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The influence of reward quality and quantity and spatial proximity on the responses to inequity and contrast in capuchin monkeys (*Cebus [Sapajus] apella*)

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Abstract

Recent evidence within the field of comparative psychology has demonstrated that small differences in procedure may lead to significant differences in outcome. Therefore, failing to fully explore the impact of different contexts on a behavior limits our ability to fully understand that behavior. A behavior that has exhibited substantial variation, both within and across studies, is animals' responses to violations of their expectations, either when expectations were based on another's outcome (inequity) or one's own previous outcome (contrast). We explored this further in capuchin monkeys, focussing on two factors that often vary in such tests but have not yet been rigorously explored: the relative values of the food rewards and the degree of separation of the subjects. Concerning the first, we examined responses to violation of expectations when the difference between what was expected (or what the partner got) and what was received differed in either quality or quantity. Concerning the second, we compared responses when the two individuals were separated by a clear partition (Barrier condition) versus sharing the same enclosure without the partition (No Barrier condition). Our results suggest that responses to inequity are most likely to emerge when the food received is low-value food, regardless of the difference between the actual and expected outcome. However, capuchins did not respond differently to different quantities of rewards, nor did the degree of separation between subjects significantly impact results. We consider the implications of this work for both studies of violation of expectation and other cognitive and behavioral tasks.

Keywords: inequity, contrast effect, social comparison, *Cebus apella*, *Sapajus apella*

The influence of reward quality, quantity and spatial proximity on the responses to inequity and contrast in capuchin monkeys (*Cebus [Sapajus] apella*)

Recent evidence shows that apparently small differences in experimental procedure can lead to big differences in outcome. For instance, among chimpanzees, whether or not subjects pass tasks designed to assess perspective taking is highly dependent on the size of the testing area (Bräuer, Call, & Tomasello, 2007; Hare, Call, Agnetta, & Tomasello, 2000; Karin-D'Arcy & Povinelli, 2002), the distance between the stimuli (Mulcahy & Call, 2009), and the design of the procedure (Melis, Call, & Tomasello, 2006). Similarly, great apes' ability to succeed in a tool use task is influenced by the placement of the tool(s) (Mulcahy & Call, 2006). Experimental variables have also been shown to impact task performance in New World monkeys. After observing a human experimenter hide a reward, squirrel monkeys and marmosets were better able to identify the location of the hidden reward when given nine possible locations as opposed to two. Apparently decreasing the probability of success by chance increased subjects' motivation to pay attention in the task (Schubiger, Kissling, & Burkart, 2016). Most of the work documenting the effect of procedural differences on behavioral outcomes has focused on cognitive tasks, but the same appears to be true for behavioral tasks. For instance, enclosure size again appears to be important in prosocial choice tasks (in cooperatively breeding primates; Burkart, Fehr, Efferson, & van Schaik, 2007; Cronin, Schroeder, Rothwell, Silk, & Snowdon, 2009), as does whether or not the food rewards are visible (reviewed in Cronin, 2012). This is an important issue for several reasons. First, failing to recognize when procedural differences are influencing results negatively impacts our understanding of a given behavior, in particular by creating apparent inconsistencies where none may exist. This may lead to an inappropriate understanding of the distribution of a behavior or ability, or a misunderstanding of how robustly an ability manifests. Moreover, it is essential to understand what factors are influencing a behavior to truly understand that behavior.

This is also an important issue in cases in which substantial variation is seen across studies. Without appropriately controlling for the experimental factors, we do not know if this variation is due to individual differences among animals, if the effect itself is weak, or if there are contextual factors that are influencing responses in meaningful ways that we need to better understand. One area in which this may be relevant is in the study of violations of expectation. A growing literature indicates that in some contexts, some species respond negatively when their expectations are violated, both in the context of inequity (expectations based on another's outcomes) and contrast (expectations based on one's previous outcomes). In the case of inequity, nonhuman species respond negatively to receiving a lower-valued reward than a partner following some form of work (e.g., exchanging a token; reviewed in Talbot, Price, & Brosnan, 2016). These negative responses typically include refusing to work or refusing to accept the lower-valued reward and are contingent upon a social partner receiving the better rewards. Negative responses to contrast also emerge when an individual receives a lower-valued reward, however, they manifest when a better reward appears to be available and are based on one's own expectations. However, there is substantial variation across species, across studies, and even across individuals within the same studies (Talbot et al., 2016).

For example, chimpanzees show substantial differences both across studies and within the same study, with some individuals showing strong responses to inequity and others showing no response at all (reviewed in Brosnan, 2013). In fact, even in studies that do find responses to inequity, we do not see responses in every individual tested (Bräuer, Call, & Tomasello, 2006, 2009; Brosnan, Hopper, Richey, Freeman, Talbot, ... & Schapiro, 2015; Brosnan, Schiff, & de

Waal, 2005; Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010; Hopper, Lambeth, Schapiro, Bernacky, & Brosnan, 2013), making perhaps the most noticeable feature of this research the variability of the response. Previous research has demonstrated that the responses are influenced by, at minimum, rank (Brosnan et al., 2010), personality (Brosnan et al., 2015), and duration of relationship (Brosnan et al., 2015; Hopper, Lambeth, Schapiro, & Brosnan, 2014). Although we have the most data on chimpanzees, there is also variation in the response across capuchin studies (Brosnan & de Waal, 2003; Dubreuil, Gentile, & Visalberghi, 2006; Fletcher, 2008; Fontenot, Watson, Roberts, & Miller, 2007; McAuliffe, Chang, Leimgruber, Spaulding, Blake, & Santos, 2015; Roma, Silberberg, Ruggiero, & Suomi, 2006; Silberberg, Crescimbene, Addessi, Anderson, & Visalberghi, 2009; Takimoto & Fujita, 2011; Takimoto, Kuroshima, & Fujita, 2009; van Wolkenten, Brosnan, & de Waal, 2007). Among squirrel monkeys, while no individuals respond negatively to inequity, there is variability among who responds negatively to contrast effects (Freeman, Sullivan, Hopper, Talbot, Holmes, …, & Brosnan, 2013; Talbot, Freeman, Williams, & Brosnan, 2011).

