Georgia State University
Digital Archive @ GSU

Psychology Honors Theses | Department of Psychology

5-6-2012

Affective Responses to Inequity in Capuchin Monkeys

Danny Fernandez
dfernandez2@student.gsu.edu

Follow this and additional works at: http://digitalarchive.gsu.edu/psych_hontheses

Recommended Citation
Fernandez, Danny, "Affective Responses to Inequity in Capuchin Monkeys" (2012). *Psychology Honors Theses.* Paper 12.

This Thesis is brought to you for free and open access by the Department of Psychology at Digital Archive @ GSU. It has been accepted for inclusion in Psychology Honors Theses by an authorized administrator of Digital Archive @ GSU. For more information, please contact digitalarchive@gsu.edu.

Affective Responses to Inequity in Capuchin Monkeys

By

Danny Fernandez

Under the Direction of Dr. Sarah F. Brosnan

ABSTRACT

Many studies have documented adverse affects to inequitable situations in non-human primates. The behaviors that have predominantly been examined include food taking, collecting, giving, and refusals between the primate subjects and the experimenters. However, no studies had looked at the affective responses to inequity in primates. In a recent study, four-year old children who were rewarded inequitably accepted the reward, however they showed affective signs of dissatisfaction. For this study, we looked for affective displays in capuchins during inequitable exchange tasks. We predicted that the capuchins that were experiencing inequity would show more signs of agitation and aggression than those in equitable situations. We saw no increase in agitation or aggression when subjects were treated inequitably. There was higher aggression towards partners who received the lower reward in inequitable situations and less agitation seen by partners during frustration controls. Future studies may find our hypothesized results using different methodologies.

INDEX WORDS: Primate, Inequity, Affective Responses, Affective behaviors, Capuchin monkeys

Affective Responses to Inequity in Capuchin Monkeys

By

Danny Fernandez

An Honors Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of

Bachelors of Science

in the College of Arts and Sciences

Georgia State University

2011

Copyright by
Danny Fernandez
201

DEDICATION

I would like to dedicate this work to my family for supporting me in all that I attempt. Without their constant help I wouldn't be where I am today nor would I be who I am today.

ACKNOWLEDGEMENTS

I would like to acknowledge Dr. Sarah Brosnan who allowed me to work in her lab for over two years. She helped me better understand all aspects of the field of research in psychology as well as helping prepare me for all the rigors that graduate school will provide. I would also like to thank the McNair Post-Baccalaureate Program for giving me the opportunity to begin my research career and always helping me with any endeavor and request.

TABLE OF CONTENTS

DEDICATION iv

ACKNOWLEDGEMENTS v

LIST OF TABLES viii

LIST OF FIGURES

1 Introduction 1

2 Experiment 9

2.1 Participants 9

2.2 Apparatus 9

2.3 Experimental Procedure 10

2.4 Coding Procedure 10

2.5 Statistics 11

3 Results 12

4 Discussion 12

REFERENCES 16

APPENDICES 24

LIST OF TABLES

Table 2 Ethogram (details of behaviors for video coding) 20

LIST OF FIGURES

Figure 1: Mean ± SEM total aggressive behaviors for subjects by condition 21

Figure 2: Mean ± SEM total aggressive behaviors for partners by condition 22

Figure 3: Mean ± SEM total agitated behaviors for subjects by condition 23

Figure 4: Mean ± SEM total agitation behaviors for partners by condition 24

1 INRODUCTION

Inequity occurs when one individual's outcomes differ from those of another, which may include different rewards or different procedures required to get those rewards (Fehr & Fischbacher, 2003; Fehr & Schmidt, 1999). Many studies have been done on the effects of inequity in both humans and primates (Brosnan & de Waal, 2003; Henrich, 2009). However, few have gone past easily and more objectively quantifiable data, such as refusals to exchange or refusals to accept rewards. These quantifiable responses included an unwillingness to participate in the task and a refusal to accept the proffered reward. No studies had been done on emotional displays, or affective responses to inequity in primates. In this study we investigated affective responses to inequity in capuchin monkeys.

In order to better understand inequity one must first understand equity and fairness. Equity is considered to consist of two parts: the reaction to one's outcome to effort and a comparison to some one else's outcome for the same amount of effort (Fehr & Fischbacher, 2003; Fehr & Schmidt, 1999). People respond poorly when they feel that they are being treated unfairly in Ultimatum games. Ultimatum games are structured decision experiments in which a "proposer" has a set amount of money and must decide how to divide the money between themselves and a "responder," who can decide to accept the proposer's offer or reject the offer. Rejection comes at a cost to both participants since neither will then receive a reward (Fehr & Schmidt, 1999; Henrich, 2009). This response is believed to come from feelings of fairness in the face of an unreasonable offer, since most offers lower than thirty percent of the total are rejected. The feeling of inequity in these studies is so great that even when dealing with actual (e.g., not hypothetical) rewards, participants choose to react to non-zero offers in this way, which is contrary to rational economic theory (Fehr & Fischbacher, 2003; Fehr & Schmidt, 1999). These

reactions to “unfair” offers are seen across cultures (Henrich, 2009). Even when rejections of an offer will not affect the amount of money a proposer gets, people still rejected unfair offers (Yamagishi et al., 2009).

