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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*

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

48 Recent evidence shows that apparently small differences in experimental procedure can
49 lead to big differences in outcome. For instance, among chimpanzees, whether or not subjects
50 pass tasks designed to assess perspective taking is highly dependent on the size of the testing
51 area (Bräuer, Call, & Tomasello, 2007; Hare, Call, Agnetta, & Tomasello, 2000; Karin-D'Arcy
52 & Povinelli, 2002), the distance between the stimuli (Mulcahy & Call, 2009), and the design of
53 the procedure (Melis, Call, & Tomasello, 2006). Similarly, great apes' ability to succeed in a tool
54 use task is influenced by the placement of the tool(s) (Mulcahy & Call, 2006). Experimental
55 variables have also been shown to impact task performance in New World monkeys. After
56 observing a human experimenter hide a reward, squirrel monkeys and marmosets were better
57 able to identify the location of the hidden reward when given nine possible locations as opposed
58 to two. Apparently decreasing the probability of success by chance increased subjects'
59 motivation to pay attention in the task (Schubiger, Kissling, & Burkart, 2016). Most of the work
60 documenting the effect of procedural differences on behavioral outcomes has focused on
61 cognitive tasks, but the same appears to be true for behavioral tasks. For instance, enclosure size
62 again appears to be important in prosocial choice tasks (in cooperatively breeding primates;
63 Burkart, Fehr, Efferson, & van Schaik, 2007; Cronin, Schroeder, Rothwell, Silk, & Snowdon,
64 2009), as does whether or not the food rewards are visible (reviewed in Cronin, 2012). This is an
65 important issue for several reasons. First, failing to recognize when procedural differences are
66 influencing results negatively impacts our understanding of a given behavior, in particular by
67 creating apparent inconsistencies where none may exist. This may lead to an inappropriate
68 understanding of the distribution of a behavior or ability, or a misunderstanding of how robustly

69 an ability manifests. Moreover, it is essential to understand what factors are influencing a
70 behavior to truly understand that behavior.

71 This is also an important issue in cases in which substantial variation is seen across
72 studies. Without appropriately controlling for the experimental factors, we do not know if this
73 variation is due to individual differences among animals, if the effect itself is weak, or if there
74 are contextual factors that are influencing responses in meaningful ways that we need to better
75 understand. One area in which this may be relevant is in the study of violations of expectation. A
76 growing literature indicates that in some contexts, some species respond negatively when their
77 expectations are violated, both in the context of inequity (expectations based on another's
78 outcomes) and contrast (expectations based on one's previous outcomes). In the case of inequity,
79 nonhuman species respond negatively to receiving a lower-valued reward than a partner
80 following some form of work (e.g., exchanging a token; reviewed in Talbot, Price, & Brosnan,
81 2016). These negative responses typically include refusing to work or refusing to accept the
82 lower-valued reward and are contingent upon a social partner receiving the better rewards.
83 Negative responses to contrast also emerge when an individual receives a lower-valued reward,
84 however, they manifest when a better reward appears to be available and are based on one's own
85 expectations. However, there is substantial variation across species, across studies, and even
86 across individuals within the same studies (Talbot et al., 2016).

87 For example, chimpanzees show substantial differences both across studies and within
88 the same study, with some individuals showing strong responses to inequity and others showing
89 no response at all (reviewed in Brosnan, 2013). In fact, even in studies that do find responses to
90 inequity, we do not see responses in every individual tested (Bräuer, Call, & Tomasello, 2006,
91 2009; Brosnan, Hopper, Richey, Freeman, Talbot, ... & Schapiro, 2015; Brosnan, Schiff, & de

92 Waal, 2005; Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010; Hopper, Lambeth, Schapiro,
93 Bernacky, & Brosnan, 2013), making perhaps the most noticeable feature of this research the
94 variability of the response. Previous research has demonstrated that the responses are influenced
95 by, at minimum, rank (Brosnan et al., 2010), personality (Brosnan et al., 2015), and duration of
96 relationship (Brosnan et al., 2015; Hopper, Lambeth, Schapiro, & Brosnan, 2014). Although we
97 have the most data on chimpanzees, there is also variation in the response across capuchin
98 studies (Brosnan & de Waal, 2003; Dubreuil, Gentile, & Visalberghi, 2006; Fletcher, 2008;
99 Fontenot, Watson, Roberts, & Miller, 2007; McAuliffe, Chang, Leimgruber, Spaulding, Blake, &
100 Santos, 2015; Roma, Silberberg, Ruggiero, & Suomi, 2006; Silberberg, Crescimbene, Addessi,
101 Anderson, & Visalberghi, 2009; Takimoto & Fujita, 2011; Takimoto, Kuroshima, & Fujita,
102 2009; van Wolkenten, Brosnan, & de Waal, 2007). Among squirrel monkeys, while no
103 individuals respond negatively to inequity, there is variability among who responds negatively to
104 contrast effects (Freeman, Sullivan, Hopper, Talbot, Holmes, . . . , & Brosnan, 2013; Talbot,
105 Freeman, Williams, & Brosnan, 2011).

