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Sarah F. Brosnan

Georgia State University, sbrosnan@gsu.edu

Catherine Talbot

Megan Ahlgren

Susan P. Lambeth

Steven J. Schapiro

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Mechanisms underlying responses to inequitable outcomes in chimpanzees, *Pan troglodytes*

Sarah F. Brosnan^{1,2}, Catherine Talbot^{1,2}, Megan Ahlgren², Susan P. Lambeth², and Steven J. Schapiro²

¹Department of Psychology and Neuroscience Institute, Georgia State University, Atlanta, GA USA

²Michale E Keeling Center for Comparative Medicine and Research, The University of Texas M. D. Anderson Cancer Center, Bastrop, TX USA

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Correspondence should be addressed to:

Sarah F. Brosnan
Department of Psychology
Georgia State University
PO Box 5010, Atlanta, GA 30302-5010 USA
Email: sbrosnan@gsu.edu

Phone: 404-413-6301

ABSTRACT

Several species of non-human primates respond negatively to inequitable outcomes, a trait shared with humans. Despite previous research, questions regarding the response to inequity remain. In this study, we replicated the methodology from previous studies to address four questions related to inequity. First, we explored the impact of basic social factors. Second, we addressed whether negative responses to inequity require a task, or exist when rewards are given for ‘free’. Third, we addressed whether differences in the experimental procedure or the level of effort required to obtain a reward affected responses. Finally, we explored the interaction between ‘individual’ expectations (based on one’s own previous experience) and ‘social’ expectations (based on the partner’s experience). These questions were investigated in 16 socially-housed adult chimpanzees using eight conditions that varied across the dimensions of reward, effort, and procedure. Subjects did respond to inequity, but only in the context of a task. Differences in procedure and level of effort required did not cause individuals to change their behavior. Males were more sensitive to social than to individual expectation, while females were more sensitive to individual expectation. Finally, subjects also increased refusals when receiving a better reward than their partner, which has not been seen previously. These results indicate that chimpanzees are more sensitive to reward inequity than procedures, and that there is interaction between social and individual expectations that depends upon social factors.

INTRODUCTION

Humans are very sensitive to inequity. Experiments in a variety of disciplines have shown that we respond quite negatively to receiving less than a partner (Fehr & Rockenbach, 2003; Kahneman, Knetsch, & Thaler, 1986; Walster [Hatfield], Walster, & Berscheid, 1978; Zizzo & Oswald, 2001). Although these responses do vary based on factors such as one's culture (Henrich et al., 2001), the quality of the relationship between the individuals involved (Attridge & Berscheid, 1994; Clark & Grote, 2003), and one's personality (Colquitt, Scott, Judge, & Shaw, 2006; Wiesenfeld, Swann Jr., Brockner, & Bartel, 2007), the presence of this response is remarkably consistent across different groups.

Humans' ability to detect inequity may derive from an evolved characteristic shared more generally among animals, rather than being a hallmark of the human species (Brosnan, in press-b). In fact, the presence of a negative response to inequitable outcomes has been documented in two non-human primate species, capuchin monkeys and chimpanzees (*Cebus apella*: Brosnan & de Waal, 2003 ; Fletcher, 2008; van Wolkenten, Brosnan, & de Waal, 2007; *Pan troglodytes*: Brosnan, Schiff, & de Waal, 2005), as well as one non-primate species, domestic dogs (*Canus domesticus*: Range, Horn, Viranyi, & Huber, 2008). In these studies, subjects had to complete some task, after which they were offered rewards that were less preferred than those their social partners had received. Subjects often refused the rewards or refused to continue participating in the test, which was interpreted as a negative reaction to inequity.

However, as in human studies, primates do not always respond to inequity. Not all studies have found this response (e.g. Bräuer et al, 2009; see below for further

discussion), and even within studies, some individuals respond while others do not (e.g. Brosnan, Schiff & de Waal, 2005). It is difficult to determine why this variation occurs, as studies vary in methodology and other differences may exist in housing or husbandry practices that affect subjects' reactions. Nonetheless, careful comparisons make it possible to identify the factors that moderate the response. Below we summarize what is known thus far and the goals of the current study.

Basic social factors, such as rank and sex are not often predictive in measuring responses to inequity. One study investigating the response in all four species of great ape found that dominants were more likely to both ignore food and leave the experimental area than subordinates, although this behavior did not vary between the conditions of equity and inequity (Bräuer et al, 2006). However, the analysis was not done for the species separately, so it is not clear which species' responses are affected by rank. No sex differences in how primates respond to inequity have been found.

Another social factor which may affect responses to inequity is group membership. This may be caused by differences in group dynamics, colony management, etc. However, differences between groups have often been confounded with differences in methodology and procedures among studies. For instance, about half of the current studies require subjects to perform a task to get a reward, while the other half have simply handed the reward for free. This procedural difference predicts responses in the majority of cases (see below for more detail; Brosnan, in press-a). Moreover, other smaller methodological differences might also prove significant. For instance, comparing chimpanzee studies, in one set of experiments, subjects sat across from each other, interacting through a booth while isolated in separate enclosures spaced

approximately 1 meter apart (Bräuer et al, 2006; 2009), while in another set of experiments, they sat directly adjacent to each other in a shared enclosure (Brosnan et al, 2005). This represents a substantial change in social arrangement.

Despite these confounds, evidence does exist that, in chimpanzees, at least, social factors affect responses. Brosnan and colleagues (2005) found that subjects' responses varied depending on the subjects' social group membership. Since Brosnan et al's study was performed at a single facility, using the same experimenters and methodology, there were no procedural or methodological differences to confound the results. Pair-housed individuals and those from a large, multi-male, multi-female group that had been formed relatively recently (within 8 years of the study) responded to rewards which were less desirable than their partners'. However, subjects from another, similarly sized, social group that had been stable for 30 years showed no such response. Thus, it may be that some feature of these chimpanzees' social environments affected their responses (a phenomenon also known in humans; Clark & Grote, 2003), although this was confounded with the length of co-housing (length of co-housing did not affect responses in another study; Bräuer et al, 2006). Hence, one of the goals of the current study was to add to this data set using experimental procedures and arrangements which were identical to the previous study (Brosnan et al, 2005) to test additional chimpanzees from stable, long term (> 30 year) social groups.

