianism in young children." *Nature* 454.7208 (2008): 1079-1083.
[14] McAuliffe, Katherine, Peter R. Blake, and Felix Warneken. "Children reject inequity out of spite." *Biology letters* 10.12 (2014): 20140743.
[15] Geraci, Alessandra, and Luca Surian. "The developmental roots of fairness: Infants' reactions to equal and unequal distributions of resources." *Developmental science* 14.5 (2011): 1012-1020.
[16] LoBue, Vanessa, et al. "When getting something good is bad: Even three□year□olds react to inequality." *Social Development* 20.1 (2011): 154-170.
[17] Sheskin, Mark, Paul Bloom, and Karen Wynn. "Anti-equality: Social comparison in young children." *Cognition* 130.2 (2014): 152-156.
[18] Tricomi, Elizabeth, et al. "Neural evidence for inequality-averse social preferences." *Nature* 463.7284 (2010): 1089-1091.
[19] Rey□Biel, Pedro. "Inequity aversion and team incentives." *The Scandinavian Journal of Economics* 110.2 (2008): 297-320.
[20] Mohnen, Alwine, Kathrin Pokorny, and Dirk Sliwka. "Transparency, inequity aversion, and the dynamics of peer pressure in teams: Theory and evidence." *Journal of Labor Economics* 26.4 (2008): 693-720.
[21] Fehr, Ernst, Helen Bernhard, and Bettina Rockenbach. "Egalitarianism in young children." *Nature* 454.7208 (2008): 1079-1083.
[22] Fehr, Ernst, Helen Bernhard, and Bettina Rockenbach. "Egalitarianism in young children." *Nature* 454.7208 (2008): 1079-1083.

What has been found in primates? Do all primates show inequity aversion? Do some species of primates show inequity aversion? Or, is inequity aversion (of the kind observed in humans) not present in primates?

There is an intuitive case that primates must have some sense of fairness (chimpanzees sharing meat after hunts[23]), but this sort of reciprocity may be fundamentally different from what the Ultimatum Game, Dictator Game, and other behavioral economic games seek to detect. Primates have mechanisms to prevent free riding. But, possessing mechanisms to combat free riding may not necessarily imply that primates possess advantageous or disadvantageous inequity aversion.

The intent of inequity aversion experimental designs is that participants are not suspicious that their choices will have reputational consequences (so that an aversion to inequity even when there is no credible threat of repercussions can be shown). Thus, for a study to provide compelling evidence of primate inequity aversion, it will have to make an effort to isolate an aversion to an inequity itself from social pressures that can cause behaviors that look like an aversion to unfairness.

Do primates have a logical use for inequity aversion? Sarah Brosnan, in her paper, "Evolution of responses to (un)fairness" [24], argues that there is a theoretical case to be made for the presence of primate inequity aversion. Namely, inequity aversion

[23] Mitani, John C., and David P. Watts. "Why do chimpanzees hunt and share meat?." Animal Behaviour 61.5 (2001): 915-924.
[24] Brosnan, Sarah F., and Frans BM de Waal. "Evolution of responses to (un) fairness." *Science* 346.6207 (2014): 1251776.

may be an evolutionarily useful mechanism to protest unequal outcomes in cooperative settings. This mechanism could take two forms. In the first form, if a primate receives less than a partner, they may protest in the hopes of receiving more just outcomes in the future. In the second form, if a primate receives more than a partner, the may wish to rebalance the relationship in the future so that the cooperative relationship does not break down.

The authors cite evidence for inequity aversion in capuchins[25], macaques[26], and chimpanzees [27] [28]. One such paper: "Mechanisms underlying responses to inequitable outcomes in chimpanzees, Pan troglodytes" [29] found evidence for advantageous inequity aversion in chimpanzees. The paper notes that social group membership could be significant: "Subjects' rank affected refusal rates. The higher-ranking of the two individuals was more likely to refuse than was the lower-ranking of the two." The paper notes that a subjects' sex also affected results. Overall, males were more likely than females to show a reaction to inequity. Further, they note "subjects were much more likely to refuse tokens than foods, probably because of the challenge of giving up food in one's possession." Finally, the authors note large discrepancies in their results

[25] Brosnan, Sarah F., and Frans BM De Waal. "Monkeys reject unequal pay." *Nature* 425.6955 (2003): 297-299.
[26] Massen, Jorg JM, et al. "Inequity aversion in relation to effort and relationship quality in long□tailed macaques (Macaca fascicularis)." *American Journal of Primatology* 74.2 (2012): 145-156.
[27] Brosnan, Sarah F., et al. "Mechanisms underlying responses to inequitable outcomes in chimpanzees, Pan troglodytes." *Animal Behaviour* 79.6 (2010): 1229-1237.
[28] Brosnan, Sarah F., Hillary C. Schiff, and Frans BM De Waal. "Tolerance for inequity may increase with social closeness in chimpanzees." *Proceedings of the Royal Society of London B: Biological Sciences* 272.1560 (2005): 253-258.
[29] Brosnan, Sarah F., et al. "Mechanisms underlying responses to inequitable outcomes in chimpanzees, Pan troglodytes." *Animal Behaviour* 79.6 (2010): 1229-1237.

between individual chimpanzees, and recommend studies with large test populations be conducted.