106 What is causing this variability? In some species, there are consistent findings that
107 suggest that we understand the variability. For instance, in squirrel monkeys, it is always the
108 males that respond negatively to contrast, and never females (Freeman et al., 2013; Talbot et al.,
109 2011). However, despite substantial effort to find differences based on sex, relationship, age,
110 personality, and other individual variables, in most cases researchers are unable to pinpoint a
111 single factor. One approach that has not yet been taken is to explore the procedural differences
112 that have been hypothesized to influence responses. A particular challenge of comparative work
113 is designing studies that are actually comparable. Across species, there is the ever-present
114 challenge of balancing procedures that are identical with those that are scaled to the species in

115 question (Pretot, Bshary & Brosnan, 2016a,b). Even within species, different populations may
116 have different preferences (even for the same foods) due to factors such as differences in
117 exposure. Moreover, differences among housing conditions may necessitate differences in
118 procedure. The former factor often varies among studies of inequity. Therefore, it may be that
119 differences in the relative magnitude or relative preference of rewards across studies, or different
120 criteria used to determine the rewards that are (presumably) expected versus received, are
121 influencing responses, despite the fact that each lab uses strict criteria to choose foods.
122 Regarding the latter, it has been previously hypothesized that how the animals are positioned
123 relative to one another influences responses (Brosnan et al., 2010). This is based on evidence
124 from human psychology studies suggesting that the spatial proximity of individuals impacts
125 social behavior (Sommer, 1965), but there is as yet no evidence in non-human species. In order
126 to test these hypotheses, we turned to capuchin monkeys, a species for which there are a
127 substantial number of studies on inequity and little understanding of why this variation occurs.

128 We first addressed the relative values of the chosen food rewards. The way in which
129 reward pairs are determined by the experimenters varies substantially across studies of inequity.
130 Most studies evaluate the quality of the rewards to the subjects on an individual basis,
131 immediately prior to testing (e.g., Brosnan & de Waal, 2003; Brosnan et al., 2010; Massen, van
132 den Berg, Spruijt, & Sterck, 2012; Neiworth, Johnson, Whillock, Greenberg, & Brown, 2009;
133 Silberberg et al., 2009; Talbot et al., 2011; van Wolkenten et al., 2007). While this rank orders
134 food values, it also is the case that different experimenters use different criteria, so it is
135 nonetheless difficult to compare relative reward differences across these studies. Moreover, in
136 other cases, researchers either used the same rewards as previous studies (Roma et al., 2006) or
137 relied on previous food preference data (Bräuer et al., 2006, 2009). Although both of these are

138 reasonable, differences in access to various food items or individuals' preferences may influence
139 subjects' valuation of rewards differently at different facilities, or at different times, or in
140 different contexts within the same facility (e.g., stimulus satiation; Hetherington, Pirie, & Nabb,
141 2002). Thus, it is important to measure each subject's current preferences in a systematic manner
142 immediately prior to testing. To do so, we used a consistent set of criteria to determine three
143 foods that varied in preference consistently across all individuals within the population.

144 Related to this, while most studies use different quality foods, often with the presumption
145 that it is easier for the subjects to distinguish visually distinct foods, it is impossible to determine
146 whether the relative preferences we obtain are at all equivalent across individuals (even if using a
147 standardized set of criteria to choose foods). Preference does not necessarily equate with value.
148 That is, you and I may both consistently choose strawberries over grapes, but for you the
149 preference may be very strong whereas for me it is not much above my indifference point. One
150 way to more accurately define reward value is cross modal scaling, in which the value of two
151 foods are compared to the value of a third, less substitutable, food (Casey, Silberberg, Paukner,
152 & Suomi, 2014; Schwartz, Silberberg, Casey, Paukner, & Suomi, 2016). Of course, when
153 possible, varying quantities of a single food type is more objective as more food is always
154 preferable to less. Many nonhuman species can differentiate different quantities (Shettleworth,
155 2009), including capuchin monkeys (Addessi, Crescimbene, & Visalberghi, 2008; Beran, Evans,
156 Leighty, Harris, & Rice, 2008; Evans, Beran, Harris, & Rice, 2009), and capuchins adjust their
157 choices to maximize the number of rewards (e.g., Brosnan, Parrish, Beran, Flemming,
158 Heimbauer, ..., & Wilson, 2011). Thus, here we compared subjects' responses to different
159 quantities of cereal, a medium-value food, which may be the most favorable for optimal
160 performance according to the Yerkes-Dodson law (Yerkes & Dodson, 1908).

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

183 condition; physical but not visual separation) to those in which they shared the enclosure (No
184 Barrier condition; no separation).

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

201 We hypothesized that the capuchins' responses would vary depending on the relative
202 difference in quality between the food items. However, because there have been no such studies,
203 we did not have any directional predictions. We also did not have a prediction for whether
204 responses would be more pronounced in either the inequity or contrast condition. Because
205 previous research has shown that capuchin monkeys are sensitive to different quantities of

206 rewards (Addressi et al., 2008; Beran et al., 2008; Brosnan et al., 2011; Brosnan et al., 2012;
207 Evans et al., 2009), we predicted that subjects would respond negatively to receiving a smaller
208 amount than anticipated. Finally, given previous inequity studies and work showing that visual
209 access influences behavioral responses in situations involving cooperation and inequity
210 (Takimoto et al., 2010), we predicted that we would see increased responses in the No Barrier
211 condition as compared to the barrier condition.