As mentioned earlier, a great deal of evidence indicates that a task is necessary, if not sufficient, to elicit a response to inequity (Brosnan, in press-a). However, no study has appropriately tested this hypothesis. Among capuchin monkeys, responses to inequity have been found in all but one study that involved a task of some sort (Brosnan & de

Waal, 2003; Fletcher, 2008; van Wolkenten, Brosnan, & de Waal, 2007; for the exception, see Silberberg et al, 2009) and in none of the studies that did not include a task (Dindo & de Waal, 2006; Dubreuil, Gentile, & Visalberghi, 2006; Roma, Silberberg, Ruggiero, & Suomi, 2006). More importantly, three of these studies utilized the same group of capuchins (Brosnan & de Waal, 2003; Dindo & de Waal, 2006; van Wolkenten et al, 2007), which controls for between-group variability and indicates that a task is essential, if not sufficient. Tamarins are more likely to respond negatively to a low value reward when work is involved than when rewards are given for free, although this, too, was a between-subjects design (Neiworth et al., 2009). Finally, chimpanzees show the same pattern; no response to inequity has been found without a task (Bräuer et al, 2006), and the presence of a task is not sufficient to elicit the response in all groups of chimpanzees (Brosnan et al, 2005; Bräuer et al, 2009). However, in none of these studies were responses to both conditions compared within the same group of subjects. Thus, a second goal of this study is to provide a direct, within-subjects test of the hypothesis that chimpanzees respond more strongly to inequity when a task is involved than when it is not.

Related to this is the question of whether different levels of effort or procedures may also elicit an inequity response. Previous work in capuchin monkeys indicated that the requirement of greater effort exacerbated the response against unequal rewards (van Wolkenten et al, 2007), but there was not a response to the effort difference itself (van Wolkenten et al, 2007; Fontenot et al, 2007). However, no studies exist for other species. Thus, to determine the generalizability of this finding, we included several variations on

procedure and effort to determine whether varying these parameters affects responses in chimpanzees.

A final issue is the relative roles of individual versus social expectations. Primates are known to respond negatively to violations of individual expectations, in which an outcome deviates from that which was anticipated based on their own previous experience (Reynolds, 1961; Roma, Silberberg, Ruggiero, & Suomi, 2006; Tinklepaugh, 1928; Wynne, 2004). However, expectations may also be based on their *partner's* previous experience, or social expectations. In other words, the primates may respond more negatively to situations in which their partner got a better reward for completing the same task (social expectations) than to situations in which the better reward was indicated beforehand, but the lesser reward was given following the task (individual expectations). Of studies directly comparing the two, some have indicated a stronger response to social than individual responses (chimpanzees: Brosnan, Schiff, & de Waal, 2005; capuchins: van Wolkenten, Brosnan, & de Waal, 2007), while others have found no response to either (capuchins: Silberberg et al, 2009; chimpanzees: the long-term group in Brosnan, Schiff & de Waal, 2005). Thus, we replicate this comparison here using a new sample of chimpanzees to obtain additional data regarding the issue.

For the current study, we tested same-sex pairs of adult chimpanzees living in social groups ranging in size from 6 to 14 group members at a facility at which no previous work on inequity had been done. We included conditions used in previous studies (Bräuer, Call, & Tomasello, 2009; Brosnan, Schiff, & de Waal, 2005) to directly compare responses between facilities (see Methods for a complete list of conditions). We additionally included new conditions to address specific questions. First, we investigated

whether basic social factors (sex and rank) affected the response. Second, we addressed the role of a task by explicitly comparing two conditions in which rewards were inequitable, but in one, subjects completed a task (exchange) to receive them and in the other, rewards were handed to the subjects ‘for free,’ with no task required. This is the first direct test of the hypothesis that the presence of a task affects the response to inequity (Brosnan, in press-a). Related to this, we addressed whether differences in the level of effort or the procedure used by the experimenter affected chimpanzees’ responses when the material outcome was held constant. Finally, we directly compared social and individual expectations to see how these expectations interacted in the chimpanzees’ behavior. This study provides the most comprehensive test to date of the ways in which chimpanzees’ behavior is or is not altered by the presence of some aspect of inequity.

METHODS

Subjects

Subjects included 16 adult chimpanzees, 10 males and six females, housed in social groups at the Michale E. Keeling Center for Comparative Medicine and Research of The University of Texas M. D. Anderson Cancer Center, Bastrop, TX, USA (hereafter referred to as Bastrop). Six of the subjects were wild-born, six were mother-reared in captivity, and four were nursery-reared in peer groups. All subjects were housed in social groups with indoor/outdoor access and extensive environmental enrichment (climbing structures, ropes and swings, barrels, and other toys). All subjects had *ad libitum* access to primate chow and water and each group received four meals of fruits and vegetables per day, as well as additional puzzle (or occupational) enrichment with food several times per week. At no time prior to or during testing were the subjects food or water deprived.

All subjects participated voluntarily, coming when called to the indoor dens of their living areas for the experiment. Separating subjects out from their social group in this way limited distractions during the experiment.

Chimpanzees were tested in same-sex pairs with a group mate. Chimpanzees were chosen to participate in the study if they reliably separated and had a potential partner from within their social group (e.g. another individual of the same sex who also reliably separated). Since chimpanzees were not separated from their partners during the study, but shared the same den through the experiment, partnerships also had to be willing to separate with each other, which meant that all partnerships were tolerant. Partnerships were not altered during the course of the study, nor were subjects used in more than one partnership. Thus, in cases in which an odd number of chimpanzees of the same sex were available from the same social group, we chose the pair which more easily separated from the rest of the group as a pair (e.g. was the most tolerant).

One of the advantages of this population was that there had been no previous studies on inequity. The only previous related work regarded prosocial behavior, but only a quarter of our subjects had participated in these tests. Four subjects (1 male, 3 female) had participated as subjects in one or more of these previous studies on prosocial behavior (Silk et al, 2005; Vonk et al, 2008; Brosnan et al, 2009). One additional subject (female) was a partner in two of the studies (Silk et al, 2005; Vonk et al, 2008), but received no training and made no choices in any test. The remaining eleven subjects had no previous experience in any test related to prosocial behavior.

Food Preference Tests

We established food preferences of the subjects through a dichotomous-choice test between a low-value food and a high-value food (Brosnan & de Waal, 2004). To determine which foods to use, all of our subjects were given a series of these choice tests for a variety of different fruits and vegetables (e.g. grapes, apple pieces, carrot pieces, cucumber pieces, potato pieces). To determine food preferences, subjects were given 10 successive trials in which the experimenter held up one food in each hand, approximately 30 cm apart, centered on the chimpanzee. Presentation of foods alternated from left to right each trial in order to control for any side biases. Subjects could indicate their choice by gesturing to the desired food item with their hand or by moving their head in front of their preferred option (some subjects had previously been trained to use their lips rather than hands to accept food from experimenters). They always received the food they indicated as soon as they made their choice. The chosen food was considered to be the preferred one.

There were two criteria for food selection. First, each chimpanzee had to prefer the same high-value food to the same low-value food at least 80% of the time (8 of 10 trials) in two consecutive sessions to be considered for the food choice pair. Second, after the preference was established, each chimpanzee was given 10 consecutive pieces of the low-value food (in a separate session) to verify that they were willing to consume all 10 pieces of the food when no other foods were available. It was critical that subjects like the low-value food in ordinary circumstances, as otherwise they would always reject it. Ultimately, all subjects preferred a single grape to a similarly-sized piece of carrot, and would eat the carrot pieces in the separate session. Therefore, these choices were used throughout, as the high- and low-value food items, respectively.