What is causing this variability? In some species, there are consistent findings that suggest that we understand the variability. For instance, in squirrel monkeys, it is always the males that respond negatively to contrast, and never females (Freeman et al., 2013; Talbot et al., 2011). However, despite substantial effort to find differences based on sex, relationship, age, personality, and other individual variables, in most cases researchers are unable to pinpoint a single factor. One approach that has not yet been taken is to explore the procedural differences that have been hypothesized to influence responses. A particular challenge of comparative work is designing studies that are actually comparable. Across species, there is the ever-present challenge of balancing procedures that are identical with those that are scaled to the species in question (Pretot, Bshary & Brosnan, 2016a,b). Even within species, different populations may have different preferences (even for the same foods) due to factors such as differences in exposure. Moreover, differences among housing conditions may necessitate differences in procedure. The former factor often varies among studies of inequity. Therefore, it may be that differences in the relative magnitude or relative preference of rewards across studies, or different criteria used to determine the rewards that are (presumably) expected versus received, are influencing responses, despite the fact that each lab uses strict criteria to choose foods. Regarding the latter, it has been previously hypothesized that how the animals are positioned relative to one another influences responses (Brosnan et al., 2010). This is based on evidence from human psychology studies suggesting that the spatial proximity of individuals impacts social behavior (Sommer, 1965), but there is as yet no evidence in non-human species. In order to test these hypotheses, we turned to capuchin monkeys, a species for which there are a substantial number of studies on inequity and little understanding of why this variation occurs.

We first addressed the relative values of the chosen food rewards. The way in which reward pairs are determined by the experimenters varies substantially across studies of inequity. Most studies evaluate the quality of the rewards to the subjects on an individual basis, immediately prior to testing (e.g., Brosnan & de Waal, 2003; Brosnan et al., 2010; Massen, van den Berg, Spruijt, & Sterck, 2012; Neiworth, Johnson, Whillock, Greenberg, & Brown, 2009; Silberberg et al., 2009; Talbot et al., 2011; van Wolkenten et al., 2007). While this rank orders food values, it also is the case that different experimenters use different criteria, so it is nonetheless difficult to compare relative reward differences across these studies. Moreover, in other cases, researchers either used the same rewards as previous studies (Roma et al., 2006) or relied on previous food preference data (Bräuer et al., 2006, 2009). Although both of these are reasonable, differences in access to various food items or individuals' preferences may influence subjects' valuation of rewards differently at different facilities, or at different times, or in different contexts within the same facility (e.g., stimulus satiation; Hetherington, Pirie, & Nabb, 2002). Thus, it is important to measure each subject's current preferences in a systematic manner immediately prior to testing. To do so, we used a consistent set of criteria to determine three foods that varied in preference consistently across all individuals within the population.

Related to this, while most studies use different quality foods, often with the presumption that it is easier for the subjects to distinguish visually distinct foods, it is impossible to determine whether the relative preferences we obtain are at all equivalent across individuals (even if using a standardized set of criteria to choose foods). Preference does not necessarily equate with value. That is, you and I may both consistently choose strawberries over grapes, but for you the preference may be very strong whereas for me it is not much above my indifference point. One way to more accurately define reward value is cross modal scaling, in which the value of two foods are compared to the value of a third, less substitutable, food (Casey, Silberberg, Paukner, & Suomi, 2014; Schwartz, Silberberg, Casey, Paukner, & Suomi, 2016). Of course, when possible, varying quantities of a single food type is more objective as more food is always preferable to less. Many nonhuman species can differentiate different quantities (Shettleworth, 2009), including capuchin monkeys (Addessi, Crescimbene, & Visalberghi, 2008; Beran, Evans, Leighty, Harris, & Rice, 2008; Evans, Beran, Harris, & Rice, 2009), and capuchins adjust their choices to maximize the number of rewards (e.g., Brosnan, Parrish, Beran, Flemming, Heimbauer, …, & Wilson, 2011). Thus, here we compared subjects' responses to different quantities of cereal, a medium-value food, which may be the most favorable for optimal performance according to the Yerkes-Dodson law (Yerkes & Dodson, 1908).

Regarding the second factor, the presence of a barrier, there is anecdotal evidence that spatial proximity influences inequity responses in chimpanzees. In all studies in which chimpanzees are sharing an enclosure, at least some subjects reacted negatively to inequity (Brosnan et al., 2005; Brosnan et al., 2010; Brosnan et al., 2015). Indeed, in the majority of interactions in these studies, the chimpanzees were in direct physical contact with one another and appeared to closely monitor their partner's outcomes. On the other hand, in a study in which chimpanzees were facing one another across a 1m wide testing area, no subject showed a negative response to inequitable rewards (Bräuer et al., 2009). Of course, one anecdote is not conclusive, and there are certainly other reasons that these results could have varied; however, this hypothesis is in line with evidence that spatial orientation is significant in cognitive tasks with humans, and in other contexts with primates. Humans prefer to sit adjacent to each other in cooperative tasks but opposite one another in competitive ones (Sommer, 1965). This may be particularly relevant in inequity paradigms, as it has been hypothesized that these negative reactions evolved in conjunction with cooperation, as a way for individuals to judge their outcomes relative to their partner's (Brosnan, 2006; Fehr & Schmidt, 1999). If this is the case, then it is possible that being in a "competitive" situation does not trigger a sensitivity to inequity in the same way that sitting side-by-side does. More simply, being adjacent improves individuals' ability to monitor their partner's rewards. Capuchins behave differently when they cannot see their partners, cooperating less (Takimoto et al., 2010) and struggling to find previous cooperative outcomes (Mendres & de Waal, 2000). This suggests that being separated from one's partner, physically or visually, can impact results within social tasks. To test this, we compared inequity responses when the subjects were separated by a clear partition (Barrier condition; physical but not visual separation) to those in which they shared the enclosure (No Barrier condition; no separation).

We examined the impact of reward value and spatial proximity on both social contrast, or inequity, and individual contrast in two populations of capuchin monkeys, one at Georgia State University's Language Research Center and one at the NICHD Laboratory of Comparative Ethology. We used a traditional procedure for testing violation of expectations, but varied the relative value of food rewards, the quantity of food rewards, and whether or not subjects were separated. For the general procedure, pairs of subjects had to alternate exchanging tokens with a human experimenter for a food reward. We compared how they responded when their partner got the same reward as them (Equity condition) to their response when their partner got a preferred reward (Inequity condition) or when both subjects were shown a preferred outcome, but given a less preferred one (Contrast condition). We varied reward value between least preferred (low-value), middle preference (medium-value), and most preferred (high-value), with values based on food preference tests run immediately prior to testing. At GSU, subjects were tested together in a large testing chamber (No Barrier condition) that could be divided in half with a barrier (Barrier condition), although due to logistics the No Barrier condition could not be run at NICHD. We also tested subjects' responses to different quantities of a medium value reward, Cheerios brand cereal, which were not utilized in the quality comparisons.

We hypothesized that the capuchins' responses would vary depending on the relative difference in quality between the food items. However, because there have been no such studies, we did not have any directional predictions. We also did not have a prediction for whether responses would be more pronounced in either the inequity or contrast condition. Because previous research has shown that capuchin monkeys are sensitive to different quantities of rewards (Addessi et al., 2008; Beran et al., 2008; Brosnan et al., 2011; Brosnan et al., 2012; Evans et al., 2009), we predicted that subjects would respond negatively to receiving a smaller amount than anticipated. Finally, given previous inequity studies and work showing that visual access influences behavioral responses in situations involving cooperation and inequity (Takimoto et al., 2010), we predicted that we would see increased responses in the No Barrier condition as compared to the barrier condition.