These responses presumably occur because of an emotional feeling of being slighted in a way that goes against our ideals of morality. Moral emotions are the link between moral standards and behaviors that rectify the injustice and maintain order on society. These responses are done to others and for the benefit of others (Haidt, 2003; Tangney, Stuewig, & Mashek, 2007). These responses do not even need to be consciously motivated to help as decision heuristics (Brosnan, 2006, 2011; Haidt, 2003). They serve as proximate mechanisms that maintain ultimate goals of fairness or cooperation (Fehr & Schmidt, 1999). This idea of responses to morality as instinctual proximate mechanisms was actually noted by Adam Smith hundreds of years ago as an adaptation for survival (see discussions in; (Wight, 2009; Brosnan, 2011). Helping in cooperative ways can actually promote others to be more generous towards you based on reputation as a good cooperator (Milinski, Semmann, & Krambeck, 2002; Nowak & Sigmund, 2005). Failing to cooperate comes at great cost because it motivates punishment towards people who are not cooperating (Fehr & Gächter, 2002; Fehr & Schmidt, 1999).

It has been proposed that these systems of feelings evolved from systems of cooperation typically seen animals (Brosnan, 2011; Flack & de Waal, 2000). Non-human primates show many complex cooperative behaviors, such as reciprocity, food sharing, reconciliation, consolation, conflict intervention, which may be rooted to deeper behaviors such as empathy and sympathy (Flack & de Waal, 2000). Several steps for the evolution of responses to inequity have been proposed. First, individuals must notice the difference between rewards or outcomes. Second, individuals must respond negatively to unequal outcomes between themselves and

others. Third, individuals may inflict a punishment to another conspecific where a cost is placed on the self for better cooperation from others in the long run (Brosnan & de Waal, 2006; Brosnan, 2011).

Equity and cooperation in tasks are seen in large, naturalistic social groups in non-human primates (Flack & de Waal, 2000). The chimpanzees that live in the Arnhem zoo will work cooperatively in order to reach leaves in large trees. The trees are surrounded by electric wires that prevent a single ape from getting to the leaves on the top of the trees. One chimpanzee will hold a branch up against the tree in order for their partner to get to the top and grab a branch full of leaves. When the chimpanzee lowers itself both of the chimpanzees will get a large portion of the leaves for themselves while giving a much smaller quantity to the rest of the group (de Waal, 1998). In cooperative situations there is an expectation of equitable food distribution where those that did the most work will get larger portions of food that represent their effort.

These ideas of fairness can be seen in the laboratory as well. In studies involving cooperation, the best results are seen when both monkeys shared rewards. In one study, capuchin monkeys needed to complete a bar pull task in order to get a reward. Both subjects were tested, in pairs, in a partitioned cage such that each conspecific only had access to one reward. There were three conditions in the experiment: solo, where only one subject was necessary to successfully pull the bar pull for their reward; mutual, where both subjects needed to pull for both to acquire rewards; and cooperative, where both needed to pull in order for one subject to receive a reward. The subjects were significantly more successful in the solo and mutual conditions when compared to the cooperative condition. However partners that allowed passive sharing after successfully pulling in the bar pull in the cooperative condition were significantly more to succeed at completing this task (de Waal & Berger, 2000). Those pairs that were more

equitable had the most success. These results were also seen in other cooperation tasks where rewards cannot be monopolized by one conspecific (de Waal & Davis, 2003) and higher valued rewards were alternated between subjects. (Brosnan, Freeman, & De Waal, 2006). If food was dominated by anyone individual within the first few trials, than cooperation broke down (de Waal & Davis, 2003).

These responses to inequity are not seen in less costly tasks. One variation of the ultimatum game was done on chimpanzee pairs. The proposer could choose and pull one of two trays that displayed different distributions of food. The responder could either accept the decision by pulling on a rope that would bring the trays forward to both chimpanzees, or refuse to pull, so that neither conspecific would get a reward. There were no significant variations between refusals regardless of whether the option selected by the proposer was the more or the less equitable (Jensen, Call, & Tomasello, 2007). I believe that these results are different from the cooperation studies because this study did not have a task where both subjects needed to cooperate. Of course being equitable on the basis of equitably sharing a reward following cooperation is necessary but not sufficient to show that primates are actually sensitive to equity (rather than just not liking getting less).

Another aspect of inequity that is frequently studied is when getting more than a partner causes a reaction in a subject (Horner, Carter, Suchak, & de Waal, 2011; Silk et al., 2005; Takimoto, Kuroshima, & Fujita, 2010). Advantageous inequity is when a subject receives a reward that is higher than that of its partner and responds, thus establishing a more equitable result (Fehr & Schmidt, 1999). Often what is really measured is willingness to feed another partner, not how one responds when they get more (Horner, et al., 2011; Silk, et al., 2005; Takimoto, et al., 2010). This prosocial behavior does occur. When chimpanzees were given the

option between choosing between two tokens from a bucket, one of which rewarded only them and the other of which rewarded both the subject and partner, chimpanzees selected the prosocial option statistically more in the presence of a partner (Horner, et al., 2011). However these results do not occur in all such tests with chimpanzees (e.g., Silk et al, 2005; for a more thorough discussion of advantageous inequity aversion, see de Waal & Suchak, 2010 or Jaeggi, Burkart, & Van Schaik, 2010).

In humans, typically responses to disadvantageous inequity are stronger than those to advantageous inequity, and non-human primates are no different (Brosnan & de Waal, 2003; Fehr & Fischbacher, 2003; Loewenstein, Thompson, & Bazerman, 1989; Silk, et al., 2005). One of the first studies to explicitly test for reactions to inequity in primates was in capuchin monkeys. In this study, experimenters compared subjects' reactions when they had to do a task, exchanging a token with a human experimenter, but sometimes received a less preferred reward than a social partner for doing so. Responses to inequity included not returning the token and failure to eat the reward. The refusal rates were higher in the inequity condition than in the control conditions in which rewards were equal between the primates (Brosnan & de Waal, 2003). Similar results were found in chimpanzees, who rejected the token and rejected the reward more during the inequity condition than during the equity condition (Brosnan, 2005). Since then, similar results have been found in other studies with capuchins and chimpanzees, as well as in domestic dogs (Range, Horn, Viranyi, & Huber, 2009; van Wolkenten, Brosnan, & de Waal, 2007).