In contrast with the results suggesting primate inequity aversion, a number of studies have argued that primates show no signs of inequity aversion. Other studies argue there that primates show no signs of AIA and the evidence for DIA is only very weak. Below, I review some of the more skeptical findings.

Katherine McAuliffe in a 2015 study approached capuchin fairness using an experimental design resembling an Ultimatum Game. The experimenters created a test apparatus where subjects could choose the item they would receive as well as the item their conspecific would receive, while their conspecific could accept or decline a particular item.

They used 3 kinds of reward, the highest value was Kix cereal, second highest value was Rice Krispies, and lowest value was a peanut shell. This created several combinations of equity or inequity. In the DIA condition, capuchins had a choice to reject a disfavored reward, while in the AIA condition, capuchins had a choice to provide their conspecific a better reward at no personal cost. The study found no statistically significant pattern of capuchins rejecting rewards in a DIA scenario or AIA scenario.

The authors concluded that they found no evidence of either AIA or DIA in capuchins. Rather, capuchins seem to make choices that maximize their own food

outcomes in costly Ultimatum Games. The authors acknowledge that their results contradict findings in studies such as "Monkeys reject unequal pay"[30] and "Inequity responses of monkeys modified by effort"[31].

One criticism of a study of this kind is capuchins had to give up a food reward in-order to demonstrate inequity aversion. Studies, since, such as "Capuchin monkeys (Cebus apella) fail to show inequality aversion in a no-cost situation"[32] have come up with designs that attempt to overcome this limitation, by making zero-cost the behavior to reject inequity.

Mark Sheskin, in a 2014 studied capuchin inequity aversion under four social test conditions and four nonsocial control conditions. In the control condition, to test for disadvantageous inequity aversion, (1) a trader offered the subject a grape and placed a lower value food item in a bucket or (2) a trader offered the subject a grape and placed a grape in a bucket. In the disadvantageous inequity aversion test condition, (3) a trader offered the subject a grape and gave a conspecific a lower value food item or (4) a trader offered the subject a grape and gave a conspecific a grape.

In these conditions, no statistically significant DIA was observed. Though, in the social condition, one capuchin reliably traded with the unequal trader. This is

[30] Brosnan, Sarah F., and Frans BM De Waal. "Monkeys reject unequal pay." *Nature* 425.6955 (2003): 297-299.
[31] van Wolkenten, Megan, Sarah F. Brosnan, and Frans BM de Waal. "Inequity responses of monkeys modified by effort." *Proceedings of the National Academy of Sciences* 104.47 (2007): 18854-18859.
[32] Sheskin, Mark, et al. "Capuchin monkeys (Cebus apella) fail to show inequality aversion in a no-cost situation." *Evolution and Human Behavior*35.2 (2014): 80-88.

interesting because it is precisely the opposite of what we would expect to observe if capuchins had DIA. One capuchin reliably showed a preference for the equal trader (what we would expect if capuchins have AIA). But, taken as a whole, these test conditions showed no statistically significant evidence for AIA.

Some improvements of the study design are likely possible. First, the study only involved 4 capuchins, which may be too small of a sample size, particularly given the potentially significant effects factors relating to social status can have on primate behavior. Second, some experimental factor could have overwhelmed capuchin inequity aversion, if such an aversion exists in a weak form. For example, capuchins could have had a preference for the trader with an overall more valuable offering because they failed to understand that they would never receive the better reward. This could explain the capuchin that preferred the unequal trader in the DIA condition and the equal trader in AIA condition, as in both of these cases the capuchin preferred the trader with the greater overall endowment.

The authors note that the capuchin that showed preferences in the social conditions was partnered with an alpha male. The authors cite a paper "Capuchin monkeys (Cebus apella) are sensitive to others' reward: an experimental analysis of food-choice for conspecifics"[33] that found some evidence suggesting that capuchins are less inclined to be prosocial towards alphas. Further, the authors note that the

[33] Takimoto, Ayaka, Hika Kuroshima, and Kazuo Fujita. "Capuchin monkeys (Cebus apella) are sensitive to others' reward: an experimental analysis of food-choice for conspecifics." *Animal cognition* 13.2 (2010): 249-261.

capuchins may have not paid sufficient attention to their partner's payoffs to form discernable preferences on the dimension of inequity.

Despite possible criticisms, this study, taken together with the one done by Katherine McAuliffe, make a strong inequity aversion in capuchins seem unlikely. However, they do not seem to conclusively rule out a weaker form of inequity aversion. It seems safe to conclude that direct, robust evidence of either AIA or DIA has been elusive. But, researchers should be careful to not draw premature conclusions

The debate is still open. Are alpha males less likely to have AIA? Are subordinates sometimes conditioned to have AIA? Far larger sample sizes would be needed to address finer points such as this one. Suppose if the tendencies of inequity aversion are affected by the dimensions of sex differences, age differences, familiarity differences, and social status differences. If this were the case, 4, 8, or even 30 test subjects might not be enough to create representative samples of primate populations.