Method

Subjects

Language Research Center

We tested six (five adult males and one adult female; age range = 7-22 years old; mean age = 12.8 years) brown capuchin monkeys (*Cebus [Sapajus] apella*) from the Language Research Center (LRC) at Georgia State University in Atlanta, GA. Two additional adult female capuchin monkeys, the lowest ranking and highest ranking in their group, were originally included in the subject pool, but were excluded from further testing because the lower-ranking did not reliably enter the test chamber with her higher-ranking partner. In such cases, we assume that the subject does not wish to participate in the task or be in proximity to a given partner and do not include them further (this criterion has been followed in other inequity work, i.e., Brosnan et al., 2010).

Monkeys were socially housed in stable, mixed-sex social groups that had been housed together for almost a decade (since July 2005 or the individual's birth, whichever came later). Each social group lived in indoor/outdoor space that included climbing structures and material enrichment. Primates received a diet including primate chow, fruit, and vegetables and were never food deprived. Fresh running water was available *ad libitum*, including during testing sessions. Subjects were tested in enclosures attached to their home cage, where all testing takes place. They had been trained to voluntarily enter these enclosures for cognitive and behavioral experiments. Subjects were not tested on days they chose not to enter the test enclosure, which they were free to do at any time without any consequences. No subject was tested on this study more than once in the same day. Monkeys were paired with individuals from their own social groups for testing.

National Institutes of Health

We tested seven male capuchin monkeys (age range = 5-10 years old; mean age = 7.5 years), from the National Institute of Health (NIH) Laboratory of Comparative Ethology in Poolesville, MD. Monkeys were housed in two pairs and one group of three with continuous auditory and tactile access to their cage mates and testing partners. All social partners were stable for at least two years. Home cages were enriched with perches, rubber and/or plastic toys and forage boards. Monkeys received a scattered feed and fresh fruit or nuts once a day and primate chow twice a day. Fresh water was supplied *ad libitum*. Subjects were tested in their home cages. No subject was tested more than once in the same day. Three of the seven NIH Animal Center subjects were housed together and therefore tested in a round robin fashion. Within the same day, monkeys only ever served as partners after they themselves had been tested as subjects. All procedures used in this research were in accordance with the American Psychological Association's guidelines for ethical conduct in the care and use of nonhuman animals in research and have been approved by the Institutional Animal Care and Use Committee of Georgia State University (A10025 & A13022) and of the National Institute of Health Animal Center (09-015).

Food Preference Tests

Prior to testing on the quality comparisons, we established preferences for three different food values, including a highly-preferred food value reward (high-value reward, or HVR), a medium-value reward (MVR), and a less-preferred food (low-value reward, or LVR). These foods were selected from among all of the foods in the capuchins' diets using the procedure and criteria discussed in the next paragraph. Prior to testing on the quantity comparisons, we established that they preferred more to less of a medium preference food that had not been used previously in quality comparison tests.

Food selection was done using a dichotomous-choice food preference test (Brosnan & de Waal, 2004) in which an experimenter offered two food rewards simultaneously and the subject was allowed to choose one of the two rewards by reaching out of the testing enclosure and selecting the preferred item. We conducted two 10-trial sessions on different days of each of the possible food pairs. Within each session, reward positions were randomized with an equal number on each side (left and right). A reward was considered to be preferred if it was chosen at least 80% of the time over the alternative food on both days by all test subjects. Note that this required the 80% threshold on *both* sessions; a session with a 70% preference and one with a 90% preference did not count. This ensured consistency. Additionally, the test would not work if the less-preferred item was one that the subjects will not eat under normal circumstances. Therefore, to ensure that subjects were willing to eat the less-preferred food item, in a separate session we presented them with 10 consecutive pieces of the lower-valued reward. If all subjects did not eat all 10 pieces, that food could not be used as the least preferred food (LVR). Subjects underwent a new food preference test at the beginning of each experiment. Note that we conducted food preference tests for both paired qualities and paired quantities to ensure that all pairings met our criterion for preference.

General Procedure

Throughout testing, we utilized an exchange procedure in which monkeys took turns exchanging an inedible token (LRC: a 2-3 cm diameter granite stone; NIH: a 1-inch metal washer) with a human experimenter in exchange for a food reward of variable value. All subjects had previous experience with exchange tasks (e.g., Brosnan et al., 2011; Paukner, Suomi, Visalberghi, & Ferrari, 2009) and therefore did not require training.

In this procedure, an experimenter first showed the token to the monkey with whom they were interacting and then held the token between cage bars for the monkey to grasp. Monkeys had up to 10 seconds to accept the token by taking it completely inside their testing enclosure, following which the experimenter extended her hand, palm up, in front of the monkeys' enclosure in a begging gesture. Monkeys had up to 30 seconds to return the token, following which the experimenter held up the appropriate food reward and offered the reward to the subject. Monkeys had up to 10 seconds to accept the reward. Thus, subjects could refuse either the token or the food.

Subjects could easily observe their partner's behavior and the rewards they received (including both the Barrier and No Barrier conditions; see below for details). To ensure that subjects could compare their own outcome to that of their partner on every trial, the experimenter always interacted with the partner first. To ensure that the presence of particular rewards did not impact their responses in the quality comparisons, two reward containers (one for the higher valued reward and one for the lower valued reward for the given test condition; see below for details) were always present in the same location, full, and within the monkeys' view, even in control tests in which only one reward was used (Equity and Contrast). In the quantity comparisons, only one reward was used in all conditions, in different quantities, so only one reward container was present.

The experimenter coded the responses of the subject and partner in real time on data sheets and all test sessions were videotaped for later analysis and coding. The inter-trial interval was approximately 5-10 seconds, or the time it took for the experimenter to record the data and the monkey to consume the food.

Food Comparisons

Food rewards and quantities were determined for each population by the food preference tests described above. Quality comparisons included High (H) vs. Low (L), which compared the HVR (LRC: grape, NIH: grape) with the LVR (LRC: bell pepper, NIH: popcorn), High (H) vs. Medium (M), which compared the HVR (LRC: grape, NIH: grape) with the MVR (LRC: cucumber piece, NIH: apple piece), and Medium (M) vs. Low (L), which compared the MVR (LRC: cucumber piece, NIH: apple piece) with the LVR (LRC: bell pepper, NIH: popcorn).

Quantity comparisons compared a larger-quantity of food with a smaller-quantity of food. Using the food preferences tests described above, we first established that the monkeys preferred more to less of a medium preference food, Cheerios (an unsweetened oat cereal), which were not used in quality comparisons. The LVR was one piece of cereal, but due to a miscommunication, for LRC capuchins the HVR was five cereal pieces and for NIH capuchins it was three pieces. Both populations passed the preference test on their respective distribution. In order to avoid confusion, subjects underwent all conditions in a particular comparison before proceeding to the next. Subjects experienced all of the quality comparisons before being tested on quantity comparisons.