However, there are other possible explanations for these outcomes. For instance, it may be that scramble competition explains their behavior, as the mere presence of the food and a partner will influence a subject's behavior. In one study, subjects received different rewards, but

no task was involved. The capuchins collected food faster when their partners did not have access to food, indicating that when no task is present the monkeys are more influenced by social facilitation than inequity (Dindo & De Waal, 2007). However, in a study explicitly comparing responses to unequal food distributions when they were or were not required to complete a task to get the rewards, it was clear that a task affected behavior. Chimpanzees did not respond to unequal outcomes when they were handed to them by experimenters, but frequently rejected their less good reward when they had to exchange to receive it (Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010). Thus, this response may be specific to situations in which individuals worked for their rewards.

It is also possible that instead of responding to inequity that the change in reward, from high to low, between sessions frustrates the subjects because they expect a higher reward (Amsel, 1992; Roma, Silberberg, Ruggiero, & Suomi, 2006; Wynne, 2004). In one study, the capuchins rejection rates were higher for the subjects that had received grapes in the previous conditions than those that had received cucumber for the duration of the experiment (Roma, et al., 2006). However, this study did not have a task, as in the original Brosnan study. Moreover, there was also never a condition in the experiment where the subject that had received grapes was also put in the same inequitable situation, in which the same subject only ate cucumbers while their partner ate grapes. Thus it was impossible to explicitly compare inequity and frustration. Brosnan and de Waal reanalyzed their data to see if the frustration effect had any influence on the rejection rates by comparing reactions to lower-value rewards depending upon what reward they had received in the previous conditions. These results actually gave more support to the reaction being caused by inequity (Brosnan & de Waal, 2006). These results are also corroborated by another study done on capuchins (van Wolkenten, et al., 2007). Finally, in

one study, no responses to the frustration affect were seen in a group of capuchins (Silberberg, Crescimbene, Addessi, Anderson, & Visalberghi, 2009). Thus while frustration is clearly also a factor, it does not seem that the "inequity response" is merely due to frustration.

The reaction to inequity may be affected by the difficulty of the task involved to get the reward. In an experiment conducted on capuchin monkeys, a basic exchange task was used to see the effects of inequity when the tasks involved different levels of effort. The procedures were similar to other inequity experiments except that in some trials, a subject received a reward for free and in others, the subject needed to exchange three times for the same reward. There were more refusals in the inequitable conditions. There was a main effect of effort, which was seen the most when a subject needed to exert more effort for a lower valued reward (van Wolkenten, et al., 2007), however there did not appear to be a separate effect of inequitable effort on responses. A similar study was done on chimpanzees that also had different levels of effort. The conditions were similar to the previous study. There was significant variation in refusals of rewards and tokens across all conditions, but there was no effect of unequal effort. Again, subjects were more likely to refuse in the inequity condition than in the gift condition, in which they got the rewards for free (Brosnan, et al., 2010). There has been one study were inequity did not decrease capuchins willingness to participate in exchange, but this study involved only unequal effort, and not unequal rewards, indicating that, again, unequal effort exacerbates existing inequity responses but does not lead to them (Fontenot, Watson, Roberts, & Miller, 2007). In studies without tasks, for both subject and partner, the effects of inequity were not seen suggesting that the task may be necessary to experience inequity.

In humans, children affective responses can show more evidence of responses to inequity than explicit measures. Most studies of inequity do not test children below the age of five

because in many previous experiments these young children hardly vocalized during the experiment, and never refused. A recent study investigated whether four-year old children experiencing inequity would show affective responses. The experimenters had kids play with blocks and then help them pick up the blocks for a sticker reward. One of the two children would always receive more stickers than their partner. The children were then asked questions involving their rewards and their distribution. The children were also coded based on affective responses, primarily their facial expressions. Based on these affective responses, the advantaged children were happy or neutral about the distribution as opposed to the disadvantaged children, who were quite unhappy with the distribution. As expected based on previous results, the older children were more likely to compare their piles and vocalize irritation over the distribution of the stickers, while the children that were four years old did not verbalize their agitation over the inequity. However, by looking at their subjective behaviors one could tell that the children were unhappier even though there were few vocalized objections (LoBue, Nishida, Chiong, DeLoache, & Haidt, 2011). We applied this method of behavioral observation to responses to inequity to capuchin monkeys.

So far there has been one other study that looked at affective responses to inequity in non-human primates, except in this study there was no task involved during that portion of their study (Fontenot, et al., 2007). As mentioned above, a task is necessary to see responses to inequity (Brosnan & de Waal, 2003; Roma, et al., 2006). We studied affective responses to inequity with a task, thus improving upon their methods since a task may be necessary to experience inequity. We decided to replicate this study using non-human primates, because these primates, too, may experience more agitation over the distributions than they indicate through their explicit refusals. Observational methods can be applied to primate behaviors in task

experiments since there could be more subtle affective responses that are not being taken into account in inequitable experiments conducted to date.