Prosocial tendencies can be fragile in humans; they may also be fragile in primates. The environment that captive primate test subjects grow up in could inhibit their development of cooperative tendencies as compared to wild primates. Would primates show more inequity aversion in experiments that better approximate natural tasks, such as hunting or foraging? Or, as I will address later in this section, if primates show framing effects (act differently in different contexts), could experimental settings

primate primates to act more selfishly? In the next subsection, I discuss prosocial donation.

Prosocial Donation

Prosocial donation is an agent's giving to another with no expectation of a reciprocal reward. In this way, evidence of prosocial donation may be presumed to be evidence for other regard.

Prosocial donation is related to inequity aversion in a few (significant) ways. First, both tendencies would seem to depend on a sense of other regard. One can theorize that a tendency to donate is in part underlain by inequity aversion. Further studies may find that strong (advantageous) inequity aversion tendencies in individual subjects correlate with strong prosocial donation tendencies. Second, we might expect similar conditions that enhance or diminish inequity aversion (social status, gender, familiarity) to also enhance or diminish prosocial donation. Finally, there are some similarities in experimental designs. Costly donation is in its structure a Dictator Game. No cost donation is in structure a dictator game where the dictator's endowment to give is distinct from their endowment to keep.

In other ways, tendencies for inequity aversion and prosocial donation may have opposing effects. For instance, Sheskin's study discussed earlier had an element of a no cost prosocial donation condition. If capuchins chose to maximize their partner's reward given their own constant reward, they were functionally participating in

prosocial donation. While if a capuchin chose to minimize their partners reward given their own constant reward, they were functionally displaying DIA. If an agent has both DIA and a preference towards prosocial donation to a similar degree, some studies may conclude that the agent has neither, when in-fact they have both, but in a conflicting fashion.

What is the evidence for prosocial donation in humans? Several studies have indicated that people have a propensity to give to others without an apparent expectation of reciprocal reward, while others have provided evidence that humans are not inclined to prosocial donation for strangers if the anonymity of their choice is convincing[34]. Further, Nicolas Claidiere et al. note that prosocial donation is slow to emerge in children (and remains instable throughout adulthood). [35] In experimental designs involving humans, donations typically come at a cost to a giver, but some studies involving primates create situations in which a subject can give to another without affecting their own outcomes.

A 2005 study "Chimpanzees are indifferent to the welfare of unrelated group members" notes that chimpanzees are more likely than other primates to demonstrate regard for others, yet in their no-cost donation experiments, chimpanzees did not

[34] Winking, J., & Mizer, N. (2013). Natural-field dictator game shows no altruistic giving. Evolution and Human Behavior, 34(4), 288-293.
[35] Claidiere, Nicolas, et al. "Selective and contagious prosocial resource donation in capuchin monkeys, chimpanzees and humans." *Scientific reports*5 (2015): 7631.

reliably donate to unrelated conspecifics.[36] A 2008 study "Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members" obtained similar results.[37] Further, a 2011 study "Collaboration encourages equal sharing in children but not in chimpanzees" found that even after conditioning chimpanzees by having them collaborate on a task, chimpanzees were unwilling to donate to their conspecifics.[38] This is evidence that primates have no tendency to donate resources.

Yet, there is some evidence that primates are willing to assist conspecifics in instrumental tasks. A 2007 study "Spontaneous Altruism by Chimpanzees and Young Children" showed that chimpanzees were willing to help conspecifics gain access to an object necessary for acquiring food.[39] Further, a 2008 study "Capuchin monkeys are sensitive to others' welfare" obtained similar results with capuchins. Namely, subjects showed a willingness to help a conspecific complete a task.

Both of these studies involve direct interaction between subjects and conspecifics. Studies with human subjects have attempted to correct for interpersonal motivations in an effort to identify a purer form of prosocial donation. By this standard, it seems unlikely that evidence for this tendency will emerge. Thus, the remaining debate

[36] Silk, J. et al. Chimpanzees are indifferent to the welfare of unrelated group members. Nature 437, 1357–1359 (2005).
[37] Vonk, J. *et al.* Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Anim. Behav.* 75, 1757–1770, 10.1016/j.anbehav.2007.09.036 (2008).
[38] Hamann, Katharina, et al. "Collaboration encourages equal sharing in children but not in chimpanzees." *Nature* 476.7360 (2011): 328-331.
[39] Warneken, Felix, et al. "Spontaneous altruism by chimpanzees and young children." *PLoS Biol* 5.7 (2007): e184.

revolves around the extent to which primates behave prosocially in their interpersonal motivation. And, whether such prosocial behaviors can meaningfully be described as 'donations.' Perhaps given that prosocial donation in humans is an inconclusive field of study in humans, it is not surprising it is an inconclusive field of study with primates.