212 Method

213 Subjects

214 *Language Research Center*

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

224 Monkeys were socially housed in stable, mixed-sex social groups that had been housed
225 together for almost a decade (since July 2005 or the individual's birth, whichever came later).
226 Each social group lived in indoor/outdoor space that included climbing structures and material
227 enrichment. Primates received a diet including primate chow, fruit, and vegetables and were
228 never food deprived. Fresh running water was available *ad libitum*, including during testing

229 sessions. Subjects were tested in enclosures attached to their home cage, where all testing takes
230 place. They had been trained to voluntarily enter these enclosures for cognitive and behavioral
231 experiments. Subjects were not tested on days they chose not to enter the test enclosure, which
232 they were free to do at any time without any consequences. No subject was tested on this study
233 more than once in the same day. Monkeys were paired with individuals from their own social
234 groups for testing.

235 *National Institutes of Health*

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

250 **Food Preference Tests**

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

258 Food selection was done using a dichotomous-choice food preference test (Brosnan & de
259 Waal, 2004) in which an experimenter offered two food rewards simultaneously and the subject
260 was allowed to choose one of the two rewards by reaching out of the testing enclosure and
261 selecting the preferred item. We conducted two 10-trial sessions on different days of each of the
262 possible food pairs. Within each session, reward positions were randomized with an equal
263 number on each side (left and right). A reward was considered to be preferred if it was chosen at
264 least 80% of the time over the alternative food on both days by all test subjects. Note that this
265 required the 80% threshold on *both* sessions; a session with a 70% preference and one with a
266 90% preference did not count. This ensured consistency. Additionally, the test would not work if
267 the less-preferred item was one that the subjects will not eat under normal circumstances.
268 Therefore, to ensure that subjects were willing to eat the less-preferred food item, in a separate
269 session we presented them with 10 consecutive pieces of the lower-valued reward. If all subjects
270 did not eat all 10 pieces, that food could not be used as the least preferred food (LVR). Subjects
271 underwent a new food preference test at the beginning of each experiment. Note that we
272 conducted food preference tests for both paired qualities and paired quantities to ensure that all
273 pairings met our criterion for preference.

274 General Procedure

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

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

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

296 comparisons, only one reward was used in all conditions, in different quantities, so only one
297 reward container was present.

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

302 **Food Comparisons**

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

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

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

328 **Conditions**

329 For each comparison, pairs underwent a series of eight tests, completing two sessions of
330 each control condition (Equity and Contrast) and four total sessions of the Inequity condition,
331 with each monkey tested twice in the subject role. Each test session consisted of a series of 40
332 alternating trials so that each individual in the pair received 20 trials per session. There were
333 three conditions. The Equity condition tested the subject's response when they received the same
334 reward as their partner (the lower-valued reward of the two in the given experiment) and thus,
335 was a baseline measure. The Contrast condition examined subjects' responses to violations of
336 individual expectations. In this condition, both subjects and partners were first shown a higher-
337 valued reward, but following exchange, received the lower-valued reward. Note that the only
338 difference between this condition and the Equity condition was the attention drawn to the higher
339 valued reward before both monkeys' exchanges. Because both monkeys got the same rewards,
340 only two total sessions were required. Each monkey was the first exchanger once for each

341 condition. The Inequity condition measured subjects' responses to receiving the lower value food
342 after observing their partner receive the higher valued reward for their exchange. Each pair
343 received four tests session (twice with each monkey in the subject role; the subject was always
344 the second exchanger). The order in which each pair experienced the conditions was randomized
345 and, for all conditions, the order in which individuals were tested in the subject role (i.e., and
346 interacted with the experimenter second) was randomized and counterbalanced.

347 **Testing the Effect of a Barrier**

348 Typically, studies of inequity conducted with apes do not include a barrier between the
349 two subjects (e.g., Brosnan et al., 2005; Brosnan et al., 2010), whereas virtually all of the studies
350 with New World monkeys included a barrier between conspecifics (e.g., Cronin & Snowdon,
351 2008; Dubreuil et al., 2006; Silberberg et al., 2009; Talbot et al., 2011; van Wolkenten et al.,
352 2007; but see Freeman et al., 2013). The flexible housing at the LRC allowed us to test the effect
353 of including a barrier using the same testing enclosure for each quality and quantity comparison,
354 which held all other factors equal. After completing the full battery of sessions with a clear
355 Lexan barrier separating the subject and partner (the Barrier condition), we re-ran all of the tests
356 at the LRC without a barrier (the No Barrier condition). We chose not to counterbalance the
357 order of testing with the LRC capuchins so that their results in the Barrier condition would be
358 directly comparable to those of the NICHD capuchins.

359 **Data analysis**

360 *Refusals*

361 Refusals consisted of 58% token refusals and 42% food refusals. There was a significant
362 difference in the frequency of token and food refusals among the conditions ($\chi^2 = 12.20$, $df = 2$, p
363 $= 0.002$). However, post hoc tests were not significant (presumably due to the small samples).

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

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

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

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

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

387 *Latency to Exchange*

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

396 **Results**

397 **Quality Comparisons**

398 *Overall*

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

402 Overall, subjects were more likely to refuse in the Inequity condition compared to the
403 Equity or Contrast conditions, and this effect was the most pronounced in comparisons in which
404 a low-value food reward (LVR) was used (either in contrast to a medium-value or a high-value
405 food reward). Considering this in detail, capuchins were 9.1 times more likely to accept than to
406 refuse either the token or the food in the reference case, Equity condition of the H v L
407 comparison (i.e., the higher value of the two rewards in the comparison was present, but no one
408 received it; intercept, odds ratio $^{1/0.11}$). Subjects were 1.6 to 2.8 times more likely to refuse either
409 the token or food in the Inequity condition than in the Equity condition (main effect of condition,

410 odds ratio 2.10, 95% CI) in all comparisons except in the H vs. M comparison
411 (condition x comparison interaction). Interestingly, refusals were not higher in the Contrast
412 condition compared to the Equity condition in any comparison. In fact, for the M vs. L
413 comparison, refusals were *lower* in Contrast than in Equity (condition x comparison interaction).
414 Finally, capuchins did not differ in their rate of refusal for the H vs. L and M vs. L comparison,
415 but they refused 5.6 times less often in the H vs. M comparison (main effect of comparison, odds
416 ratio $1/0.18$).