Thus, we studied the affective responses to inequity in capuchin monkeys. These monkeys are known to refuse rewards in inequitable situations (see above), however they are also prone what appear to be emotional outbursts when they are the subjects in inequity studies. We used four pairs of capuchin monkeys and ran a typical inequity experiment. We coded the interactions between them using an ethogram, or template for behaviors, we had developed. We hypothesized that we would see affective differences in the primates across the different conditions. We specifically predicted that there would be more signs of irritation when primates were experiencing inequity, measured through signs of aggression and agitation, than in equitable situations when they are still receiving a lower valued reward, but their partner is as well.

2 EXPERIMENT

2.1Participants

The participants in this study were eight male and female brown capuchin monkeys that were housed in two separate groups at the Language Research Center at Georgia State University. The capuchins were housed in an outdoor/indoor facility with places for climbing and movement as well as extensive enrichment. Water and food were provided *ad libitum*. The feeding schedule was followed regardless of the monkeys' participation in the testing.

2.2 Apparatus

Testing was conducted in the monkeys' home enclosure, but in a separate testing chamber to reduce distractions from the group. They voluntarily entered a transfer cage from their main cage, at which point they were transferred to a testing chamber. The chamber was separated in

the middle, forming two compartments with a Plexiglas partition that allowed both monkeys to see, hear, and touch one another, but prevented them from stealing each others' rewards.

The rewards used in the study were a piece of grape (high value reward), a piece of cucumber (medium value reward), and a piece of green pepper (low value reward). The items used as the rewards were not changed throughout the course of the study. We used small granite rocks as the tokens in the exchange tests.

All tests were recorded with a Canon digital video camera. The trials were viewed using a Toshiba digital video player and recorder which allowed us to stop and start, rewind, and view at a slower speed as necessary to acquire the information. These were used adjacent to computers running Excel, so that data could be entered directly in to the spreadsheet program. This was more efficient and also restricted the possibility for data loss.

2.3 Experimental Procedure

For the experiment, the monkeys participated in exchange tasks in order to receive a reward. Rewards were displayed in bowls present and visible to both subjects during all testing. For the task, the monkey had to take a token from the experimenter's hand and then return it. There were three different conditions for this experiment: inequity baseline, in which the partner exchanged for a high value reward then the subject exchanged for a medium value reward; equity baseline, in which both exchanged for the medium value reward; and high value reward baseline, in which both were shown the high value reward and then received the medium value reward after a completed exchange. Subjects completed three sessions of each condition. Each session consisted of forty trials in which the subject and the partner alternated exchanging after every trail.

2.4 Coding Procedure

All sessions were coded for both state and point behaviors (refer to table 2.l, for a more in depth look at the coding procedure see the Appendix). State behaviors were coded during each exchange, and began the moment the subject grabbed the token until they received a reward, if they successfully exchanged, and for a second period during the five seconds following the exchange. The state behaviors coded included whether the capuchin appeared calm or agitated. Being calm was classified as being still, moving slowly, softly cooing, or grooming oneself or the partner. Being agitated was classified as pouncing, vocalizing while barring teeth (except for coos), self-scratching, fear grimacing (both lips pulled back showing teeth), and banging or throwing the token.

Point behaviors were coded every time they occurred from the exchange of the token until the start of the next trial, which was the next token exchange. These behaviors were aggression and food related behaviors, which consisted of reaching and food acquisition. Aggressive behaviors were classified as swiping, attempting to bite, and screaming. These behaviors were also coded for who they were directed at, either the partner or the experimenter. Reaching was characterized for each individual reaching through the cage until at least the elbow was on the other side of the cage. Only each individual reach was counted, meaning the arm had to be pulled all the way back to the inside of the cage for the behavior to count again. These behaviors were also recorded for who they are directed at, either the partner or the experimenter. Reaching for the experimenter was not counted when they were holding a token. Reaching for the partner was not counted unless they had food. Acquisition was any acquisition of food from the partner.

2.5 Statistics

The analysis was done using a Friedman's one-way analysis of variance. This statistic was chosen because we were looking at the variance of the behaviors between multiple conditions. The non-parametric test was chosen as we had a small sample size, making it more likely that the central tendency changed by outliers (non-parametric tests compare medians instead of means). An alpha of .05 was considered significant. All statistics were two-tailed.

3 RESULTS

Subjects showed no change in their state behavior across conditions. Subjects showed no differences in aggression (Figure 1; $x^2(2,8)= 1.75$, $p>.4169$; or agitation (Figure 3; $x^2(2,8)=2.25$, $p>.3247$). Partners, on the other hand, did show some changes. Partners were less aggressive during the HVR condition than during the other conditions (Figure 2; $x^2(2,8)= 6.44$, $p<.04$). And more agitated during token exchanges in the inequitable condition (Figure 4;$x^2(2,8)= 8.03$, $p<.018$). The remaining point behaviors have been coded but not organized for analysis so their data was excluded from this text. They will be prepared and analyzed in the near future.

4 DISCUSSION

Our hypothesis was not supported by the results. Subjects did not display more aggression or agitation during trials in which they were receiving inequitable outcomes. This is surprising because anecdotally it was believed that they were prone to increased agitation when receiving inequitable rewards. However, it should be noted that in studies of disadvantageous inequity, the responses being measured is a lack of interaction with the experimenters in the form of refusing to exchange or accept a reward (Roma, et al., 2006). It is possible that the lack of responses could be a form of reaction to the inequity that follows from not wanting to engage with the experiment. It's also possible that the reaction is purely overt, and therefore there isn't a need for an affective response. This could be tested by looking at a species for which there are no

overt response, such as orangutans (Brosnan, Flemming, Talbot, Mayo, & Stoinski, 2011) or squirrel monkeys (Talbot, Freeman, Williams, & Brosnan, 2011).