Training

Prior to the study, all subjects had been trained to exchange an inedible token for a food reward (this food reward was not used in subsequent testing). Tokens consisted of polyvinyl chloride (PVC) pipes 20 cm in length and 1.9 cm in diameter. For an exchange interaction, the experimenter positioned herself at eye level with the subject, showed the token to the chimpanzee, and then gave it to the chimpanzee. After the chimpanzee took the token completely inside the enclosure, the experimenter held her hand outstretched, palm up, with fingertips a few inches from the caging. Upon returning the token into the experimenter's hand, the chimpanzee was given a food reward. Subjects met criterion when they returned at least 18 of 20 tokens in a single session; in practice, chimpanzees typically returned the token on all 20 trials.

Testing

Chimpanzees were tested as same sex pairs with another adult from their social group. All pairs remained the same throughout the course of testing, and no subject participated in more than one pair. All testing was done in the indoor dens that were part of the chimpanzees' living environment. The pair members shared the same den and thus were not separated from each other during the course of testing. No pair was tested more often than once per day.

Each subject underwent a series of eight tests, completing two sessions of each test in the subject role (and two additional sessions in the partner role; see below for details). The order of sessions was randomized for each pair. There were three conditions in which the actions of both individuals, the procedure, and the rewards received were the same (the ETLV, ETHV, and FC conditions, see Table 1). For these conditions, in which

each member of the pair was functionally in the subject role, each pair (instead of each individual) received two sessions of each test, and it was randomly decided which individual went first on the first session (the other went first on the second session). Thus due to these symmetrical conditions, each pair received a total of 26 test sessions, rather than 32.

Each test session consisted of 50 alternating trials between the partner and subject, so that each individual received 25 trials per test session, beginning with the partner on trial 1. Trials were separated only by the time it took the experimenter to record the response and prepare for the next trial, which was approximately 5 seconds.

In trials in which exchange was required, the chimpanzee had up to 10 seconds to accept the token and then up to 30 additional seconds to complete the exchange (the mean latency for a completed exchange was 4.37 seconds). Exchanges were considered successful if the subject returned the token to the experimenter's hand. Sharing the token with a partner, pushing the token out of the mesh (away from the experimenter's hand), or placing the token down inside the cage and ignoring it were not considered successful exchanges (see Table 2). When the token had been returned, the experimenter held it up in front of, but out of reach of, the chimpanzee, then lifted the correct reward from the container visible to both chimpanzees and gave it to the chimpanzee that had just completed the exchange. If no exchange was required, food rewards were held up in the same manner, but without the token. Subjects occasionally did not take these rewards, again either refusing to accept them, sharing them with their partner, ignoring them, or throwing them away (see Table 2). These results were considered a refusal to accept the reward.

Both reward containers (one for the low-value food and one for the high-value food) were always present, full, and in the same position, regardless of whether they were used in the session, so that the presence of either of these rewards did not cue the subject or create differences in reactions. Responses were immediately recorded on data sheets by the experimenter and all test sessions were videotaped for later analysis and coding.

Test Conditions

The goal of the experiment was to determine how different rewards and different procedures (e.g. level of effort or time delay) affect responses to inequity. In order to accomplish this, we varied 1) whether the subject and partner had to exchange for the reward, 2) which reward the subject and partner received, and 3) whether there was a delay in receiving the reward after completing the test (see Table 1 for a summary). We designed the study so that tests of different hypotheses varied on only a single one of these dimensions. However, because there were three factors involved, some of the tests varied on more than one parameter (e.g. different delay and different food rewards). We primarily discuss only those pairs in which a single factor varied, but discuss below three instances in which another comparison is included to test a specific prediction.

To test whether or not the chimpanzees responded when the other received a different reward, we included three conditions; an Inequity Test and two same-reward controls. There were no procedural differences between these tests; all individuals exchanged in every trial. For the Inequity Test (IT), both chimpanzees completed an exchange, however the subject received a low-value carrot and the partner received a high-value grape. In the Equity Test, Low Value (ETLV), both chimpanzees completed an exchange and received the low-value carrot. The Equity Test, High Value (ETHV)

was the same, except both chimpanzees received a high-value grape. To test how subjects responded when their partner got a better reward, we compared subjects' reactions in the IT to their reactions in the ETLV. To compare how partners responded when the subject got a less good reward, we compared partners' reactions in the IT to their reactions in the ETHV.

To compare social and individual expectations, we included a test which was identical to the ETLV, except that the subjects both saw a grape prior to every exchange. In this test, the Food Control (FC), both chimpanzees were shown a grape until they gestured toward it, but after completing the exchange, received a low-value carrot. Note that the FC differs from the ETLV only in the way the chimpanzees' attention was drawn to the grape; the bucket of grapes was present in the same location for every test, including the ETLV. We also compared the FC to the IT test, although these two tests differed on two dimensions, to see which reaction was stronger.

To compare the two previous methodologies, we compared the IT to the Gift Reward (GR) Test, in which the subject received a carrot and the partner a grape, but both individuals received their respective reward for 'free', without having to exchange a token beforehand. Although the GR and IT differ on two parameters (the presence of a task and the length of the interaction; exchange took 4.37 seconds on average), they are appropriate for comparing methodologies. Note also that the results from the Delay Test (10-second delay) indicate that a delay twice this long is not sufficient, alone, to cause a response.

Finally, we examined the effects of effort and procedure. In the Delay Test (DT), both individuals exchanged and received a grape (as in the ETHV), however the subject

was given a 10-second delay between returning the token and receiving their reward. The subjects' behavior in the DT could be compared to their behavior in the ETHV to see whether the addition of a delay caused changes in their response. It is also possible that a delay is not sufficient to trigger a response, but that a difference in the level of effort is. To investigate this, we developed two tests, the Differential Exchange, Low Value (DETLV), in which both chimpanzees received a carrot, but the subject received theirs for free, while the partner had to complete an exchange, and the Differential Exchange High Value (DETHV), which was identical, except that both chimpanzees received a grape. Both of these tests could be compared to the Equity Tests (e.g. compare DETLV and ETLV and compare DETHV and ETHV) to see whether the presence of an exchange caused a difference in response. These latter comparisons also differ on two parameters; there is an exchange present in some conditions, and these conditions will last somewhat longer. However the results of the DT rule out the effect of a delay alone on the chimpanzees' responses.

Dependent variables

For all conditions, the variables of interest were how the subject responded to the food and the token (if present). As discussed above, subjects could refuse to accept the token or the reward by ignoring it, refusing it, rejecting it, or sharing it (see Table 2 for definitions). Subjects who refused the token or did not complete the exchange were not given a food reward and therefore, had no opportunity to refuse to accept the reward. In conditions in which exchange was not used, only subjects' interactions with the food were measured. It is possible that these different types of refusals may indicate different levels of arousal on the part of the subjects. However, as no differences were found (see

Results for statistics), analyses were done with the types of refusals combined into a single measure.