Endowment Effect

The endowment effect is the phenomena observed in humans whereby agents place a premium on objects that they happen to already possess. In humans, this effect can apply to major items, such as houses, or more trivial items, such as coffee mugs. There is evidence this effect applies to humans, though its strength varies across individuals and contexts.[40] Is there a consensus that this effect also applies to primates?

In a Laurie Santos paper entitled: "Innate constraints on judgment and decision-making?", she writes "...we explored whether monkeys' [capuchins] loss aversion could potentially lead them to demonstrate an endowment effect.... This is exactly what we observed: Monkey owners were extremely reluctant to trade the good they owned."[41]

[40] Kahneman, Daniel, Jack L. Knetsch, and Richard H. Thaler. "Anomalies: The endowment effect, loss aversion, and status quo bias." *The journal of economic perspectives* 5.1 (1991): 193-206.
[41] Santos, Laurie R., and Venkat Lakshminarayanan. "Innate constraints on judgment and decision-making? Insights from children and non-human primates." *The innate mind: foundations and the future (eds P. Carruthers, S. Laurence & S. Stich)* (2008): 293-310.

A 2008 paper "Endowment effect in capuchin monkeys", presented evidence for an endowment effect in capuchins[42]. The study involved 5 capuchins and 5 trading tasks. The first trading task was designed to establish a baseline for how capuchins valued two distinct food items. Participants were given 12 tokens, each of which was exchangeable for either a fruit disc or chunk of cereal. Participants traded for the two food items in nearly identical proportions, suggesting that they placed similar values on the two foods.

In experiment one, subjects were either given 12 items of fruit or 12 items of cereal and given an option to trade individual items of their endowment for the food item they were not endowed with. Participants traded less than their indicated preferences in the baseline tests would suggest. Experiment two sought to address whether capuchins are simply reluctant to trade food items. Subjects were endowed a food of low value and were allowed to trade for a food of greater value. In this condition, all participants traded significantly more than chance for the food item of greater value. Experiment three sought to establish an estimate of the transaction cost of trading. All participants were shown to be willing to trade a token for a single oat, suggesting that their transaction cost was at most one oat. Experiment four sought to provide evidence that the observed endowment effect was not in-fact simply a function of impatience. Capuchins were endowed with almonds in shells and given the

[42] Lakshminaryanan, Venkat, M. Keith Chen, and Laurie R. Santos. "Endowment effect in capuchin monkeys." *Philosophical Transactions of the Royal Society B: Biological Sciences* 363.1511 (2008): 3837-3844.

opportunity to trade to almonds outside their shells. Although a capuchin could more quickly eat an almond by trading its in-shell almond for a shelled almond, capuchins typically kept the in-shell almonds they were endowed with.

Indications of the endowment effect have also been found in orangutans[43], chimpanzees[44], and gorillas[45]. The chimpanzee study involved three distinct contexts, in which participants were endowed with either a dipstick or sponge (preferred) associated with the ability to access a either oatmeal or juice (preferred) and provided an option to trade for the other tool, which was associated with the ability to access the other food item. In the first condition, no food was present. In the second condition, both food items were visible, but unobtainable. In the third condition, both food items were accessible given the appropriate tool. The study found that participants had a stronger endowment effect in the obtainable condition. The view that primates have an endowment effect at this point seems relatively uncontroversial.

Framing Effect

The framing effect is the phenomena in which an agent's payoff preferences are affected by environmental contexts. One mechanism for this effect is priming. For example, we might predict that a person primed by an example of a person who won a

[43] Flemming, Timothy M., et al. "The endowment effect in orangutans." (2012).
[44] Brosnan, Sarah F., et al. "Evolution and the expression of biases: situational value changes the endowment effect in chimpanzees." *Evolution and Human Behavior* 33.4 (2012): 378-386.
[45] Drayton, Lindsey A., et al. "Endowment effects in gorillas (Gorilla gorilla)." *Journal of Comparative Psychology* 127.4 (2013): 365.

lot of money gambling may be willing to bet more aggressively than if they were primed by an example of a person who lost a lot of money gambling.

Studies have indicated framing effects in bonobos and chimpanzees[46], as well as capuchins[47]. In the study, "Bonobos and chimpanzees exhibit human-like framing effects.", framing effects were studied on 23 free ranging chimpanzees and 17 free ranging bonobos subjects. Experimenters offered participants a gain framing, where apes were initially presented one piece of food. If the subject picked the option, half of the time he/she would receive the piece of food presented, and half the time the he/she would receive two pieces of the presented food. The second deal experimenters offered was the loss frame, where apes were initially presented two pieces of food. If a subject picked the option, half of the time, he/she would receive both pieces of the presented food, and half the time he/she would receive only one piece of the presented food. Both the chimps and bonobos in the study showed a statistically significant preference for the gain condition, which is a result we would expect from a similar experiment with human subjects.