Despite the fact that our predictions were not met we found another unanticipated reaction. The most interesting finding in this experiment was that subjects were more likely to be agitated when receiving the higher value reward in the inequitable condition during the exchange. One possibility for this is that the rewards, while obviously inequitable in terms of value were also unequal in terms of size. The piece of grape being given to the partner was much smaller than the piece cucumber. When the subject finished its grape instantaneously its partner would still have been eating its reward making it appear to always have a reward across the testing session. Another possibility is that they were concerned about their partner's reaction to their better reward, and so they were agitated. That is, if they thought that their partner would try to take their food, they may have become more agitated.

Another interesting finding was that aggression was significantly lowered during the HVR condition for partners. This is strange because other than the starting order of receiving rewards, there were no differences in procedure or outcome between the subjects. Thus in our study, we found that the frustration of getting less than one was initially shown actually reduced aggression, even though it has been shown to increase rates of rejection in studies of frustration. This actually makes sense if subjects were responding either by refusing or by affective responses. That is, subjects were not showing affective responses, possibly because they were communicating their feelings through refusals. Subjects may have show less aggression in the frustration condition because of increased refusal rates.

Despite the results, there are other ways to measure these behaviors and it is possible that other studies would find different results. First, we are in the process of analyzing the point

behaviors, to see if we get variation in these behaviors that were not seen in the state behaviors. Additionally, currently studies of affective responses to inequity are being replicated in other species, namely orangutans and chimpanzees, to see if these responses will be seen in other species. In particular, orangutans show no overt responses to inequity, so if there is a tradeoff between overt and affective responses, it is possible that we will see more variation in reactions in this species. Additionally, this was the first such study attempted in any non-human species, and as such was a learning experience. We spent six months designing the initial ethogram, but after additional efforts in other species have slightly adapted the capuchin ethogram. Other students are assisting with data coding to see if this modified procedure produces different results.

From this study I have found that the work of a graduate student is more rigorous than I had originally assumed. After two years working on the same experiment I learned that science is never a straight line from idea to its results. The best you can ever do is to adapt to each situation as it comes. If I could go back and start this study again the one thing I would change would be time management. I'm sure that if I had been better organized I would have completed all of the behavioral coding by at least three to five months. You can't wait until you have more time to complete work, but instead you have to make it. The only thing that I would have done to improve this study is to have had two people code one session every two to three weeks to ensure that the inter-rater reliability would be high throughout the study.

Overt responses are a great way to study inequity. There is very little dispute as to how these behaviors are coded. These methods led to one the most important findings there is regarding inequity in capuchins and chimpanzees (Brosnan & de Waal, 2003; van Wolkenten, et al., 2007). However without the ability to linguistically vocalize their aversion to inequity, we

may not be seeing all responses to inequity (LoBue, et al., 2011). In this study we attempted to bridge the gap between what is overtly seen and what we affectively expected. Although we found little evidence in this particular context, future work will help to uncover whether other such situations exist, based on the pioneering work of this honors thesis.

References

Amsel, A. (1992). Frustration theory: Many years later. *Psychological Bulletin, 112*(3), 396-399.

Brosnan, S., & de Waal, F. B. M. (2003). Monkeys reject unequal pay. *Nature, 425*(6955), 297-299.

Brosnan, S., & de Waal, F. B. M. (2006). Partial support from a non-replication: comment on Roma, Silberberg, Ruggiero, and Suomi (2006). *Journal of comparative psychology, 120*(1), 74-75.

Brosnan, S. F. (2006). At a Crossroads of Disciplines. *Social Justice Research, 19*(2), 218-227.

Brosnan, S. F. (2011). An evolutionary perspective on morality. *Journal of Economic Behavior & Organization, 77*(1), 23-30.

Brosnan, S. F., Freeman, C., & De Waal, F. B. M. (2006). Partner's Behavior, Not Reward Distribution, Determines Success in an Unequal Cooperative Task in Capuchin Monkeys. *American Journal of Primatology, 68*(7), 713-724.

Brosnan, S. F., Flemming, T., Talbot, C. F., Mayo, L., & Stoinski, T. (2011). Orangutans (Pongo pygmaeus) do not form expectations based on their partner's outcomes. *Folia Primatologica, 82*(1), 56-70.

Brosnan, S. F., Talbot, C., Ahlgren, M., Lambeth, S. P., & Schapiro, S. J. (2010). Mechanisms underlying responses to inequitable outcomes in chimpanzees, Pan troglodytes. *Animal Behaviour, 79*(6), 1229-1237.

de Waal, F. (1998). *Chimpanzee politics: Power and sex among apes (rev. ed.)*. Baltimore, MD US: Johns Hopkins University Press.

de Waal, F. B. M., & Berger, M. L. (2000). Payment for labour in monkeys. *Nature, 404*(6778).

de Waal, F. B. M., & Davis, J. M. (2003). Capuchin cognitive ecology: Cooperation based on projected returns. *Neuropsychologia, 41*(2), 221-228.

de Waal, F. B. M., & Suchak, M. (2010). Prosocial primates: selfish and unselfish motivations. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1553), 2711-2722.

Dindo, M., & De Waal, F. B. M. (2007). Partner effects on food consumption in brown capuchin monkeys. *American Journal of Primatology, 69*(4), 448-456.

Fehr, E., & Fischbacher, U. (2003). The nature of human altruism. *Nature, 425*(6960), 785-791.

Fehr, E., & Gächter, S. (2002). Altruistic punishment in humans. *Nature, 415*(6868), 137-140.