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

426 *Barrier Conditions*

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

433 $p = .013$ (albeit without significantly impacting responses across test conditions or comparisons;
434 see next paragraph), and latency to exchange, Step 2: $\chi^2(5) = 64.70, p < .001$.

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

444 **Quantity Comparisons**

445 *Overall*

446 In the two quantity comparisons, the capuchins varied significantly among food
447 comparisons (which overlapped with population comparisons) but not test conditions in their rate
448 of refusal, $\chi^2(5) = 14.30, p = .014$ (Table 5) and in their latency to exchange, $\chi^2(5) = 15.81,$
449 $p = .007$ (Table 6).

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

456 exchange than the LRC capuchins ($M = 0.19$, $SD = 0.93$ refusals per session) in the 5 vs. 1
457 comparison (effects of comparison).

458 *Barrier Conditions*

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

462 **Discussion**

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

473 Considering these findings in more detail, capuchin monkeys were more likely to respond
474 to inequity when there was a low-value reward present (i.e., in the H vs. L and M vs. L
475 conditions) as compared to the H vs. M condition. Similarly, capuchins took longer to complete
476 token exchanges in the Inequity and Contrast conditions when a low-value reward was present,
477 as compared to conditions in which both subjects received the same reward (Equity) or both
478 rewards were relatively more preferred (i.e., in the H vs. M comparison). Given that we had

479 several different MVRs and LVRs, but subjects only refused for the LVRs, it seems unlikely that
480 this result is due to greater differences in relative value. Thus, the presence of a particularly low-
481 value food reward – but one that the subjects are willing to eat **at least** 10 times in a row in a non-
482 experimental context – appears necessary to generate responses to violations of expectations.

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

500 Intriguingly, the capuchins did not respond to violations based on different quantities, in
501 either the Inequity or Contrast conditions. This is somewhat surprising because we know that

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

521 One other possibility is that this was due to the food we chose for the quantity tests
522 (pieces of Cheerios brand cereal, an unsweetened 'o' shaped oat cereal). In the quality tests,
523 subjects never refused more preferred foods (i.e., the MVR or HVR), leading us to hypothesize
524 that the cereal pieces were too high in value for them to refuse, no matter what their partner

525 received. To provide an initial test of this hypothesis, we conducted post-hoc food preference
526 tests comparing five of the GSU monkeys' preference for one piece of cereal (the smallest
527 quantity used in this study, and therefore the most equivalent to the LVR in the quality tests) to
528 the low, medium and high value foods used with the LRC monkeys in the quality comparison.
529 Potentially supporting this hypothesis, we found that cereal pieces were of medium value, and in
530 particular, were consistently preferred over the lower value food. Thus, for future studies we
531 recommend that quantity tests be based upon a less preferred food.

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

548 Although we are certain that there are a multitude of factors influencing responses to
549 inequity, these results strongly suggest that at least some of the differences we are seeing across
550 studies are due to procedural differences. Specifically, refusals due to inequitable outcomes are
551 most likely to emerge when a low-value (but still liked) food is used. We hypothesize that
552 differences in the relative preferences of different foods may have influenced responses in
553 different studies, leading to variation in outcomes. Whereas it is often tempting to treat
554 differences in outcome across different studies as contradictory, in reality, both are providing key
555 data to help us understand the context surrounding a phenomenon. By far the most productive
556 avenue is to try to determine what key factors are influencing a response and what that tells us
557 about the nature of the behavior. By better understanding the contexts in which animals respond
558 to inequity, or show any behavior, we come closer to understanding the causes and consequences
559 of that behavior, and the specific influence of context on that animal or species.
560

561 References

- 562 Addressi, E., Crescimbene, L., & Visalberghi, E. (2008). Food and token quantity discrimination
563 in capuchin monkeys (*Cebus apella*). *Animal Cognition*, *11*, 275-282.
- 564 Addressi, E., Paglieri, F., Beran, M. J., Evans, T. A., Macchitella, L., De Petrillo, F., & Focaroli,
565 V. (2013). Delay choice versus delay maintenance: Different measures of delayed
566 gratification in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*,
567 *127*, 392-398.
- 568 Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models
569 using lme4. *Journal of Statistical Software*, *67*, 1–48.
- 570 Beran, M. J., Evans, T. A., Leighty, K. A., Harris, E. H., & Rice, D. (2008). Summation and
571 quantity judgments of sequentially presented sets by capuchin monkeys (*Cebus apella*).
572 *American Journal of Primatology*, *70*, 191-194.
- 573 Beran, M. J., Perdue, B. M., Parrish, A. E., & Evans, T. A. (2012). Do social conditions affect
574 capuchin monkeys' (*Cebus apella*) choices in a quantity judgment task? *Frontiers in*
575 *Psychology*, *3*, 492.
- 576 Bräuer, J., Call, J., & Tomasello, M. (2006). Are apes really inequity averse? *Proceedings of the*
577 *Royal Society B: Biological Sciences*, *273*, 3123–3128.
- 578 Bräuer, J., Call, J., & Tomasello, M. (2007). Chimpanzees really know what others can see in a
579 competitive situation. *Animal Cognition*, *10*, 439–448.
- 580 Bräuer, J., Call, J., & Tomasello, M. (2009). Are apes inequity averse? New data on the token-
581 exchange paradigm. *American Journal of Primatology*, *71*, 175–181.
- 582 Brosnan, S. F. (2006). Nonhuman species' reactions to inequity and their implications for
583 fairness. *Social Justice Research*, *19*, 153–185.