In a conceptually similar study "The evolution of decision-making under risk: framing effects in monkey risk preferences", five capuchins, traded tokens for two options with the same average value, but where one option was framed as having

[46] Krupenye, Christopher, Alexandra G. Rosati, and Brian Hare. "Bonobos and chimpanzees exhibit human-like framing effects." *Biology letters* 11.2 (2015): 20140527.
[47] Lakshminarayanan, Venkat R., M. Keith Chen, and Laurie R. Santos. "The evolution of decision-making under risk: framing effects in monkey risk preferences." *Journal of Experimental Social Psychology* 47.3 (2011): 689-693.

upside potential and one was framed as having downside risk.[48] The study found that capuchins preferred a risky loss to a sure loss and a safe gain to a risky gain. In other words, the capuchins were more risk averse when presented with gains than when presented with losses.

There are relatively few studies on primate framing effects. Early indications seem to suggest the effect applies to primates. There is little controversy over this topic, though perhaps if more studies are done, controversies will emerge.

Section 3
Behavioral Economic Findings with Humans

In this section, I will review some of the important findings that behavioral economics has attained with humans, but not primates. This will be relevant for section 4, where I provide an overview of the criticisms of behavioral economics and in section 5, where I make suggestions for improving our behavioral studies with primate subjects.

Behavioral economics in most, if not all, of its various subsets has reached a greater degree of both breadth and precision with humans than with primates. There are many possible explanations for this reality. For one, researchers may find it easier to design experimental methods for human participants. Taken together with the fact that

[48] Lakshminarayanan, Venkat R., M. Keith Chen, and Laurie R. Santos. "The evolution of decision-making under risk: framing effects in monkey risk preferences." *Journal of Experimental Social Psychology* 47.3 (2011): 689-693.

it is less expensive and time consuming to field studies with human participants, it might simply be a matter of practicality. Or, there might be less interest in the cognitive functions of primates. Finally, human behavior could just be more sophisticated than primate behavior, and thus researchers have more things to find by studying humans. In any of these cases, findings with humans can serve as a source of ideas to push the frontiers of primate behavioral economics.

Individual Differences

Behavioral economics has studied the effects on economic behavior for a broad range of participant characteristics. These include gender, age, cognitive ability, past experiences, and others. As an example of differences in cognitive ability, researchers have found evidence that participants with greater numeracy scores are relatively less sensitive to how a risk is framed and will tend to take relatively risk neutral decisions.[49] As an example of gender differences, it has been found in a range of studies that women are, on average, more risk averse than men.[50]

Some portions of gender differences are likely explained by differing levels of hormones (such as testosterone) that affect behavior.[51] A study, "Gender differences in

[49] Peters, Ellen, and Irwin P. Levin. "Dissecting the risky-choice framing effect: Numeracy as an individual-difference factor in weighting risky and riskless options." *Judgment and Decision Making* 3.6 (2008): 435.
[50] Byrnes, James P., David C. Miller, and William D. Schafer. "Gender differences in risk taking: A meta-analysis." (1999): 367.
[51] Stanton, Steven J., et al. "Low-and high-testosterone individuals exhibit decreased aversion to economic risk." *Psychological science* 22.4 (2011): 447-453.

financial risk aversion and career choices are affected by testosterone" used cheek swabs and found that women with relatively higher testosterone showed less risk aversion than their peers and that higher testosterone levels were associated with high risk career choices among women.[52] [53] Others have sought to build models based on behavioral concepts. For example, a paper, "The roots of entrepreneurship and labour demand: Individual ability and low risk aversion" uses the concept of individual differences in risk aversion and its interplay with real world risks and rewards in a model of the decision making of those who chose to become entrepreneurs.[54]

These observations relating to individual differences provide material for speculation. Would we expect a female with high numeracy to be less risk averse than a male with high testosterone?

Mental States and Brain Structures

Researchers have sought to identify the effects of certain mental illnesses on economic decision making with some success. As an example of such an effect, people with bipolar disorder are known to be at risk of reckless behaviors, like drug use or gambling. One study, "Altered risk-aversion and risk-seeking behavior in bipolar

[52] Sapienza, Paola, Luigi Zingales, and Dario Maestripieri. "Gender differences in financial risk aversion and career choices are affected by testosterone." *Proceedings of the National Academy of Sciences* 106.36 (2009): 15268-15273.
[53] Cramer, Jan S., et al. "Low risk aversion encourages the choice for entrepreneurship: an empirical test of a truism." *Journal of economic behavior & organization* 48.1 (2002): 29-36.
[54] Van Praag, C. Mirjam, and Jan S. Cramer. "The roots of entrepreneurship and labour demand: Individual ability and low risk aversion." *Economica*68.269 (2001): 45-62.

disorder", found confirming evidence that people with bipolar disorder are more likely to take risks and obtained results suggesting that those with bipolar disorder are less sensitive to control conditions that adjust how a risk is framed.[55] This finding may be of theoretical interest as it suggests that differing levels of risk aversion may be mediated by differing reactions to framing. If this were the case, it could beg the question of the extent risk aversion a unique trait in itself, and the extent it is a product of a more general framing effect.