Fehr, E., & Schmidt, K. M. (1999). A theory of fairness, competition, and cooperation. *The Quarterly Journal of Economics, 114*(3), 817.

Flack, J. C., & de Waal, F. B. M. (2000). `Any animal whatever. Darwinian building blocks of morality in monkeys and apes. *Journal of Consciousness Studies, 7*(1-2), 1-29.

Fontenot, M. B., Watson, S. L., Roberts, K. A., & Miller, R. W. (2007). Effects of food preferences on token exchange and behavioural responses to inequality in tufted capuchin monkeys, Cebus apella. *Animal Behaviour, 74*(3), 487-496.

Haidt, J. (2003). The moral emotions. *Handbook of affective sciences*, 852-870.

Henrich, J. (2009). In Search of Homo Economicus: Behavioral Experiments in 15 Small-Scale Societies. In G. M. Hodgson (Ed.), *Darwinism and Economics* (pp. 110-115): Elgar Reference Collection. International Library of Critical Writings in Economics, vol. 233. Cheltenham, U.K. and Northampton, Mass.: Elgar.

Horner, V., Carter, J. D., Suchak, M., & de Waal, F. B. M. (2011). Spontaneous prosocial choice by chimpanzees. *PNAS Proceedings of the National Academy of Sciences of the United States of America, 108*(33), 13847-13851.

Jaeggi, A. V., Burkart, J. M., & Van Schaik, C. P. (2010). On the psychology of cooperation in humans and other primates: combining the natural history and experimental evidence of

prosociality. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1553), 2723-2735.

Jensen, K., Call, J., & Tomasello, M. (2007). Chimpanzees are rational maximizers in an ultimatum game. *Science, 318*(5847), 107-109.

LoBue, V., Nishida, T., Chiong, C., DeLoache, J. S., & Haidt, J. (2011). When getting something good is bad: Even three,Äêyear,Äêolds react to inequality. *Social Development, 20*(1), 154-170.

Loewenstein, G. F., Thompson, L., & Bazerman, M. H. (1989). Social utility and decision making in interpersonal contexts. *Journal of Personality and Social Psychology, 57*(3), 426-441.

Milinski, M., Semmann, D., & Krambeck, H.-J. (2002). Reputation helps solve the 'tragedy of the commons'. *Nature, 415*(6870), 424-426.

Nowak, M. A., & Sigmund, K. (2005). Evolution of indirect reciprocity. *Nature, 437*(7063), 1291-1298.

Range, F., Horn, L., Viranyi, Z. f., & Huber, L. (2009). The absence of reward induces inequity aversion in dogs. *PNAS Proceedings of the National Academy of Sciences of the United States of America, 106*(1), 340-345.

Roma, P. G., Silberberg, A., Ruggiero, A. M., & Suomi, S. J. (2006). Capuchin monkeys, inequity aversion, and the frustration effect. *Journal of comparative psychology, 120*(1), 67-73.

Silberberg, A., Crescimbene, L., Addessi, E., Anderson, J. R., & Visalberghi, E. (2009). Does inequity aversion depend on a frustration effect? A test with capuchin monkeys (Cebus apella). *Animal Cognition, 12*(3), 505-509.

Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., et al. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. *Nature, 437*(7063), 1357-1359.

Takimoto, A., Kuroshima, H., & Fujita, K. (2010). Capuchin monkeys (Cebus apella) are sensitive to others‚Äô reward: An experimental analysis of food-choice for conspecifics. *Animal Cognition, 13*(2), 249-261.

Talbot, C. F., Freeman, H. D., Williams, L. E., & Brosnan, S. F. (2011). Squirrel monkeys' response to inequitable outcomes indicates a behavioural convergence within the primates. *Biology Letters, 7*(5), 680-682.

Tangney, J. P., Stuewig, J., & Mashek, D. J. (2007). Moral Emotions and Moral Behavior. *Annual Review of Psychology, 58*, 345-372.

van Wolkenten, M., Brosnan, S. F., & de Waal, F. B. M. (2007). Inequity responses of monkeys modified by effort. *PNAS Proceedings of the National Academy of Sciences of the United States of America, 104*(47), 18854-18859.

Wight, J. B. (2009). Adam smith on instincts, affection, and informal learning: Proximate mechanisms in multilevel selection. *Review of Social Economy, 67*(1), 95-113.

Wynne, C. D. L. (2004). Animal behaviour: fair refusal by capuchin monkeys. *Nature, 428*(6979), 140.

Yamagishi, T., Horita, Y., Takagishi, H., Shinada, M., Tanida, S., & Cook, K. S. (2009). The private rejection of unfair offers and emotional commitment. *PNAS Proceedings of the National Academy of Sciences of the United States of America, 106*(28), 11520-11523.