- 584 Brosnan, S. F. (2013). Justice and fairness related behaviors in non-human primates.
585 *Proceedings of the National Academy of Sciences of the United States of America*, 110,
586 10416–10423.
- 587 Brosnan, S. F., & De Waal, F. B. M. (2003). Monkeys reject unequal pay. *Nature*, 425, 297-299.
- 588 Brosnan, S. F., & de Waal, F. B. M. (2004). A concept of value during experimental exchange in
589 brown capuchin monkeys, *Cebus apella*. *Folia Primatologica*, 75, 317–330.
- 590 Brosnan, S. F., Hopper, L. M., Richey, S., Freeman, H. D., Talbot, C. F., Gosling, S. D., ... &
591 Schapiro, S. J. (2015). Personality influences responses to inequity and contrast in
592 chimpanzees. *Animal Behaviour*, 101, 75-87.
- 593 Brosnan, S. F., Parrish, A., Beran, M. J., Flemming T., Heimbauer, L., Talbot, C. F., Lambeth, S.
594 P., Schapiro S. J. & Wilson, B. J. (2011). Responses to the Assurance game in monkeys,
595 apes, and humans using equivalent procedures. *Proceedings of the National Academy of*
596 *Sciences*, 108, 3442- 3447.
- 597 Brosnan, S. F., Schiff, H. C., & De Waal, F. B. (2005). Tolerance for inequity may increase with
598 social closeness in chimpanzees. *Proceedings of the Royal Society of London B:*
599 *Biological Sciences*, 272, 253-258.
- 600 Brosnan, S. F., Talbot, C.F., Ahlgren, M., Lambeth, S. P., & Schapiro, S. J. (2010). Mechanisms
601 underlying responses to inequitable outcomes in chimpanzees, *Pan troglodytes*. *Animal*
602 *Behaviour*, 79, 1229-1237.
- 603 Burkart, J. M., Fehr, E., Efferson, C., & van Schaik, C. P. (2007). Other-regarding preferences in
604 a non-human primate: Common marmosets provision food altruistically. *Proceedings of*
605 *the National Academy of Sciences*, 104, 19762-19766.

- 606 Casey, A. H., Silberberg, A., Paukner, A., & Suomi, S. J. (2014). Defining reward value by
607 cross-modal scaling. *Animal Cognition*, *17*, 177-183.
- 608 Cronin, K. A. (2012). Prosocial behaviour in animals: the influence of social relationships,
609 communication and rewards. *Animal Behaviour*, *84*, 1085-1093.
- 610 Cronin, K. A., Schroeder, K. K., Rothwell, E. S., Silk, J. B., & Snowdon, C. T. (2009).
611 Cooperatively breeding cottontop tamarins (*Saguinus oedipus*) do not donate rewards to
612 their long-term mates. *Journal of Comparative Psychology*, *123*, 231-241.
- 613 Cronin, K. A., & Snowdon, C. T. (2008). The effects of unequal reward distributions on
614 cooperative problem solving by cottontop tamarins, *Saguinus oedipus*. *Animal*
615 *Behaviour*, *75*, 245-257.
- 616 Dubreuil, D., Gentile, M. S., & Visalberghi, E. (2006). Are capuchin monkeys (*Cebus apella*)
617 inequity averse? *Proceedings of the Royal Society of London B: Biological Sciences*, *273*,
618 1223-1228.
- 619 Evans, T. A., Beran, M. J., Harris, E. H., & Rice, D.F. (2009). Quantity judgments of
620 sequentially presented food items by capuchin monkeys (*Cebus apella*). *Animal*
621 *Cognition*, *12*, 97-105.
- 622 Fehr, E., & Schmidt, K. M. (1999). A theory of fairness, competition, and cooperation. *The*
623 *Quarterly Journal of Economics*, *114*, 817-868.
- 624 Fletcher, G. E. (2008). Attending to the outcome of others: Disadvantageous inequity aversion in
625 male capuchin monkeys (*Cebus apella*). *American Journal of Primatology*, *70*, 901-905.
- 626 Fontenot, M. B., Watson, S. L., Roberts, K. A., & Miller, R. W. (2007). Effects of food
627 preferences on token exchange and behavioural responses to inequality in tufted capuchin
628 monkeys, *Cebus apella*. *Animal Behavior*, *74*, 487-496.