We also measured subjects' latency to return the token as an additional measure of hesitation or change in motivation. Latency was measured from the time the chimpanzee grasped the token from the experimenter to the time the experimenter brought it fully back to the other side of the mesh. This was required as chimpanzees sometimes allowed the experimenter to grasp the distal end of the token (a piece of PVC pipe) but did not let go of their own end. Thus, the chimpanzee had to fully relinquish the token before the interaction was considered complete.

Finally, we looked at the effects of several basic social factors, including the subjects' sex and rank. All subjects were paired with same sex partners. For rank, we measured only which chimpanzee was dominant to the other in dyadic interactions with no other chimpanzee present, as these were the conditions under which the test took place. We did not attempt to quantify rank distance differences between the different partnerships.

Statistics

In order to determine whether there was variation between the conditions, omnibus Friedman's tests were run (the condition of sphericity was violated, contraindicating parametric tests). Comparisons between males and females were done using Mann-Whitney U nonparametric tests for unrelated samples. Comparisons between two conditions within a sex category were done using Wilcoxon Sign Rank nonparametric tests for related samples. For the Wilcoxon tests, some ns differ from the number of subjects due to ties. All p-values are 2-tailed.

All analyses were done on the data collected by the experimenter. One-third (33%) of the data were re-coded from the video tapes by coders blind to the hypotheses to verify its accuracy. Coders showed high agreement on whether or not an interaction resulted in a rejection (agreed on 98.5% of trials, Cohen's $\kappa = 0.87$).

RESULTS

Overall refusals

We first investigated whether there was variation between the eight conditions utilized in the experiment. Overall, subjects showed significant variation in their refusal rates across the eight conditions (Friedman's test: $\chi^2=34.955$, $df=7$, $p < 0.001$). Subjects were less likely to refuse the food than tokens (Wilcoxon signed ranks test; $T+ = 120$, $n = 16$, $p < 0.001$). Chimpanzees also showed significant variation in token rejections (only 7 conditions, as no tokens were used in the Gift Reward condition; Friedman's test: $\chi^2=23.110$, $df=6$, $p = 0.001$). Although subjects did refuse foods in some situations, there was no variation based upon only food refusals, probably due to the small sample size (Friedman's test: $\chi^2=10.068$, $df=7$, $p = 0.185$). To include both all eight conditions and all possible mechanisms of refusal, we completed all subsequent analyses using the total refusal rate.

Sex & Rank Difference

Subjects' rank did affect refusal rates. The higher ranking of the two individuals was more likely to refuse than the lower-ranking of the two (Mann-Whitney U test; $U = 90.5$, $n = 16$, $p = 0.015$).

Subjects' sex also affected results. Overall, males were more likely than females to show a reaction to inequity (Mann-Whitney U test; $U = 106$, $n = 16$, $p = 0.022$; see

Figure 1). This was manifest as different reactions to the different conditions. Males were more likely to refuse to participate in the Inequity test (IT) than the equity conditions, either involving exchange (ETLV; $T+ = 55$, $n = 10$, $p = 0.005$) or not (FC; $T+ = 40$, $n = 9$, $p = 0.038$). Males did not differ between the latter two conditions (comparing ETLV and FC; $T+ = 33.5$, $n = 9$, $p = 0.192$).

Females, on the other hand, did not respond differently to the Inequity Test (IT) condition as compared to the equity conditions (Wilcoxon Sign rank test, all $ps > 0.05$). They were, however, significantly more likely to refuse to participate in the FC than the inequity test ($T+ = 15$, $n = 5$, $p = 0.042$) and marginally more likely to refuse to participate in the FC than in the low-value equity condition ($T+ = 14$, $n = 5$, $p = 0.080$). Due to this sex difference in response in the IT condition, males and females were addressed separately in subsequent analyses, unless otherwise indicated.

Comparing task and 'gift' methodologies

Males responded to inequity only in the context of a task. They were significantly more likely to participate (e.g. refused less often) in the Gift Reward (GR) condition than in the inequity condition (IT; $T+ = 55$, $n = 10$, $p = 0.005$). Females responded only marginally differently between the two conditions ($T+ = 10$, $n = 4$, $p = 0.066$), although this similarity was because they did not often refuse in the inequity condition, not because they refused frequently in the GR condition.

Responses to procedural and effort variations

Although food differences are often used to generate inequity, differences in procedure or effort may also lead to the same outcome. Subjects did not react to the delay, refusing no more often in this condition than in the equity test (Wilcoxon Sign

rank test comparing DT to ETHV, Males: $T+ = 32.5$, $n = 9$, $p = 0.235$; Females: $T+ = 6$, $n = 4$, $p = 0.705$). Negative reactions may also increase if different tasks are required. However, chimpanzees' responses did not vary depending upon whether or not the partner had to exchange (the subject always exchanged; Wilcoxon Sign Rank test comparing ETLV and DETLV, Males: $T+ = 30$, $n = 10$, $p = 0.797$; Females: $T+ = 11.5$, $n = 5$, $p = 0.276$; comparing ETHV and DETHV; Males: $T+ = 18.5$, $n = 9$, $p = 0.084$; Females: $T+ = 6$, $n = 4$, $p = 0.713$).

Types of refusals

Males and females did not differ on their response to any of the four different types of refusals (Wilcoxon, all $p > 0.14$), thus in this case, we combined the sexes for analysis. There was an effect of refusal type (Friedman's test: $\chi^2 = 18.722$, $df = 3$, $p < 0.001$), likely due to the very low rate of sharing in both the food and token conditions. Subjects were more likely to refuse the token than a food reward (refusal: $T+ = 28$, $n = 7$, $p = 0.018$, share: $T+ = 21$, $n = 6$, $p = 0.026$, reject: $T+ = 28$, $n = 7$, $p = 0.018$, and a trend in this direction for ignore: $T+ = 25$, $n = 7$, $p = 0.063$).

Latency to refuse

We examined the latency to return the token to the experimenter (this includes only 7 conditions, because there was no task in the GR condition). There was no overall effect on latency (Friedman's test: $\chi^2 = 6.255$, $df = 2$, $p = 0.395$).