Table 1 Ethogram (details of behaviors for video coding)

Classification of Behavior	Descriptions of Behaviors
State Behavior: Calm	Not moving Languidly moving Soft cooing Calm grooming
State Behavior: Agitated	Self scratching Agitated pouncing Vocalizing (except for cooing) Banging or throwing token Fear grimace
Point Behavior: Reaching	Sticking hand through the mesh
Point Behavior: Acquisition	Taking food from partners cage

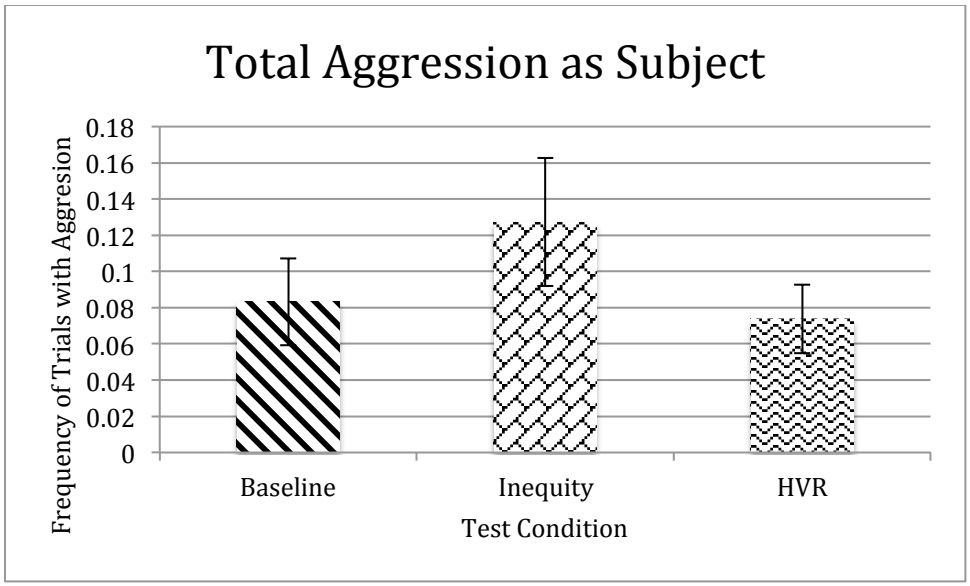

Figure 1: Mean ± SEM total aggressive behaviors for subjects by condition. No significant differences were seen.

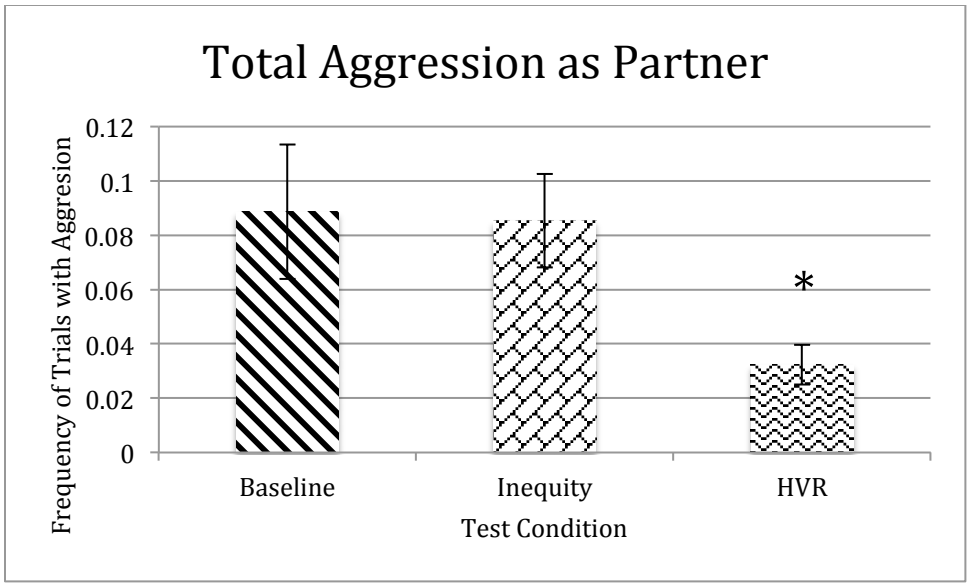

Figure 2: Mean ± SEM total aggressive behaviors for partners by condition. The asterisk indicates that partners' aggression was significantly reduced in the HVR condition as compared to the other two.

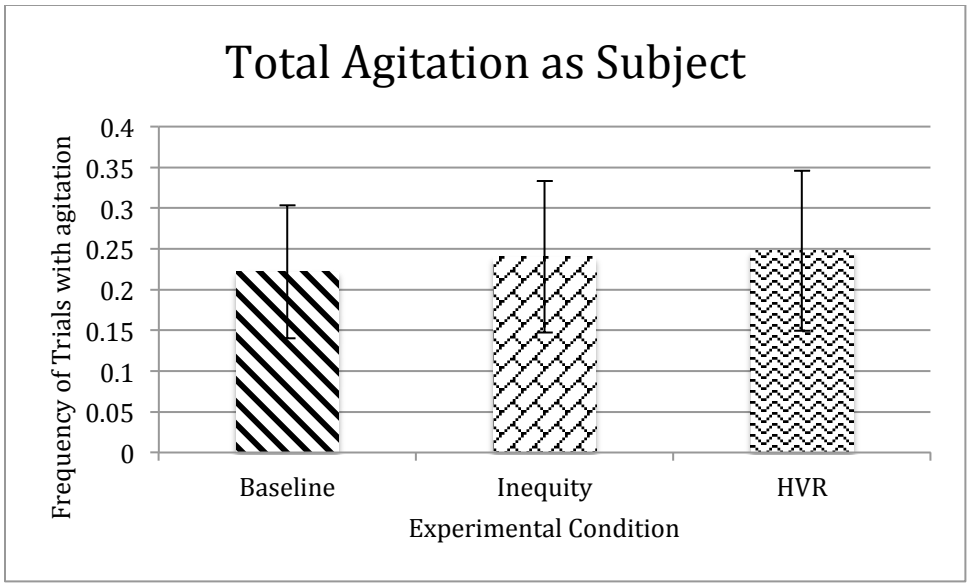

Figure 3: Mean ± SEM total agitated behaviors for subjects by condition. No significant differences were seen.