We did not initially conduct preference tests comparing cereal to the food items used in the quality tests prior to testing, because cereal was never tested in comparison to any of these foods. However, to provide an initial test of a hypothesis that emerged from our results (see Discussion), after testing we compared the preference of five of the GSU monkeys who were in the original study for one piece of cereal (the smallest quantity used in this study, and therefore the most equivalent to the LVR in the quality tests) to the low, medium and high value foods used with the LRC monkeys in the quality comparison. Every subject preferred a grape to a Cheerio, and all but one subject preferred the cereal to the lowest value reward (two monkeys preferred cereal to the MVR, two monkeys preferred the MVR, and one was indifferent between the MVR and a Cheerio).

Conditions

For each comparison, pairs underwent a series of eight tests, completing two sessions of each control condition (Equity and Contrast) and four total sessions of the Inequity condition, with each monkey tested twice in the subject role. Each test session consisted of a series of 40 alternating trials so that each individual in the pair received 20 trials per session. There were three conditions. The Equity condition tested the subject's response when they received the same reward as their partner (the lower-valued reward of the two in the given experiment) and thus, was a baseline measure. The Contrast condition examined subjects' responses to violations of individual expectations. In this condition, both subjects and partners were first shown a higher-valued reward, but following exchange, received the lower-valued reward. Note that the only difference between this condition and the Equity condition was the attention drawn to the higher valued reward before both monkeys' exchanges. Because both monkeys got the same rewards, only two total sessions were required. Each monkey was the first exchanger once for each condition. The Inequity condition measured subjects' responses to receiving the lower value food after observing their partner receive the higher valued reward for their exchange. Each pair received four tests session (twice with each monkey in the subject role; the subject was always the second exchanger). The order in which each pair experienced the conditions was randomized and, for all conditions, the order in which individuals were tested in the subject role (i.e., and interacted with the experimenter second) was randomized and counterbalanced.

Testing the Effect of a Barrier

Typically, studies of inequity conducted with apes do not include a barrier between the two subjects (e.g., Brosnan et al., 2005; Brosnan et al., 2010), whereas virtually all of the studies with New World monkeys included a barrier between conspecifics (e.g., Cronin & Snowdon, 2008; Dubreuil et al., 2006; Silberberg et al., 2009; Talbot et al., 2011; van Wolkenten et al., 2007; but see Freeman et al., 2013). The flexible housing at the LRC allowed us to test the effect of including a barrier using the same testing enclosure for each quality and quantity comparison, which held all other factors equal. After completing the full battery of sessions with a clear Lexan barrier separating the subject and partner (the Barrier condition), we re-ran all of the tests at the LRC without a barrier (the No Barrier condition). We chose not to counterbalance the order of testing with the LRC capuchins so that their results in the Barrier condition would be directly comparable to those of the NICHD capuchins.

Data analysis

Refusals

Refusals consisted of 58% token refusals and 42% food refusals. There was a significant difference in the frequency of token and food refusals among the conditions ($\chi^2 = 12.20$, df = 2, $p = 0.002$). However, post hoc tests were not significant (presumably due to the small samples).

We therefore used the overall refusal rate (combining refusals to exchange the token with refusals to consume food rewards) for all analyses. To determine which factors influenced the occurrence of refusals in the quality comparisons, we fitted generalized linear mixed-effects models (GLMMs) with refusal as a binomial dependent variable. We used the glmer function of the lme4 package (Bates et al., 2015) in R statistical software version 3.3.0 (R Development Core Team, 2016). Individual identity was included as a random effect to account for different baseline rates of refusal. As fixed effects, we included test condition (Equity, Inequity and Contrast), the three quality comparisons (H vs. L, M vs. L, and H vs. M), and their interaction.

To further evaluate the effect of a barrier on refusals for the population of LRC capuchins, we used a sequential regression analysis. In Step 1, we refitted the condition x comparison model for this reduced sample. In Step 2, we entered barrier (0/1) as a binomial predictor and its two-way interactions to assess its effect on refusals beyond that of condition and comparison.

Finally, we fitted a GLMM to determine which factors influenced refusals in the quantity comparisons. As fixed effects, we included test condition, the two quantity comparisons (LRC: 5 vs. 1, NIH: 3 vs. 1), and their interaction. For the LRC capuchins, we compared refusals in the Barrier and No Barrier conditions using a paired *t*-test.

We also fitted null models, containing only the intercept and the random effect. We used likelihood ratio tests and compared Akaike's Information Criterion (AIC) to assess whether a factor significantly improved model fit over a reduced model without that factor.

A second coder, blind to the hypotheses, coded 20% of all test trials from video, measuring each monkey's response. Inter-rater reliability was calculated using the Kappa coefficient. Inter-rater reliability was excellent (agreed on 99.5% of trials, Cohen's $\kappa = 0.90$).

Latency to Exchange

To determine which factors influenced capuchin monkeys' latency to return the token, we fitted linear mixed-effects models (LMMs) with the lmer function of the lme4 package (Bates, Maechler, Bolker, & Walker, 2015) in R statistical software version 3.3.0 (R Development Core Team, 2016). Model specifications were identical to those for refusal, except with latency to exchange as a continuous dependent variable. The restricted maximum likelihood (REML) approach was used for parameter estimation; *p*-values were calculated based on Satterthwaite approximated degrees of freedom obtained with the lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2015).

Results

Quality Comparisons

Overall

The capuchins varied significantly among the test conditions and food comparisons in their rate of refusal, $\chi^2(8) = 367.85$, $p < .001$ (Table 1, Figure 1A and 1B), and in their latency to exchange, $\chi^2(8) = 75.36$, $p < .001$ (Table 2; Figure 1C and 1D).

Overall, subjects were more likely to refuse in the Inequity condition compared to the Equity or Contrast conditions, and this effect was the most pronounced in comparisons in which a low-value food reward (LVR) was used (either in contrast to a medium-value or a high-value food reward). Considering this in detail, capuchins were 9.1 times more likely to accept than to refuse either the token or the food in the reference case, Equity condition of the H v L comparison (i.e., the higher value of the two rewards in the comparison was present, but no one received it; intercept, odds ratio $^{1}/_{0.11}$). Subjects were 1.6 to 2.8 times more likely to refuse either the token or food in the Inequity condition than in the Equity condition (main effect of condition, odds ratio 2.10, 95% CI) in all comparisons except in the H vs. M comparison (condition x comparison interaction). Interestingly, refusals were not higher in the Contrast condition compared to the Equity condition in any comparison. In fact, for the M vs. L comparison, refusals were *lower* in Contrast than in Equity (condition x comparison interaction). Finally, capuchins did not differ in their rate of refusal for the H vs. L and M vs. L comparison, but they refused 5.6 times less often in the H vs. M comparison (main effect of comparison, odds ratio $^{1}/_{0.18}$).