Another study, "Euthymic patients with bipolar disorder show decreased reward learning in a probabilistic reward task" found that people with bipolar disorder are slower to learn the reward structures in probabilistic games.[56]

Related to the findings with bipolar disorder, researchers have studied relationships between a participant's mood at a given time and their risk taking. One study, "The influence of positive and negative mood states on risk taking, verbal fluency, and salivary cortisol" primed participants with either positive or negative (moods). The researchers theorized that participants in better moods would be less risk averse. The study did not find a significant result for this hypothesis, though it did confirm that manic depressants appear more risk seeking.[57]

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[55] Altered risk-aversion and risk-seeking behavior in bipolar disorder."
[56] Pizzagalli, Diego A., et al. "Euthymic patients with bipolar disorder show decreased reward learning in a probabilistic reward task." *Biological psychiatry* 64.2 (2008): 162-168.
[57] Clark, L., S. D. Iversen, and G. M. Goodwin. "The influence of positive and negative mood states on risk taking, verbal fluency, and salivary cortisol." *Journal of Affective Disorders* 63.1 (2001): 179-187.

Neuroscience studies, such as "Neurocognitive development of risk aversion from early childhood to adulthood", have sought to identify neural markers that can be associated with varying degrees of risk aversion[58] [59], risk assessment[60], inequity aversion[61], prosocial donation, and the endowment effect[62].

Behavioral economics in groups

Researchers have connected the phenomena of social contagion with how people frame risks,[63] and have attempted to explain financial crises by augmenting traditional economic models with behavioral variables.[64] [65]

Taken together, these experimental methods are reflective of some relative advantages in studying human behavioral economics. With human subjects, researchers are able to field participants with specific mental characteristics, such as personality traits, mental illnesses, and general intelligence measures. While, with primates, far less is known about how to measure their moods, general intelligence, and mental

[58] Paulsen, David, et al. "Neurocognitive development of risk aversion from early childhood to adulthood." *Frontiers in human neuroscience* 5 (2012): 178.
[59] Gonzalez, Cleotilde, et al. "The framing effect and risky decisions: Examining cognitive functions with fMRI." *Journal of economic psychology* 26.1 (2005): 1-20.
[60] Hsu, Ming, et al. "Neural systems responding to degrees of uncertainty in human decision-making." *Science* 310.5754 (2005): 1680-1683.
[61] Sanfey, Alan G., et al. "The neural basis of economic decision-making in the ultimatum game." *Science* 300.5626 (2003): 1755-1758.
[62] Knutson, Brian, et al. "Neural antecedents of the endowment effect." *Neuron*58.5 (2008): 814-822.
[63] Scherer, Clifford W., and Hichang Cho. "A social network contagion theory of risk perception." *Risk analysis* 23.2 (2003): 261-267.
[64] Coudert, Virginie, and Mathieu Gex. "Does risk aversion drive financial crises? Testing the predictive power of empirical indicators." *Journal of Empirical Finance* 15.2 (2008): 167-184.
[65] Barberis, Nicholas. "Psychology and the Financial Crisis of 2007-2008." (2011).

pathologies (the rare instances in which chimpanzee have killed in-group peers is as possible example of primate psychological outliers, though the phenomenon is not yet well understood.[66]) Even if we were to make progress in categorizing primates by personal characteristics, using such controls require large sample sizes that are likely out of reach. Though, one can make an argument that primate studies would benefit from perhaps even larger sample sizes than human studies: If we think we understand the confounding variables for primates less well, we might need even larger sample sizes to overcome these confounding variables. In the next section, I will review common criticisms of behavioral economics as a field of study.

Section 4
Criticisms of Behavioral Economics

Behavioral economics, on the whole has been well received as a major contribution to economics. Though, it has faced a fair bit of skepticism and critical debate. For the purposes of this paper, the lines of criticism can be broadly fit into two distinct, though not mutually exclusive, groups. One, that the methods researchers in the field have employed are flawed in important ways. And two, that the underlying concepts of behavioral economics are either unusual or inaccurate models for reality. In

[66] Watts, David P. "Intracommunity coalitionary killing of an adult male chimpanzee at Ngogo, Kibale National Park, Uganda." *International Journal of Primatology* 25.3 (2004): 507-521.

this section I will briefly overview the technical criticisms of statistical methods, representative samples, experimental soundness of behavioral economics, as well the conceptual criticisms of behavioral economics. With each topic, I will attempt to address its relevance to studies involving primates.

Technical Criticisms

The technical criticisms of behavioral economics are probably best understood as a part of a broader controversy about social sciences. Perhaps the most prominent framing of the problem is the so called 'replication crisis', which refers to the soundness of core statistical methodologies, particularly in psychology. Some argue the crisis is exaggerated,[67] but others take it very seriously.[68] I highlight two major statistical issues. Namely, researcher degrees of freedom and the file drawer.