- 629 Freeman, H. D., Sullivan, J., Hopper, L. M., Talbot, C. F., Holmes, A. N., Schultz-Darken, N.,
630 ... Brosnan, S. F. (2013). Different responses to reward comparisons by three primate
631 species. *PLoS ONE*, 8, e76297.
- 632 Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000). Chimpanzees know what conspecifics
633 do and do not see. *Animal Behaviour*, 59, 771-785.
- 634 Hetherington, M. M., Pirie, L. M., & Nabb, S. (2002). Stimulus satiation: effects of repeated
635 exposure to foods on pleasantness and intake. *Appetite*, 38, 19-28.
- 636 Hopper, L. M., Lambeth, S. P., Schapiro, S. J., Bernacky, B., & Brosnan, S. F. (2013). The
637 ontogeny of social comparisons in rhesus macaques (*Macaca mulatta*). *Journal of*
638 *Primateology*, 2, 109.
- 639 Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Brosnan, S. F. (2014). Social comparison
640 mediates chimpanzees' responses to loss, not frustration. *Animal Cognition*, 17, 1303-
641 1311.
- 642 Karin-D'Arcy, R. M., & Povinelli, D. J. (2002). Do chimpanzees know what each other see? A
643 closer look. *International Journal of Comparative Psychology*, 15, 21-54.
- 644 Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2015). lmerTest: tests for random
645 and fixed effects for linear mixed effect models (lmer objects of lme4 package). R
646 package version 2-0.
- 647 Massen, J. J., van den Berg, L. M., Spruijt, B. M., & Sterck, E. H. (2012). Inequity aversion in
648 relation to effort and relationship quality in long-tailed Macaques (*Macaca*
649 *fascicularis*). *American Journal of Primatology*, 74, 145-156.

- 650 McAuliffe, K., Chang, L. W., Leimgruber, K. L., Spaulding, R., Blake, P. R., & Santos, L. R.
651 (2015). Capuchin monkeys, *Cebus apella*, show no evidence for inequity aversion in a
652 costly choice task. *Animal Behaviour*, *103*, 65–74.
- 653 Melis, A. P., Call, J., & Tomasello, M. (2006). Chimpanzees (*Pan troglodytes*) conceal visual
654 and auditory information from others. *Journal of Comparative Psychology*, *120*, 154-162.
- 655 Mendres, K. A., & de Waal, F. B. M. (2000). Capuchins do cooperate: the advantage of an
656 intuitive task. *Animal Behaviour*, *60*, 523-529.
- 657 Mulcahy, N. J., & Call, J. (2006). How great apes perform on a modified trap-tube task. *Animal*
658 *cognition*, *9*, 193-199.
- 659 Mulcahy, N. J., & Call, J. (2009). The performance of bonobos (*Pan paniscus*), chimpanzees
660 (*Pan troglodytes*), and orangutans (*Pongo pygmaeus*) in two versions of an object-choice
661 task. *Journal of Comparative Psychology*, *123*, 304-309.
- 662 Neiworth, J. J., Johnson, E. T., Whillock, K., Greenberg, J., & Brown, V. (2009). Is a sense of
663 inequity an ancestral primate trait? Testing social inequity in cotton top tamarins
664 (*Saguinus oedipus*). *Journal of Comparative Psychology*, *123*, 10-17.
- 665 Paukner, A., Suomi, S.J., Visalberghi, E., Ferrari, P.F. (2009). Capuchin monkeys display
666 affiliation towards humans who imitate them. *Science*, *325*, 880-883.
- 667 Prétôt, L., Bshary, R., & Brosnan, S. F. (2016a). Comparing species decisions in a dichotomous
668 choice task: adjusting task parameters improves performance in monkeys. *Animal*
669 *Cognition*, *19*, 819-834.
- 670 Prétôt, L., Bshary, R., & Brosnan, S. F. (2016b). Factors influencing the different performance of
671 fish and primates on a dichotomous choice task. *Animal Behaviour*, *119*, 189-199.

- 672 R Development Core Team (2016). R: A language and environment for statistical computing.
673 Vienna, Austria: R Foundation for Statistical Computing.
- 674 Roma, P. G., Silberberg, A., Ruggiero, A. M., & Suomi, S. J. (2006). Capuchin monkeys,
675 inequity aversion, and the frustration effect. *Journal of Comparative Psychology, 120*,
676 67-73.
- 677 Schubiger, M. N., Kissling, A., & Burkart, J. M. (2016). How task format affects cognitive
678 performance: A memory test with two species of New World monkeys. *Animal*
679 *Behaviour, 121*, 33-39.
- 680 Schwartz, L. P., Silberberg, A., Casey, A. H., Paukner, A., & Suomi, S. J. (2016). Scaling reward
681 value with demand curves versus preference tests. *Animal Cognition, 19*, 631-641.
- 682 Shettleworth, S. J. (2009). Numerical competence. In *Cognition, evolution, and behavior* (2nd
683 ed., pp. 340–370). New York, NY: Oxford University Press.
- 684 Silberberg, A., Crescimbene, L., Addessi, E., Anderson, J. R., & Visalberghi, E. (2009). Does
685 inequity aversion depend on a frustration effect? A test with capuchin monkeys (*Cebus*
686 *apella*). *Animal Cognition, 12*, 505-509.
- 687 Sommer, R. (1965). Further studies of small group ecology. *Sociometry, 28*, 337-348.
- 688 Takimoto, A., Kuroshima, H., & Fujita, K. (2010). Capuchin monkeys (*Cebus apella*) are
689 sensitive to others' reward: An experimental analysis of food-choice for conspecifics.
690 *Animal Cognition, 13*, 249–261.
- 691 Takimoto, A., & Fujita, K. (2011). I acknowledge your help: Capuchin monkeys' sensitivity to
692 others' labor. *Animal Cognition, 14*, 715-725.