Response of the partner

We compared the refusal rate for each *partner* in the Inequity Test (IT: that is, the partner received a grape and the other chimpanzee – the subject – received a carrot) to both their refusal rates in the ETHV and their own refusal rate in the IT when they got the

lower-value carrot (e.g. were the subject, as a control for responses to different rewards in general). Subjects' refusal rates varied across these three conditions (Friedman's test: $\chi^2=18.264$, $df=2$, $p < 0.001$). Post hoc comparisons revealed that, as is expected, part of this variation was due to a higher refusal rate when individuals received a carrot in the IT (subject role) as compared to when they received a grape in the IT (partner role; $T+=76$, $n = 12$, $p = 0.004$). However, subjects receiving a grape also refused more often when their partner got a carrot as compared to when their partner also got a grape (e.g. comparing the IT partner behavior and the ETHV: $T+=95$, $n =14$, $p=0.008$). There was no difference in latency between these three conditions (Friedman's test: $\chi^2=3.500$, $df=2$, $p = 0.174$). Finally, we considered the Gift Reward condition, however only one subject ever refused the grape (she did so 4 times). Similarly, the majority of refusals by individuals in the partner role of the IT were refusals to exchange; only two subjects ever refused a grape.

DISCUSSION

Chimpanzees in this study responded to inequity between themselves and a partner, either refusing to complete the exchange task or refusing to accept the food rewards when a partner received a better food reward for completing the same task. Subjects were much more likely to refuse tokens than foods, likely because of the challenge of giving up food in one's possession. Thus, in some situations chimpanzees are basing their expectations for their own outcomes on their knowledge of the outcomes of others. These results reiterate the importance of social expectations in chimpanzees' decision-making.

Unlike in previous studies, we find a sex difference in the response to inequity. Specifically, males responded to violations of social expectations, or inequity, refusing to

complete the interaction with the experimenter when the partner received a better outcome (reward; IT) more often than when the partner got the same low-value reward (ETLV). Females, on the other hand, were more sensitive to violations of individual expectations; they did not show any difference in response when they received less than their partner (IT) as compared to situations in which both individuals received the same low-value reward (ETLV). However, they showed a significantly increased refusal rate when they and their partner were shown a high-value food rewards, but were given a low-value reward for completing the task (FC).

This sex difference, which has not been reported previously (chimpanzees: Brosnan et al, 2005; Bräuer et al, 2009; capuchins: van Wolkenten et al, 2007; tamarins: Neiworth et al, 2009), fits with chimpanzee behavior. Chimpanzee males typically spend their days together, and their interactions are characterized by extensive male-male coalitions and alliances (de Waal, 1982, 1992; Goodall, 1986). Due to these interactions, males may be sensitive to situations in which they receive less than another male. In humans, such variance is hypothesized to signal a change in one's status relative to the partner, and hence represent a threat to one's position (Lind & Tyler, 1998; Tyler & Lind, 1992), which may also be true in chimpanzees. Human males are also hypothesized to be more involved in decisions regarding justice than females (e.g. Singer et al., 2006), which could also be true in other primates, including chimpanzees.

Females, on the other hand, have a different social structure and so may have different motivations than males. Females in the wild typically forage and spend the majority of their time with only their offspring as company, and are much less engaged in

coalitions and alliances than are males (Goodall, 1986). Thus, the females may be much less focused on their rank, and the implications of different rewards for their rank.

Chimpanzees' responses also varied dependent upon their rank, with high-ranking individuals refusing more frequently than their lower-ranking partners. Higher-ranking individuals should be more accustomed to receiving the better reward, however a rank difference has been found in only one other study, and did not affect reactions between equity and inequity conditions (Bräuer et al, 2006). The absence of an effect of rank in other studies (Brosnan et al, 2005; see also studies on capuchin monkeys: van Wolkenten et al, 2007) may be because inequity was caused by the experimenter, not a conspecific. Thus, reactions may have been directed at the experimenter rather than the partner.

These results also affirm the hypothesis that reactions to inequity are more likely when a task of some sort (here, exchange) is used (Brosnan, in press-a; Neiworth et al, 2009). Chimpanzees did not respond to inequity of rewards if those rewards were simply handed to the individuals for 'free,' without a task being required. Although previous correlational data implied this relationship (see Introduction), this experiment provided the first study in which both conditions were counterbalanced within the same series of sessions in the same subjects.

There are several possible explanations for this phenomenon. A rather prosaic point is that these subjects are captive, and they routinely (often daily) receive food handouts from humans. These rewards are typically not distributed perfectly evenly (despite caregivers' best efforts), and the primates have undoubtedly learned that their actions do not affect the outcome. In fact, at the Bastrop chimpanzee facility, subjects have been trained in a procedure, cooperative feeding, designed to ensure that all animals,

including subordinates, receive a full portion of desirable foods during the four daily enrichment meals. In this procedure, dominant individuals are rewarded with extra treats for not stealing the subordinates' food (Bloomsmith, Laule, Alford, & Thurston, 1994; Schapiro, Bloomsmith, & Laule, 2003). Thus, one level of inequity is systematically created (extra treats for dominants) to avoid more excessive and variable inequity at another level (dominants stealing the food of others). Chimpanzees at the Bastrop facility are therefore already accustomed to some inequity in a situation with 'free' handouts, and thus may not expect equity (Bräuer et al, 2006).

A second possible explanation is that primates respond differently to others' rewards acquired by 'good fortune' than they do to rewards that required the effort of others to obtain. In a cooperative species, individuals who can assess their relative level of effort and reward as compared to their partners will benefit by ceasing interactions that do not provide a net benefit and continuing those that do. However, even among these species, there is no fitness benefit to reacting against other individuals' good fortune, if these benefits were not gained at one's own expense. This fits with a previous hypothesis that joint efforts require joint payoffs to be sustainable (van Wolckenten et al, 2007). It is possible that the presence of a task when other conspecifics are present triggers these joint behaviors, hence the influence of the task on inequity responses in the present set of experiments. Further tests investigating this response in cooperative versus non-cooperative situations or species may help to tease apart these two hypotheses.

This study also demonstrates that, at least under situations of moderate effort, chimpanzees respond to differences in material outcome, not differences in either procedure or the level of effort required to achieve a reward. The presence of a delay (10

seconds, DT) between the completion of the task and the receipt of the reward did not affect responses, as compared to the situation in which both chimpanzees were rewarded within the same time frame (no delay; ETHV). This delay represented what could be a frustrating inequality in the procedure used to distribute the rewards. However, this condition also involved high-value food items, which may have ameliorated the chimpanzees' reactions. Moreover, 10 seconds may not have been a sufficient delay; it is well within the capabilities of chimpanzees to delay gratification for this period of time in experimental (Beran & Evans, 2006; Dufour, Sterck, Pele, & Theirry, 2007) and natural (e.g. meat sharing, Gomes & Boesch, 2009) situations.

The chimpanzees also responded similarly when their partner got the same reward as they did for 'free' versus when both individuals had to exchange to receive the reward (e.g. DETLV vs ETLV and DETHV vs ETHV). These data are in accord with those from capuchin monkeys, who do not respond to differences in effort only (van Wolkenten, Brosnan, & de Waal, 2007; Fontenot et al, 2007). Thus, this study, taken with previous work on capuchins, provides strong evidence that effort differentials alone are not sufficient to trigger a response to inequity, either in chimpanzees or, more broadly, among primates.