Researcher degrees of freedom refers to the extent in which a study lacks clearly delineated independent and dependent variables and/or a predetermined plan for analyzing data. If a study has substantial researcher degrees of freedom, it presents a risk that researchers can find misleading, statistically significant results, which is typically taken to be a p-value equal to or less than .05 (the probability of observing an equal or greater effect at random is less than 5%). A problem emerges because if there

[67] Pashler, Harold, and Christine R. Harris. "Is the replicability crisis overblown? Three arguments examined." *Perspectives on Psychological Science* 7.6 (2012): 531-536.
[68]

are 10 perfectly plausible ways to statistically describe a study, the probability of finding a statistically significant result becomes much greater than 5%.

The file drawer is a separate, but related issue. It describes a phenomenon where researchers in labs across the world all run large numbers of studies, but tend to only publish when they find interesting results. This means the total number of trials it took to for an effect to appear can be, in reality, far greater than the number of reported trials for a particular study. As a result, p-values once again become a potentially misleading measure, even if the underlying study has few researcher degrees of freedom.

One partial solution to the researchers degrees of freedom problem would be to establish a norm where researchers declare how they will analyze a study before they gather results.[69] A second partial solution, which addresses both the researcher degrees of freedom and file drawer problem is replication (either pre-replication, where the same lab re-runs an experiment before publishing, or replication by separate labs altogether) which effectively reduces the researcher degrees of freedom for a given experiment's analysis. Meta-analysis of the results within and between fields is third promising solution.[70]

However, Pre-reporting norms, replication, and other ideas have limitations that are worth considering. For one, a study can become influential before its results have

[69] Schweinsberg, Martin, et al. "The pipeline project: Pre-publication independent replications of a single laboratory's research pipeline." *Journal of Experimental Social Psychology* 66 (2016): 55-67.
[70] Schooler, Jonathan W. "Metascience could rescue the'replication crisis'." *Nature* 515.7525 (2014): 9.

been replicated, and if it subsequently fails to be replicated, it can remain influential. There are a number of reasons that studies have staying power even if they fail to be replicated, for example: the failed replication studies may receive less attention, researchers may be skeptical of the quality of the replication, or researchers may sometimes assume that there is at least some truth to the original result. Second, some argue that there are strong career incentives to publish new findings, so it will always be difficult to prevent bad actors from deviating from statistical best practices.[71] Finally, others argue that replication is inherently difficult and produces misleading results of its own.[72]

The replication crisis is of central importance in primate behavioral economics. The controversy in each topic reviewed in section 2 at some level is a debate about replicability. And, however big a problem replication is generally, there is a case one can make that it is an even larger problem for primate research.

Producing replications of a primate study is more time consuming than for human studies, which one would expect to intensify the structural incentive barriers to widespread replication mentioned above. Primate studies also often involve the use of experimental habitats unique to a specific lab and interactions between researchers and subjects. Because the effects of habitats and researcher interactions are difficult to

[71] Everett, Jim AC, and Brian D. Earp. "A tragedy of the (academic) commons: interpreting the replication crisis in psychology as a social dilemma for early-career researchers." Frontiers in psychology 6 (2015).
[72] Stroebe, Wolfgang, and Fritz Strack. "The alleged crisis and the illusion of exact replication." *Perspectives on Psychological Science* 9.1 (2014): 59-71.

communicate, it would seem that doubts one has about the feasibility of exact replication in primate studies are at least as convincing as with human studies.

A second active debate in psychology relates to doubts about how well the typical set of participants in a study represent the broader population. Because studies are easiest to do on or near college campuses, a majority of samples are skewed in potentially important ways. The acronym WEIRD (which stands for 'western', 'educated', 'industrialized', 'rich', 'democratic') has become a popular label for the problem.[73] The factors it names are often relevant for behavioral economics. Priming effects (like anchoring), the endowment effect, risk aversion, inequity aversion, and prosociality all plausibly could vary meaningfully in their strength across cultural contexts. Researchers have sought cross validations by applying similar techniques in non-industrial societies[74][75], which has enriched the literature, but perhaps isn't yet enough.

Representativeness is a challenge for primate research as well: it may be the case that lab animals are not representative of their species, or that animals in one lab are not representative of animals in another lab. The ability to run a diverse set of tests on large number of primates raised under similar conditions would help to address valid

[73] Jones, Dan. "A WEIRD view of human nature skews psychologists' studies." *Science* 328.5986 (2010): 1627-1627.
[74] Henrich, Joseph, et al. "In search of homo economicus: behavioral experiments in 15 small-scale societies." *The American Economic Review*91.2 (2001): 73-78.
[75] Tracer, DavidP. "Selfishness and Fairness in Economic and Evolutionary Perspective: An Experimental Economic Study in Papua New Guinea 1." *Current Anthropology* 44.3 (2003): 432-438.

concerns that environmental factors are a poorly understood confounding variable. As it stands today, findings from labs are made more persuasive if corroborated both by other labs and by findings with wild primates. But, any given primate lab tends to have unique capabilities and populations, and the set of possible experiments with wild primates is different than what can be done with captive primates. The fact that there are differences within the set of labs for a given species, and differences between labs as a whole and the wild, taken together, makes conclusive, highly replicated findings difficult to obtain. So, while research with humans has been criticized for using samples that might be too homogenous, arguably, the primate literature would benefit precisely from a more homogeneous pool of subjects.