- 693 Talbot, C. F., Freeman, H. D., Williams, L. E., & Brosnan, S. F. (2011). Squirrel monkeys'
694 response to inequitable outcomes indicates a behavioural convergence within the
695 primates. *Biology Letters*, 7, 680–682.
- 696 Talbot, C.F., Price, S.A., Brosnan, S.F. (2016). Inequity responses in nonhuman animals. In C.
697 Sabbagh & M. Schmitt (Eds.), *Handbook of Social Justice Theory and Research* (pp.387-
698 403). New York: Springer.
- 699 van Wolkenten, M., Brosnan, S. F., & de Waal, F. B. M. (2007). Inequity responses of monkeys
700 modified by effort. *Proceedings of the National Academy of Sciences*, 104, 18854–18859.
- 701 Yerkes, R. M., & Dodson, J. D. (1908). The relation of strength of stimulus to rapidity of habit
702 formation. *Journal of comparative neurology and psychology*, 18, 459-482.
- 703

704 Table 1

705 *GLMM for Refusals in Quality Comparisons*

Variable	<i>b</i>	<i>SE</i>	95% CI	OR	OR 95% CI	<i>z</i>	<i>p</i>
<i>Fixed effects</i>							
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
<i>Random effects</i>							
Subject ID	<i>SD</i>	0.78					

706 *Note.* *N* = 6840. OR = Odds ratio. Reference categories: ^aEquity, ^bH vs. L.

707

708 Table 2

709 *GLMM for Latency to Exchange in Quality Comparisons*

Variable	<i>b</i>	<i>SE</i>	95% CI	<i>df</i>	<i>t</i>	<i>p</i>
<i>Fixed effects</i>						
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
<i>Random effects</i>						
Subject ID	<i>SD</i>	1.26				

710 *Note.* *N* = 6460. OR = Odds ratio. Reference categories: ^aEquity, ^bH vs. L.

711

712 Table 3

713 *GLMM for Refusals in Quality Comparisons in LRC Population*

Variable	<i>b</i>	<i>SE</i>	95% CI	OR	OR 95% CI	<i>z</i>	<i>p</i>
<i>Fixed effects</i>							
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
<i>Random effects</i>							
Subject ID	<i>SD</i>	0.83					

714 *Note.* *N* = 4320. OR = Odds ratio. Reference categories: ^aEquity, ^bH vs. L.

715

716

717 Table 4

718 *GLMM for Latency to Exchange in Quality Comparisons in LRC Population*

Variable	<i>b</i>	<i>SE</i>	95% CI	<i>df</i>	<i>t</i>	<i>p</i>
<i>Fixed effects</i>						
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
<i>Random effects</i>						
Subject ID	<i>SD</i>	0.40				

719 *Note.* *N* = 4151. OR = Odds ratio. Reference categories: ^aEquity, ^bH vs. L.

720

721 Table 5

722 *GLMM for Refusals in Quantity Comparisons*

Variable	<i>b</i>	<i>SE</i>	95% CI	OR	OR 95% CI	<i>z</i>	<i>p</i>
<i>Fixed effects</i>							
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
<i>Random effects</i>							
Subject ID	<i>SD</i>	1.32					

723 *Note.* *N* = 2280. OR = Odds ratio. Reference categories: ^aEquity, ^b5 vs. 1.

724

725

726 Table 6

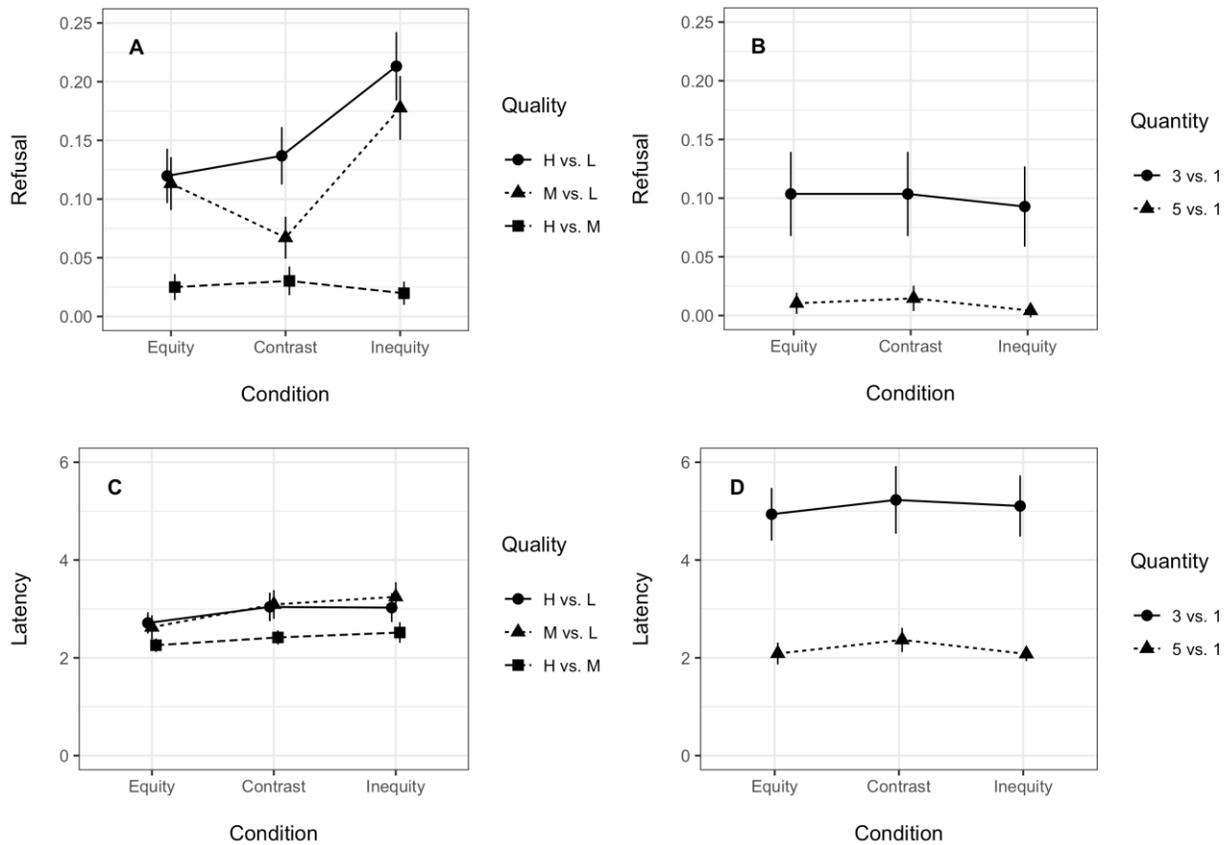
727 *GLMM for Latency to Exchange in Quantity Comparisons*