Latencies to exchange were longer in the Inequity condition in which the subject got the least preferred food whereas the partner received higher value food (either the medium or higher value reward). However, unlike in the exchange data, latencies in the Contrast condition were similar to those in the Inequity condition rather than those in the Equity condition. On average, capuchins exchanged the token after 2.3 to 3.8 seconds in the reference case, Equity with H vs. L (intercept, 95% CI). In comparison, latency to exchange was 0.35 seconds longer in the Contrast condition and 0.36 seconds longer in the Inequity condition (main effect of condition). Similar to refusals, latencies to exchange did not differ between the H vs. L and M vs. L comparison, but were 0.47 shorter in the H vs. M comparison (main effect of comparison).

Barrier Conditions

The results for the LRC monkeys in the barrier conditions (i.e., barrier present vs. barrier absent) mirrored the overall findings described above for the quality comparisons. Capuchins varied significantly among the barrier conditions (Figure 2A and 2C) and food comparisons (Figure 2B and 2D) in their rate of refusal (Table 3), Step 1: $\chi^2(8) = 245.05$, $p < .001$, and in their latency to exchange (Table 4), Step 1: $\chi^2(8) = 67.21$, $p < .001$. Additionally, the barrier conditions significantly improved model fit for both rate of refusal, Step 2: $\chi^2(5) = 14.53$,

p = .013 (albeit without significantly impacting responses across test conditions or comparisons; see next paragraph), and latency to exchange, Step 2: $\chi^2(5) = 64.70$, $p < .001$.

The refitted models for both measures replicate the effects of test condition, comparison, and their interaction described above (Tables 3 and 4). For refusals, there were no significant effects of barrier or its interactions with test condition and comparison. Improved model fit was likely driven by a marginally significant comparison x barrier condition such that, across all test conditions and food comparisons, there tended to be more refusals in the presence of a barrier in the H vs. M comparison than in the H vs. L or M vs. L comparisons. Latencies to exchange, however, were 0.8 to 1.4 seconds longer when the barrier was present than when it was not (effect of barrier). This effect was most evident in the H vs. L comparison but less so in the M vs. L comparison and the H vs. M comparison (comparison x barrier interaction).

Quantity Comparisons

Overall

In the two quantity comparisons, the capuchins varied significantly among food comparisons (which overlapped with population comparisons) but not test conditions in their rate of refusal, $\chi^2(5) = 14.30$, $p = .014$ (Table 5) and in their latency to exchange, $\chi^2(5) = 15.81$, $p = .007$ (Table 6).

In the reference case, Equity with 1 cheerio, the LRC capuchins virtually never refused the token or the food, regardless of what other food was present (*M* = 0.86, *SD* = 2.30 refusals per 20 trials in a session), and exchanged the token after 1.1 to 3.1 seconds (intercepts). There was neither a difference in refusals nor in latency to exchange between the test conditions. However, the NIH capuchins in the 3 vs. 1 comparison were significantly more likely to refuse (*M* = 2.00, *SD* = 3.30 refusals per session) and showed 1.5 to 4.3 seconds longer latencies to exchange than the LRC capuchins (*M* = 0.19, *SD* = 0.93 refusals per session) in the 5 vs. 1 comparison (effects of comparison).

Barrier Conditions

LRC capuchins in the 5 vs. 1 comparison showed both higher rates of refusal (Figure 2A) and longer latency to exchange the token (Figure 2D) when the barrier was present than when it was not, refusals: $t(719) = -3.78$, $p < .001$, latency: $t(705) = -5.58$, $p < .001$.

Discussion

In order to explore factors that may be impacting the variability among capuchins' responses in inequity studies, we examined whether the relative value of rewards and the presence of a barrier impacted responses to inequity in capuchin monkeys. We additionally investigated whether using differences in reward quantity might impact responses differently than the typically used differences in reward quality. The relative quality of proffered versus received rewards did indeed influence responses to inequity and contrast, with a particularly strong effect of the least-preferred food option. On the other hand, subjects did not respond differently to different quantities of rewards. Moreover, while the presence of a barrier significantly increased refusals in the High vs. Medium food comparison, improving model fit, it did not impact the rate of refusals across the different conditions and food comparisons.

Considering these findings in more detail, capuchin monkeys were more likely to respond to inequity when there was a low-value reward present (i.e., in the H vs. L and M vs. L conditions) as compared to the H vs. M condition. Similarly, capuchins took longer to complete token exchanges in the Inequity and Contrast conditions when a low-value reward was present, as compared to conditions in which both subjects received the same reward (Equity) or both rewards were relatively more preferred (i.e., in the H vs. M comparison). Given that we had several different MVRs and LVRs, but subjects only refused for the LVRs, it seems unlikely that this result is due to greater differences in relative value. Thus, the presence of a particularly low-value food reward – but one that the subjects are willing to eat at least 10 times in a row in a non-experimental context – appears necessary to generate responses to violations of expectations.

There are two possible – and not mutually exclusive – explanations for why this would be the case. First, receiving a particularly low-value food when a highly valued food is present may increase the level of frustration. Alternately (or in addition), it may be that when the value of both rewards is relatively high, the cost of foregoing the reward to express frustration is too high, even if they are frustrated. We cannot distinguish between these with the current data because our dependent measure does not assess whether they *notice* a violation of expectations; instead, we measure whether they *respond* to a violation of expectations by turning down a proffered reward. This inequity response is quite costly and may require substantial ability to inhibit their prepotent tendency to accept a relatively high valued food reward; recall that our criterion for the low-value reward was that they would accept and consume 10 pieces of it in the absence of other food rewards, so even the “low” value food is one that they will typically happily consume. Overall, while it is clear that this response is to the violation of social expectations (i.e., they only refuse the LVR when their partner gets a better outcome), it appears to be the absolute value of the less preferred option, rather than the relative difference in value, that drives responses. Again, this is likely due to the low cost of turning down less preferred rewards (or the high cost of turning down those that are preferred), combined with frustration when better rewards go to the partner.

Intriguingly, the capuchins did not respond to violations based on different quantities, in either the Inequity or Contrast conditions. This is somewhat surprising because we know that capuchin monkeys can differentiate between quantities (Beran et al., 2008; Evans et al., 2009), make decisions based on relative quantities (Brosnan et al., 2011), and in our preference tests, all monkeys discriminated and subsequently preferred the greater to the lesser quantity. There are several potential reasons why they did not respond. First, it is important to note that it is unlikely that the monkeys were unable to discriminate the quantity differences chosen for the current study (1 vs. 5 and 1 vs. 3). Capuchin monkeys, including some of the same subjects tested in the present study, reliably choose the larger of two quantities of 1-5 food items, including visible (Addessi et al., 2008) and non-visible sets shown briefly, and even track additions to these sets (Beran et al., 2008). Despite this, it is possible that subjects were more interested in *what* their partner received or what they had previously received rather than *how much* they received. Indeed, although items were presented sequentially to maximize the chances that subjects recognized that different quantities were present (this procedure was followed in both the preference tests and the study itself), it is possible that they failed to recognize this cue with respect to their partner, lost track of how many items their partner received, or simply did not pay attention. Similarly, a previous study found that social manipulation did not affect capuchin monkeys' risk taking behavior in a relative quantity task, even when the partner monkey received the subject monkey's unchosen food set (Beran, Perdue, Parrish, & Evans, 2012). These findings suggest that insensitivity to quantity differences may be driven, at least in part, by differential motivation and/or attention rather than insensitivity to inequity *per se*.