A third debate about the human literature relates to the underlying soundness of popular research techniques. In behavioral studies there is often a risk that results can be systematically skewed by participants whose actions are partially motivated by incentives extrinsic to the explicit test conditions or by participants whose actions are motivated by inferences they form about the concept underlying an experiment.

As an example of the latter, if a participant thinks a game was designed by a lab in the hopes of finding evidence for prosocial donation, he or she might--in an act of prosociality towards the researchers-- deliberately act prosocially. Similarly, in the case

of a study, like the one by Frans De Waal discussed in section 2[76], that finds evidence of cooperation, one might worry that the capuchins had been conditioned via implicit or explicit encouragement by their caretakers, over time, to engage in helping tasks.

There, as well, are cases where primate subjects pose just the opposite challenge that human intelligence does. Namely, it is difficult to know that extent to which primates are consciously aware of the conditions of an experiment. In the case of Sheskin's study[77] described in section 2, for example, it is possible to argue that capuchins have some inequity aversion, but their strong self-interest overwhelms their ability to learn how to attend to their weaker preference for equity.

Finally, an acute criticism with respect to behavioral economics is the narrow range of incentives that experiments can simulate. For instance, no lab can test the relationship between risk aversions in an experiment where they ask participants to put their entire net worth at risk. Nor could any lab test the extent to which life threatening circumstances effects prosociality. A similar inability to test the effects of extreme circumstances is present in the primate literature. Might primate subjects show a bit less risk aversion if they perceived some sort of imminent danger, like a predatory animal or

[76] Mendres, Kimberly A., and Frans BM de Waal. "Capuchins do cooperate: the advantage of an intuitive task." *Animal Behaviour* 60.4 (2000): 523-529.
[77] Sheskin, Mark, et al. "Capuchin monkeys (Cebus apella) fail to show inequality aversion in a no-cost situation." *Evolution and Human Behavior*35.2 (2014): 80-88.

the risk of starvation? For both humans and primates, observational studies help to bridge this gap.[78]

Conceptual Criticisms

Some argue that, regardless of whether behavioral biases are a statistically valid, replicable phenomena, their explanatory power has been overstated. One line of argument for this position is that the causes of the apparent biases we observe could be best explained with classical economics if only we better understood an agent's underlying incentives. In other words, it is practically difficult, but not theoretically impossible, to explain any apparently irrational behavior as an expression of rational self interest. As an example, suppose a study observes that owners of underwater homes are reluctant to stop making payments, even when the monetary logic for doing seems overwhelming.[79] It is tempting to conclude that these owners are making irrational choices because of the endowment effect or status quo bias. But, it could just as well be, that as outside observers, we fail recognize what turns out to be an entirely rational logic. The homeowners could be responding to an incentive to avoid the significant social cost of defaulting on their mortgages, have a good reason to protect their credit rating, or any number of other difficult to perceive motivations. It could also

[78] Stone, Anita I. "Ecological risk aversion and foraging behaviors of juvenile squirrel monkeys (Saimiri sciureus)." *Ethology* 113.8 (2007): 782-792.
[79] Wilkinson-Ryan, Tess. "Breaching the mortgage contract: the behavioral economics of strategic default." *Vand. L. Rev.* 64 (2011): 1545.

be that the homeowners simply do not know that they are foregoing a more optimal decision.

It is possible to tell similar stories with primates to explain away what appear to be biases. For instance, any study that claims to find evidence for primate inequity aversion has to address whether the effect is only present because there is no condition of anonymity. Further, studies of the endowment effect have to provide compelling evidence that reluctance to trade is not only an expression of impatience or distrust.[80]

A second line of criticism takes a more practical form, arguing that in the long term or in aggregates, the behavioral biases of individuals are likely to cancel each other out, get competed away, or otherwise become trivial as compared to more fundamental incentive effects. Primates may be able to provide useful evidence for this line of debate. Why do chimpanzees appear to be risk averse, or why do capuchins appear to have an endowment effect? Are these anomalous behaviors that emerge under highly specific contexts? Or, does it seem like behaviors that are in some way essential to their species? If the latter seems to be the case, why?

Section 5
Future Directions for Primate Behavioral Economics

[80] Lakshminaryanan, Venkat, M. Keith Chen, and Laurie R. Santos. "Endowment effect in capuchin monkeys." *Philosophical Transactions of the Royal Society B: Biological Sciences* 363.1511 (2008): 3837-3844.

There are many directions researchers in the field of primate behavioral economics can take in the coming years. I think three in particular would be most beneficial, based on my experience writing this paper. First, I think researchers might standardize more of their techniques, so that replication becomes easier. Second, researchers might focus less on experiments that relate to other-regard and focus more on strengthening the evidence for general biases, like the endowment effect and risk aversion. Finally, researchers might find more evidence for how individual differences affect primate behavioral biases. If the field had better established expectations for the extent to which, for example, gender and status of subjects changes results, I think its conclusions could be more convincing and useful for researchers in related fields as well as for the outside world.