Variable	<i>b</i>	<i>SE</i>	95% CI	<i>df</i>	<i>t</i>	<i>p</i>
<i>Fixed effects</i>						
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
<i>Random effects</i>						
Subject ID	<i>SD</i>	1.20				

728 *Note.* *N* = 2201. OR = Odds ratio. Reference categories: ^aEquity, ^b5 vs. 1.

729

730



731

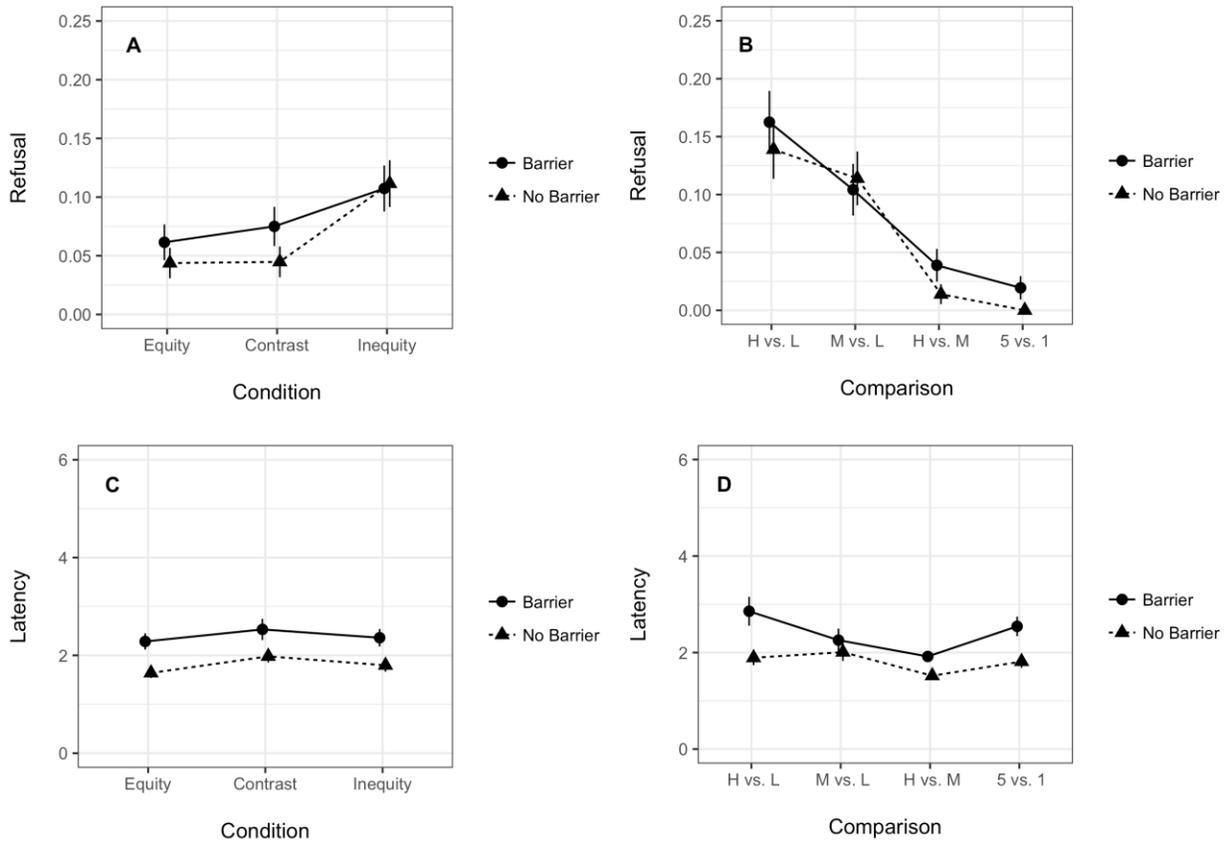
732 *Figure 1.* Mean number of refusals (A and B) and mean latency to exchange (C and D) by test condition

733 and food comparison (quality: A and C, quantity: B and D). Error bars indicate standard errors. All

734 subjects completed all quality comparisons; NIH capuchins were tested on 3 items vs. 1 item, LRC

735 capuchins on 5 items vs. 1 item.

736



737

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

741

742

743