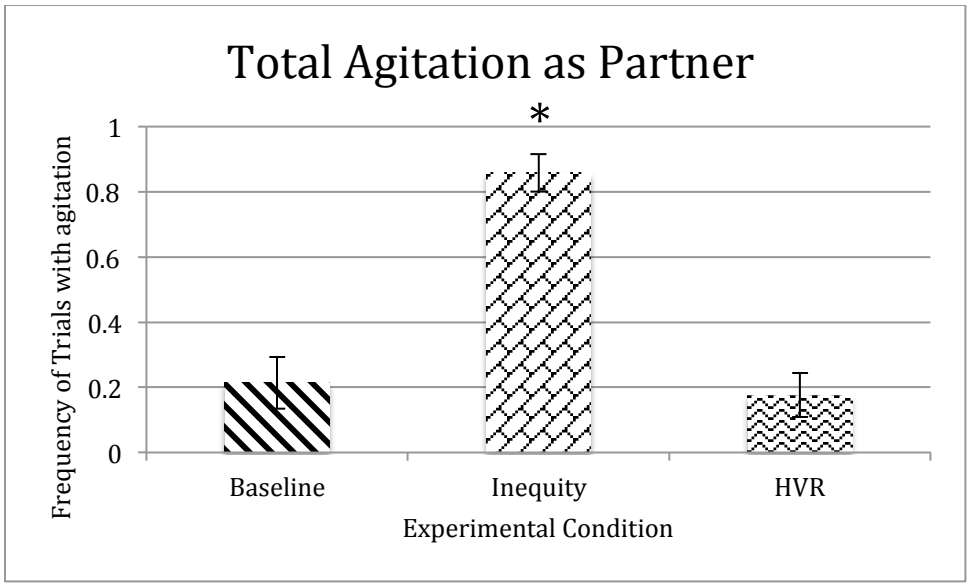

Figure 4: Mean ± SEM total agitation behaviors for partners by condition. The asterisk indicates that partners' agitation was significantly enhanced in the Inequity condition as compared to the other two.

Appendix

Subjective Responses to Disadvantageous & Advantageous Inequality

Capuchin Ethogram

October 10, 2010

Coders will be blind to the condition.

This coding template will be used for both the capuchin monkeys and the chimpanzees, however there are slightly different ethograms due to different behaviors, so **please be sure you are using the correct ethogram for your species!**

The following are the four categories of behavior that will be coded. Each category matches a category/behavior on the coding sheet (in Excel).

STATE BEHAVIORS

The following two behaviors should be recorded **twice**, once during the exchange and once in the 5 seconds following.

We define 'during exchange' as from the time the primate receives the token to the time the primate receives the food. We define '5 seconds following' as the 5 seconds immediately subsequent to receiving the food. If the monkey is out of the frame for more than 3 seconds during the exchange do not code the state behavior. If there are fewer than 5 seconds following receipt of the food before the experimenter starts the next trial with the partner, cease recording and record the dominant state during the available time period.

In each case, please record the dominant behavior during that time period. That is, the monkey should be primarily calm or primarily agitated. If it is not clear, that is, if the primate is showing roughly equal amounts of both behaviors, please do not enter in data.

Calm/Content: the capuchin is still (e.g. not pacing or jumping), moving languidly, soft cooing, calmly grooming self or partner.

Agitated: The primate is agitated. For capuchins, this includes self-scratching, agitated pouncing (e.g. several leaps in a row), vocalizing (except for coos), banging token against floor or wall of the cage, throwing token, bobbing the head, flashing teeth during token exchange, and fear grimacing (both lips pulled back showing teeth).

POINT BEHAVIORS

The following behaviors are recorded as they occur, and are recorded each time that they occur. The Excel data sheet will tabulate each instance. These behaviors should be recorded throughout

the duration of each trial (e.g. from the handing of the token until the experimenter begins the partner's trial).

Aggressive: Aggressive behaviors are always directed at another individual, either the partner or the experimenter. For capuchins, aggressive behaviors include swiping with the hand, attempting to bite (or biting), and screaming at the partner. A swipe is similar to a reach except it is done much faster.

Record whether the aggressive incident was directed at the **partner** or at the **experimenter**. This is on the Excel data sheet.

Food-related Behavior- Food related behaviors are those that take place specifically in the context of food. We specify two types of food-related behaviors below.

Reaching: One individual begs for food from partner or the experimenter, by sticking out the hand out. Each reach through the mesh counts **once**. The arm must be **at least elbows length** out of the cage or through the median to count. Reaching directed at the experimenter does not count if they are holding a token, this is a food related behavior, and this counts **only when they are holding food**. Reaching directed at the partner does not count if they do not have food; again this is a food related behavior. During the HVR trials the must monkey reach or gesture that they are aware of the high value reward before being exchanged the low value reward. Do not count the reach for the high value reward for the subject being shown the food but do count the partners' reach for the food. Also, when the subject is being given its reward after an exchange, do not count this reach. If the partner monkey reaches, do count this reach.

. Record whether the begging behavior was directed at the **partner** or at the **experimenter**. This is on the Excel data sheet.

Acquisition: Instances in which one capuchin obtains food from another primate. This includes passive sharing, in which the recipient takes food from the possessor without a response from the possessor; active sharing, in which the possessor deliberately gives food to the recipient; and stealing, in which an individual attempts or successfully grabs food from the possessor, who tries to stop the individual or is visibly agitated by the stealing. We will NOT separate these categories and include any acquisition of food. If you notice active sharing or stealing (both of which are rare), please make a note of it on the data sheet.