We unexpectedly found that chimpanzees were more likely to refuse a high-value grape when their partner got a lower-value carrot than when their partner also received a grape. This is quite interesting in light of the current debate in the literature regarding the role of prosocial preferences in primates' behavior. Focusing only on chimpanzees, several studies explicitly designed to look for prosocial preferences in chimpanzees have found no evidence that chimpanzees behave in ways that benefit their partners, even

when it costs them nothing (Jensen, Hare, Call, & Tomasello, 2006; Silk et al., 2005; Vonk et al., 2008; prosocial preferences have been found in similar experimental designs in capuchin monkeys, Lakshminarayanan & Santos, 2008; de Waal et al, 2008, Takimoto et al, 2009, and marmosets, Burkart et al, 2007, but not tamarins, Cronin et al, 2009). However, chimpanzees do provide helping behavior in non-food related situations (Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Warneken & Tomasello, 2006; Yamamoto & Tanaka, 2009). Thus it has been argued that chimpanzees do not show prosocial preferences in the context of food rewards, due to the inherent competition (Warneken et al, 2007).

Nonetheless, this paper provides the first experimental evidence that chimpanzees respond behaviorally to receiving more food than a conspecific partner. In the current study, chimpanzees who received a higher-value grape refused to participate more often when the other chimpanzee received an inferior carrot (e.g. IT subject) than they did when the other chimpanzee also received a grape (e.g. ETHV). This reaction was not seen in previous studies of inequity in primates, either among chimpanzees (Brosnan et al, 2005) or capuchin monkeys (Brosnan & de Waal, 2003; van Wolkenten et al, 2007). These results do not indicate what motivations underlay this behavior; their response may have been due to prosocial motivations, but may also have resulted from concern over accepting a higher-value reward in the presence of a conspecific (e.g. potential retaliation).

Responses to inequity have now been investigated in four studies utilizing three different colonies of chimpanzees (see Table 3 for details of each study). Based on this, it is clear that the reaction to inequity is quite variable, both between and within groups.

This is not a surprise, as this variability is also found for other social behaviors in primates (e.g. prosocial behavior: Silk et al, 2005; Warneken et al, 2007; Jensen et al, 2006; social learning: Frigaszy & Visalberghi, 1996; Bonnie & de Waal, 2007). Several possibilities are emerging as potential mediators. First, the physical arrangement of the subjects may affect social interactions. Moreover a task is apparently necessary (if not sufficient). Finally, the length of time that the social group has been stable does not appear to be related to subjects' responses. However, this is a coarse measure of social group dynamics, and further studies investigating the effect of relationships in more detail are required.

The response to inequity appears to be widely present in chimpanzees. However, there is variability in the response, likely due to both procedural factors involved in the experiments and socio-ecological factors like sex, rank, and relationship quality. Such variability, found in other social behaviors as well, highlights the flexibility of chimpanzee social cognition, and the importance of studying a large and diverse sample of chimpanzees. We further demonstrate the necessity of a task in eliciting a response to social expectations. However, differences in either the procedure or the amount of effort required to receive a reward do not elicit responses to inequity. Finally, we find that chimpanzees are sensitive to overcompensation, or receiving a greater reward, as well as undercompensation, or receiving a lesser one. This indicates that social expectations can be both positive and negative, and provides the first evidence of behavior consistent with prosocial outcomes in a food-related experimental task in chimpanzees. It seems likely that this sensitivity to social expectations evolved in the context of sociality, and may be found in a wide variety of other cooperative species.

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1 FIGURE CAPTIONS

2 **Figure 1:** The percent of total refusals (combining refusals to return the token and
3 refusals to accept the food reward) for chimpanzees in each of the 8 conditions, divided
4 by sex (males are hatched bars, females are solid bars). Significant differences between
5 males and females in an individual condition are indicated by asterisks below the x-axis.
6 Males were much more likely to refuse to complete the interaction in the Inequity test, in
7 which their partner got a better reward, than in either of the control tests in which their
8 partner received the same reward (ETLV and ETHV) or the test in which they saw the
9 better reward but received the lower value one (FC). Males also did not respond to
10 unequal rewards when no task was used (GR). Significance indicated by solid horizontal
11 bar; differences are significant at the $p < 0.05$ level from the IT, indicated by a bold
12 hatch. Females were much more likely to refuse to complete the interaction in the Food
13 Control test (FC), in which they were initially shown a high value reward, but received a
14 lower-value one upon completing the exchange, a response consistent with violation of
15 expectations. Significance indicated by dotted horizontal bar; differences are significant
16 at the $p < 0.05$ level from the FC, indicated by a bold hatch. For a description of the
17 conditions, see Table 1.

18

19 **Figure 2:** The percent of total refusals (combining refusals to return the token and
20 refusals to accept the food reward) for chimpanzees in each of the 8 conditions, broken
21 down by the four types of refusals (see Table 2 for more details on these refusals).
22 Overall, sharing was the least common form of refusal, and tokens were refused much
23 more often than was food. For a description of the conditions, see Table 1.

Table 1: Description of experimental conditions.

Abbreviation	Condition Name	Exchange	Food	Description
<i>ETLV</i>	Equity test, low value	Both exchange	Both low value (carrot)	Both subject and partner exchanged for low value reward.
<i>ETHV</i>	Equity test, high value	Both exchange	Both high value (grape)	Both subject and partner exchanged for high value reward.
<i>FC</i>	Food control	Both exchange	Both see high value (grape) before exchange, receive low value (carrot) following exchange	Prior to exchange, high value reward is held in front of exchanger and then is placed back in container. After successful completion of exchange, exchanger receives low value reward.
<i>IT</i>	Inequity test	Both exchange	Subject low value (carrot) Partner high value (grape)	Partner exchanges for high value reward and subject exchanges for low value reward.
<i>GR</i>	Gift reward	NO exchange	Subject low value (carrot) Partner high value (grape)	Partner is given a high value reward for 'free' (e.g. without exchange) and then subject is given a low value reward.
<i>DT</i>	Delay test	Both exchange, subject waits 10 sec after exchange before receiving food	Both high value (grape)	Partner exchanges for a high value reward and subject exchanges and must wait 10 seconds before receiving high value reward.
<i>DETLV</i>	Differential exchange test, low value	Subject exchanges Partner does not exchange	Both low value (carrot)	Partner is given a low value reward for 'free' (e.g. without exchange) and subject must exchange for a low value reward.
<i>DETHV</i>	Differential exchange test, high value	Subject exchanges Partner does not exchange	Both high value (grape)	Partner is given a high value reward for 'free' (e.g. without exchange) and subject must exchange for a high value reward.

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Table 2: Description of dependent variables for returning the tokens and accepting the rewards.