One other possibility is that this was due to the food we chose for the quantity tests (pieces of Cheerios brand cereal, an unsweetened 'o' shaped oat cereal). In the quality tests, subjects never refused more preferred foods (i.e., the MVR or HVR), leading us to hypothesize that the cereal pieces were too high in value for them to refuse, no matter what their partner received. To provide an initial test of this hypothesis, we conducted post-hoc food preference tests comparing five of the GSU monkeys' preference for one piece of cereal (the smallest quantity used in this study, and therefore the most equivalent to the LVR in the quality tests) to the low, medium and high value foods used with the LRC monkeys in the quality comparison. Potentially supporting this hypothesis, we found that cereal pieces were of medium value, and in particular, were consistently preferred over the lower value food. Thus, for future studies we recommend that quantity tests be based upon a less preferred food.

Considering our final key finding, the barrier between the monkeys did not significantly impact responses. Given that the referent in inequity comparisons is the other monkey, it is perhaps somewhat surprising that the presence or absence of a barrier did not influence responses to inequity. However, we speculate that this is due to the fact that capuchin monkeys are generally quite tolerant of each other and thus may choose to sit relatively close to one another regardless of whether there is a barrier between them. Moreover, because we only tested pairings in which both subjects voluntarily entered the testing chamber, we were by definition only testing pairs who were sufficiently tolerant of one another that they were willing to separate from their group together, which presumably means that they were willing to sit in close proximity regardless of the barrier. Of course, this is good news from the perspective of comparing the ape studies (typically done with no barrier) to the monkey studies (typically done with a barrier), as it means that these results should be relatively comparable. Nonetheless, in most cases, including both barrier conditions in the current study, subjects are still adjacent and side-by-side. We predict that spatial proximity and the orientation of the individuals relative to one another are likely to be important in other contexts, such as when individuals have a greater spatial distance or are oriented across from one another rather than side-by-side (Brosnan et al., 2010).

Although we are certain that there are a multitude of factors influencing responses to inequity, these results strongly suggest that at least some of the differences we are seeing across studies are due to procedural differences. Specifically, refusals due to inequitable outcomes are most likely to emerge when a low-value (but still liked) food is used. We hypothesize that differences in the relative preferences of different foods may have influenced responses in different studies, leading to variation in outcomes. Whereas it is often tempting to treat differences in outcome across different studies as contradictory, in reality, both are providing key data to help us understand the context surrounding a phenomenon. By far the most productive avenue is to try to determine what key factors are influencing a response and what that tells us about the nature of the behavior. By better understanding the contexts in which animals respond to inequity, or show any behavior, we come closer to understanding the causes and consequences of that behavior, and the specific influence of context on that animal or species.

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Table 1

GLMM for Refusals in Quality Comparisons

Variable	*b*	*SE*	95% CI	OR	OR 95% CI	*z*	*p*
Fixed effects							
Intercept	**-2.19**	**0.25**	**(-2.67, -1.70)**	**0.11**	**(0.07, 0.18)**	**-8.83**	**< .001**
Condition[a]							
Contrast	0.16	0.16	(-0.15, 0.47)	1.18	(0.86, 1.60)	1.03	.302
Inequity	**0.74**	**0.15**	**(0.45, 1.03)**	**2.10**	**(1.58, 2.81)**	**5.04**	**< .001**
Comparison[b]							
M vs. L	-0.07	0.16	(-0.39, 0.25)	.93	(0.68, 1.29)	-0.41	.680
H vs. M	**-1.72**	**0.26**	**(-2.23, -1.21)**	**.18**	**(0.11, 0.30)**	**-6.64**	**< .001**
Condition x Comparison							
Contrast / M vs. L	**-0.76**	**0.25**	**(-1.25, -0.28)**	**0.47**	**(0.29, 0.75)**	**-3.11**	**.002**
Constrast / H vs. M	0.04	0.35	(-0.66, 0.73)	1.04	(0.52, 2.07)	0.10	.918
Inequity / M vs. L	-0.18	0.21	(-0.60, 0.24)	0.84	(0.55, 1.27)	-0.84	.399
Inequity / H vs. M	**-0.99**	**0.38**	**(-1.73, -0.24)**	**0.37**	**(0.18, 0.78)**	**-2.60**	**.009**
Random effects							
Subject ID	*SD*	0.78					

Note. N = 6840. OR = Odds ratio. Reference categories: [a]Equity, [b]H vs. L.

Table 2

GLMM for Latency to Exchange in Quality Comparisons

Variable	*b*	*SE*	95% CI	*df*	*t*	*p*
Fixed effects						
Intercept	**3.07**	**0.37**	**(2.33, 3.82)**	**34**	**11.47**	**< .001**
Condition[a]						
Contrast	**0.35**	**0.17**	**(0.03, 0.68)**	**15050**	**2.94**	**.003**
Inequity	**0.36**	**0.16**	**(0.04, 0.69)**	**15050**	**3.04**	**.002**
Comparison[b]						
M vs. L	-0.04	0.17	(-0.36, 0.29)	15050	-0.29	.768
H vs. M	**-0.47**	**0.16**	**(-0.79, -0.15)**	**15050**	**-4.00**	**< .001**
Condition x Comparison						
Contrast / M vs. L	0.04	0.23	(-0.42, 0.50)	15050	0.25	.800
Contrast / H vs. M	-0.20	0.23	(-0.65, 0.25)	15050	-1.21	.227
Inequity / M vs. L	0.21	0.24	(-0.25, 0.67)	15050	1.24	.218
Inequity / H vs. M	-0.11	0.23	(-0.56, 0.34)	15050	-0.68	.499
Random effects						
Subject ID	*SD*	1.26				

Note. N = 6460. OR = Odds ratio. Reference categories: [a]Equity, [b]H vs. L.