<i>Chimpanzee Behavior</i>	<i>Token Variables</i>	<i>Reward Variables</i>
Refuse	Does not accept token w/in 10 seconds	Does not accept food w/in 5 seconds
Ignore	Does not return token w/in 30 seconds	Does not eat food for 30 seconds
Share	Allows partner to take token (no protest)	Allows partner to take food (no protest)
Reject	Push out token	Push away food

Table 3: Comparison of previous studies of inequity completed at Yerkes (Brosnan et al, 2005), Leipzig (Bräuer et al 2006; 2009), and Bastrop (current study).

	Yerkes			Leipzig		Bastrop	
	<i>Long-term</i>	<i>Short-term</i>	<i>Pair-housed</i>	<i>Bräuer et al 2006</i>	<i>Bräuer et al 2009</i>	<i>Males</i>	<i>Females</i>
Group stability (years)	30	8	Variable	6	6+*	30+	
Social group	Multi-male, multi-female		Pair-housed	Multi-male, multi-female		Multi-male, multi-female	
Individuals tested	1M, 9F	4M, 2F	2M, 2F	13, sex not reported	2M, 4F	10M, 6F	
Tests	ETLV, IT, FC			ETLV, ETHV, IT	ETLV, IT	ETLV, ETHV, FC, IT, GR, DT, DETLV, DETHV	
Task?	Exchange			No	Exchange	Exchange	
Orientation	Side-by-side			Across#	Across#	Side-by-side	
Physically interact?	Yes			No (separated)#	No (separated)#	Yes	
Social contrast	No	Yes	Yes	No	No	Yes	No
Individual contrast	No	No	No	No	No	No	Yes
Effect of rank	No	No	No	Yes&	No	Yes	Yes

38 LITERATURE CITED

- 39 Attridge, M., & Berscheid, E. (1994). Entitlement in romantic relationships in the United
40 States. In M. J. Lerner & G. Mikula (Eds.), *Entitlement and the affectional bond:
41 justice in close relationships*. New York: Plenum.
- 42 Beran, M. J., & Evans, T. A. (2006). Maintenance of delay of gratification by four
43 chimpanzees (*Pan troglodytes*): The effects of delayed reward visibility,
44 experimenter presence, and extended delay intervals. *Behavioural Processes*, 73,
45 315-324.
- 46 Bloomsmith, M. A., Laule, G. E., Alford, P. L., & Thurston, R. H. (1994). Use of training
47 to moderate chimpanzee aggression during feeding. *Zoo Biology*, 13(6), 557-566.
- 48 Bonnie, K., & de Waal, F. B. M. (2007). Copying without rewards: socially influenced
49 foraging decisions among brown capuchin monkeys. *Animal Cognition*.
- 50 Bräuer, J., Call, J., & Tomasello, M. (2006). Are apes really inequity averse? *Proc. R.
51 Soc. Lond. B*, 273, 3123-3128.
- 52 Bräuer, J., Call, J., & Tomasello, M. (2009). Are apes inequity averse? New data on the
53 token-exchange paradigm. *American Journal of Primatology*, 7, 175-181.
- 54 Brosnan, S. F. (in press-a). The Evolution of Inequity. In D. Houser & K. McCabe (Eds.):
55 Elsevier.
- 56 Brosnan, S. F. (in press-b). Responses to inequity in nonhuman primates. In P. W.
57 Glimcher, C. Camerer, E. Fehr & R. Poldrack (Eds.), *Neuroeconomics: Decision
58 making and the brain*: Elsevier.
- 59 Brosnan, S. F., & de Waal, F. B. M. (2003). Monkeys reject unequal pay. *Nature*, 425,
60 297-299.

- 61 Brosnan, S. F., & de Waal, F. B. M. (2004). Socially learned preferences for
62 differentially rewarded tokens in the brown capuchin monkey, *Cebus apella*.
63 *Journal of Comparative Psychology*, *118*(2), 133-139.
- 64 Brosnan, S. F., Schiff, H. C., & de Waal, F. B. M. (2005). Tolerance for inequity may
65 increase with social closeness in chimpanzees. *Proc. R. Soc. Lond. B*, *1560*, 253-
66 258.
- 67 Brosnan, S. F., Henrich, J., Mareno, M. C., Lambeth, S., Schapiro, S., & Silk, J. B.
68 (2009). Chimpanzees (*Pan troglodytes*) do not develop contingent reciprocity in
69 an experimental task. *Animal Cognition*. DOI 10.1007/s10071-009-0218-z
- 70 Burkart, J., Fehr, E., Efferson, C., & van Schaik, C. P. (2007). Other-regarding
71 preferences in a non-human primate: Common marmosets provision food
72 altruistically. *Proceedings of the National Academy of Sciences*, *104*(50), 19762-
73 19766.
- 74 Clark, M. S., & Grote, N. K. (2003). Close Relationships. In T. Millon & M. J. Lerner
75 (Eds.), *Handbook of psychology: Personality and social psychology* (Vol. 5, pp.
76 447-461). New York: John Wiley & Sons.
- 77 Colquitt, J. A., Scott, B. A., Judge, T. A., & Shaw, J. C. (2006). Justice and personality:
78 using integrative theories to derive moderators of justice effects. *Organizational*
79 *Behavior and Human Decision Processes*, *100*, 110-127.
- 80 Cronin, K. A., Schroeder, K. K. E., Rothwell, E. S., Silk, J. B., & Snowdon, C. (2009).
81 Cooperatively breeding cottontop tamarins (*Saguinus oedipus*) do not donate
82 rewards to their long-term mates. *Journal of Comparative Psychology*, *123*(231-
83 241).

- 84 de Waal, F. B. M. (1982). *Chimpanzee Politics: Power and sex among apes*. Baltimore:
85 The Johns Hopkins University Press.
- 86 de Waal, F. B. M. (1992). Coalitions as part of reciprocal relations in the Arnhem
87 chimpanzee colony. In A. H. Harcourt & F. B. M. de Waal (Eds.), *Coalitions and*
88 *Alliances in Humans and Other Animals* (pp. 233-258). Oxford: Oxford
89 University Press.
- 90 de Waal, F. B. M., Leimgruber, K., & Greenberg, A. (2008). Giving is self-rewarding for
91 monkeys. *Proceedings of the National Academy of Sciences*, *105*, 13685-13689.
- 92 Dindo, M., & De Waal, F. B. M. (2006). Partner effects on food consumption in brown
93 capuchin monkeys. *American Journal of Primatology*, *69*, 1-6.
- 94 Dubreuil, D., Gentile, M. S., & Visalberghi, E. (2006). Are capuchin monkeys (*Cebus*
95 *apella*) inequity averse? *Proc. R. Soc. Lond. B*, *273*, 1223-1228.
- 96 Dufour, V., Sterck, E. H. M., Pele, M., & Theirry, B. (2007). Chimpanzee (*Pan*
97 *troglydytes*) anticipation of food return: coping with waiting time in an exchange
98 task. *Journal of Comparative Psychology*, *121*(2), 145-155.
- 99 Fehr, E., & Rockenbach, B. (2003). Detrimental effects of sanctions on human altruism.
100 *Nature*, *422*, 137-140.
- 101 Fletcher, G. E. (2008). Attending to the outcome of others: Disadvantageous inequity
102 aversion in male capuchin monkeys (*Cebus apella*). *American Journal of*
103 *Primatology*, *70*, 901-905.
- 104 Fontenot, M. B., Watson, S. L., Roberts, K. A., & Miller, R. W. (2007). Effects of food
105 preferences on token exchange and behavioural responses to inequality in tufted
106 capuchin monkeys, *Cebus apella*. *Animal Behavior*, *74*, 487-496.