Table 3

GLMM for Refusals in Quality Comparisons in LRC Population

Variable	*b*	*SE*	95% CI	OR	OR 95% CI	*z*	*p*
Fixed effects							
Intercept	**-2.57**	**0.40**	**(-3.36, -1.79)**	**0.08**	**(0.03, 0.17)**	**-6.43**	**< .001**
Condition[a]							
Contrast	0.13	0.27	(-0.41, 0.67)	1.13	(0.67, 1.94)	0.48	0.634
Inequity	**1.15**	**0.24**	**(0.67, 1.62)**	**3.14**	**(1.95, 5.07)**	**4.70**	**< .001**
Comparison[b]							
M vs. L	-0.30	0.27	(-0.82, 0.23)	0.74	(0.44, 1.26)	-1.10	.270
H vs. M	**-2.10**	**0.44**	**(-2.96, -1.23)**	**0.12**	**(0.05, 0.29)**	**-4.74**	**< .001**
Barrier	0.29	0.25	(-0.19, 0.78)	1.34	(0.82, 2.18)	1.18	.237
Condition x Comparison							
Contrast / M vs. L	-0.28	0.34	(-0.94, 0.37)	0.75	(0.39, 1.45)	-0.84	.399
Contrast / H vs. M	0.05	0.45	(-0.83, 0.94)	1.06	(0.44, 2.55)	0.12	.904
Inequity / M vs. L	0.21	0.29	(-0.37, 0.78)	1.23	(0.69, 2.18)	0.71	.481
Inequity / H vs. M	**-1.13**	**0.48**	**(-2.07, -0.18)**	**0.32**	**(0.13, 0.83)**	**-2.34**	**.019**
Condition x Barrier							
Contrast / Barrier	0.16	0.31	(-0.44, 0.77)	1.18	(0.64, 2.16)	0.53	.595
Inequity / Barrier	-0.30	0.28	(-0.84, 0.25)	0.74	(0.43, 1.28)	-1.07	.286
Comparison x Barrier							
M vs. L / Barrier	-0.29	0.24	(-0.75, 0.18)	0.75	(0.47, 1.20)	-1.20	.231
H vs. M / Barrier	*0.80*	*0.41*	*(-0.00, 1.60)*	*2.22*	*(1.00, 4.95)*	*1.96*	*.050*
Random effects							
Subject ID	*SD*	0.83					

Note. *N* = 4320. OR = Odds ratio. Reference categories: [a]Equity, [b]H vs. L.

Table 4

GLMM for Latency to Exchange in Quality Comparisons in LRC Population

Variable	*b*	*SE*	95% CI	*df*	*t*	*p*
Fixed effects						
Intercept	**1.69**	**0.22**	**(1.26, 2.11)**	**21**	**8.94**	**< .001**
Condition[a]						
Contrast	*0.30*	*0.19*	*(-0.07, 0.67)*	*6072*	*1.82*	*.068*
Inequity	**0.39**	**0.19**	**(0.02, 0.76)**	**6072**	**2.38**	**.018**
Comparison[b]						
M vs. L	0.04	0.19	(-0.33, 0.41)	6072	0.24	.812
H vs. M	*-0.28*	*0.19*	*(-0.64, 0.09)*	*6072*	*-1.71*	*.088*
Barrier	**1.08**	**0.17**	**(0.75, 1.42)**	**6072**	**7.24**	**< .001**
Condition x Comparison						
Contrast / M vs. L	0.28	0.23	(-0.17, 0.73)	6072	1.40	.163
Contrast / H vs. M	-0.02	0.23	(-0.47, 0.43)	6072	-0.09	.930
Inequity / M vs. L	-0.02	0.23	(-0.48, 0.43)	6072	-0.11	.912
Inequity / H vs. M	*-0.34*	*0.23*	*(-0.78, 0.11)*	*6072*	*-1.70*	*.088*
Condition x Barrier						
Contrast / Barrier	-0.17	0.19	(-0.54, 0.19)	6072	-1.05	.293
Inequity / Barrier	-0.22	0.19	(-0.58, 0.15)	6072	-1.32	.186
Comparison x Barrier						
M vs. L / Barrier	**-0.73**	**0.19**	**(-1.10, -0.35)**	**6072**	**-4.38**	**< .001**
H vs. M / Barrier	**-0.55**	**0.19**	**(-0.92, -0.19)**	**6072**	**-3.39**	**< .001**
Random effects						
Subject ID	*SD*	0.40				

Note. N = 4151. OR = Odds ratio. Reference categories: [a]Equity, [b]H vs. L.

Table 5

GLMM for Refusals in Quantity Comparisons

Variable	*b*	*SE*	95% CI	OR	OR 95% CI	*z*	*p*
Fixed effects							
Intercept	**-5.79**	**0.90**	**(-7.55, -4.03)**	**0.00**	**(0.00, 0.02)**	**-6.45**	**< .001**
Condition[a]							
Contrast	0.35	0.60	(-0.82, 1.53)	1.42	(0.44, 4.61)	0.59	.556
Inequity	-0.94	0.85	(-2.60, 0.72)	0.39	(0.07, 2.05)	-1.11	.266
Comparison[b]: 3 vs. 1	**3.22**	**1.04**	**(1.18, 5.26)**	**24.96**	**(3.25, 191.91)**	**3.09**	**.002**
Condition x Comparison							
Contrast/ 3 vs. 1	-0.35	0.67	(-1.66, 0.96)	0.70	(0.19, 2.61)	-0.53	.598
Inequity / 3 vs. 1	0.80	0.90	(-0.96, 2.57)	2.23	(0.38, 13.01)	0.89	.372
Random effects							
Subject ID	*SD*	1.32					

Note. *N* = 2280. OR = Odds ratio. Reference categories: [a]Equity, [b]5 vs. 1.

Table 6

GLMM for Latency to Exchange in Quantity Comparisons

Variable	*b*	*SE*	95% CI	*df*	*t*	*p*
Fixed effects						
Intercept	**2.09**	**0.51**	**(1.09, 3.09)**	**32**	**5.98**	**< .001**
Condition[a]						
Contrast	*0.28*	*0.22*	*(-0.15, 0.71)*	*6017*	*1.86*	*.063*
Inequity	-0.01	0.22	(-0.44, 0.42)	6017	-0.06	.955
Comparison[b]: 3 vs. 1	**2.89**	**0.72**	**(1.50, 4.28)**	**35**	**5.91**	**< .001**
Condition x Comparison						
Contrast / 3 vs. 1	0.01	0.37	(-0.72, 0.74)	6019	0.04	.969
Inequity / 3 vs. 1	0.13	0.37	(-0.60, 0.86)	6018	0.52	.605
Random effects						
Subject ID	*SD*	1.20				

Note. *N* = 2201. OR = Odds ratio. Reference categories: [a]Equity, [b]5 vs. 1.

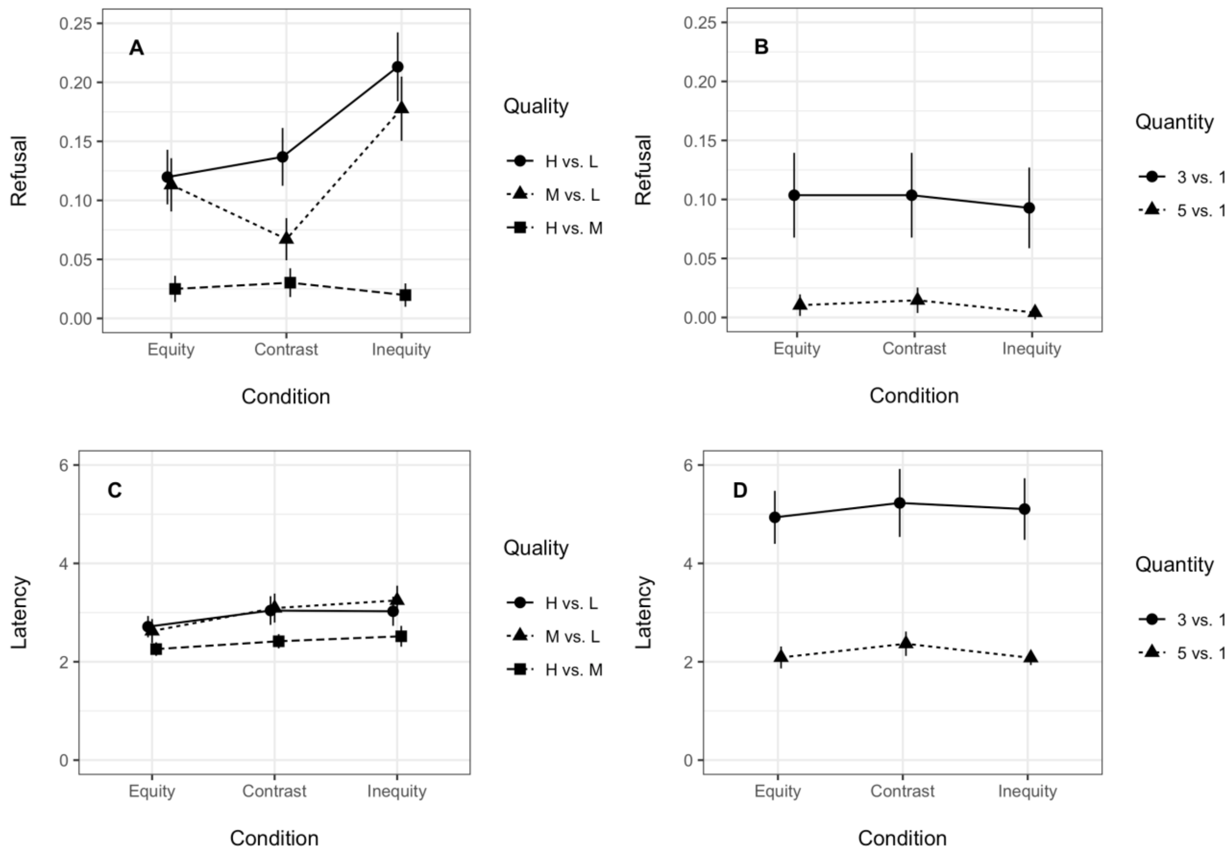

Figure 1. Mean number of refusals (A and B) and mean latency to exchange (C and D) by test condition and food comparison (quality: A and C, quantity: B and D). Error bars indicate standard errors. All subjects completed all quality comparisons; NIH capuchins were tested on 3 items vs. 1 item, LRC capuchins on 5 items vs. 1 item.

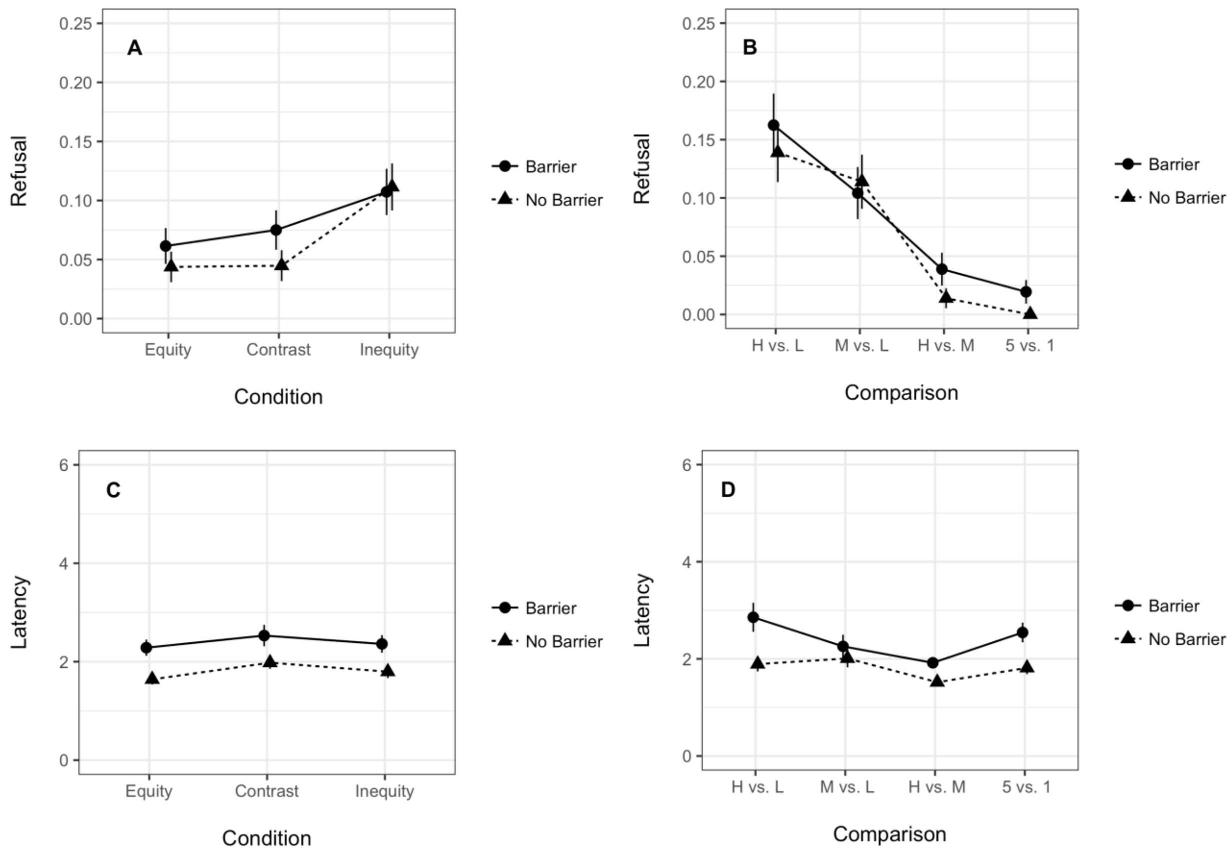

Figure 2. Mean number of refusals (A and B) and mean latency to exchange (C and D) by presence of a barrier (LRC population only). Measures plotted by test condition (A and C) and food comparison (B and D). Error bars indicate standard errors.