- 107 Fragaszy, D. M., and Visalberghi, E. (1996). Social learning in monkeys: primate
108 "primacy" reconsidered. In a. B. G. G. J. C. M. Heyes (Ed.), *Social Learning in*
109 *Animals: The Roots of Culture* (pp. 65-84). San Diego: Academic Press, Inc.
- 110 Gomes, C. M., & Boesch, C. (2009). Wild chimpanzees exchange meat for sex on a long-
111 term basis *PLoS ONE*, 4(4), e5116.
- 112 Goodall, J. (1986). *The Chimpanzees of Gombe*. Cambridge, Massachusetts: The Belknap
113 Press of Harvard University Press.
- 114 Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., et al. (2001). In
115 search of Homo Economicus: Behavioral experiments in 15 small-scale societies.
116 *American Economic Review*, 91, 73-78.
- 117 Jensen, K., Hare, B., Call, J., & Tomasello, M. (2006). What's in it for me? Self-regard
118 precludes altruism and spite in chimpanzees. *Proc. R. Soc. Lond. B*, 273, 1013-
119 1021.
- 120 Kahneman, D., Knetsch, J. L., & Thaler, R. (1986). Fairness as a constraint on profit
121 seeking: entitlements in the market. *The American Economic Review*, 76, 728-
122 741.
- 123 Lakshminarayanan, V., & Santos, L. R. (2008). Capuchin monkeys are sensitive to
124 others' welfare. *Current Biology*, R999-R1000.
- 125 Lind, E. A., & Tyler, T. R. (1998). *The social psychology of procedural justice*. New
126 York: Plenum.
- 127 Mundry, R., & Fischer, J. (1998). Use of statistical programs for nonparametric tests of
128 small samples often leads to incorrect P values: examples from Animal
129 Behaviour. *Animal Behaviour*, 56, 256-259.

- 130 Neiworth, J. J., Johnson, E. T., Whillock, K., Greenberg, J., & Brown, V. (2009). Is a
131 sense of inequity an ancestral primate trait? Testing social inequity in cotton top
132 tamarins (*Saguinus oedipus*). *Journal of Comparative Psychology*, *123*(1), 10-17.
- 133 Range, F., Horn, L., Viranyi, Z., & Huber, L. (2008). The absence of reward induces
134 inequity aversion in dogs. *PNAS*.
- 135 Reynolds, G. S. (1961). Behavioral Contrast. *Journal of the Experimental Analysis of*
136 *Behavior*, *4*, 441-466.
- 137 Roma, P. G., Silberberg, A., Ruggiero, A. M., & Suomi, S. J. (2006). Capuchin monkeys,
138 inequity aversion, and the frustration effect. *Journal of Comparative Psychology*,
139 *120*(1), 67-73.
- 140 Schapiro, S. J., Bloomsmith, M. A., & Laule, G. E. (2003). Positive reinforcement
141 training as a technique to alter nonhuman primate behavior: Quantitative
142 assessments of effectiveness. *Journal of Applied Animal Welfare Science*, *6*(3),
143 175-187.
- 144 Silberberg, A., Crescimbene, L., Addessi, E., Anderson, J. R., & Visalberghi, E. (2009).
145 Does inequity aversion depend on a frustration effect? A test with capuchin
146 monkeys (*Cebus apella*). *Animal Cognition*, *12*(3), 505-509.
- 147 Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., et al.
148 (2005). Chimpanzees are indifferent to the welfare of unrelated group members.
149 *Nature*, *437*, 1357-1359.
- 150 Singer, T., Seymour, B., O'Doherty, J. P., Stephan, K. E., Dolan, R. J., & Frith, C. D.
151 (2006). Empathetic neural responses are modulated by the perceived fairness of
152 others. *Nature*, *439*, 466-469.

- 153 Takimoto, A., Kuroshima, H., & Fujita, K. (2009). Capuchin monkeys (*Cebus apella*) are
154 sensitive to others' reward: an experimental analysis of food-choice for
155 conspecifics. *Animal Cognition*.
- 156 Tinklepaugh, O. L. (1928). An experimental study of representative factors in monkeys.
157 *Journal of Comparative Psychology*, 8, 197-236.
- 158 Tyler, T. R., & Lind, E. A. (1992). A relational model of authority in groups. In M.
159 Zanna (Ed.), *Advances in experimental social psychology*. New York: Academic
160 Press.
- 161 Tyler, T. R., & Smith, H. J. (1990). Social justice and social movements. In *Handbook of*
162 *Social Psychology* (pp. 595-629).
- 163 van Wolkenten, M., Brosnan, S. F., & de Waal, F. B. M. (2007). Inequity responses in
164 monkeys modified by effort. *Proceedings of the National Academy of Sciences*,
165 *104*(47), 18854-18859.
- 166 Vonk, J., Brosnan, S. F., Silk, J. B., Henrich, J., Richardson, A. S., Lambeth, S., et al.
167 (2008). Chimpanzees do not take advantage of very low cost opportunities to
168 deliver food to unrelated group members. *Animal Behaviour*, *75*(5), 1757-1770.
- 169 Walster [Hatfield], E., Walster, G. W., & Berscheid, E. (1978). *Equity: Theory and*
170 *research*. Boston: Allyn and Bacon.
- 171 Warneken, F., Hare, B., Melis, A. P., Hanus, D., & Tomasello, M. (2007). Spontaneous
172 altruism by chimpanzees and young children. *PLoS Biology*, *5*(7), e184.
- 173 Warneken, F., & Tomasello, M. (2006). Altruistic helping in human infants and young
174 chimpanzees. *Science*, *311*, 1301-1303.

- 175 Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., et al.
176 (1999). Cultures in chimpanzees. *Nature*, 399, 682-685.
- 177 Wiesenfeld, B. M., Swann Jr., W. B., Brockner, J., & Bartel, C. A. (2007). Is more
178 fairness always preferred? Self-esteem moderates reactions to procedural justice.
179 *Academy of Management Journal*, 50(5), 1235-1253.
- 180 Wynne, C. D. L. (2004). Fair refusal by capuchin monkeys. *Nature*, 428, 140.
- 181 Yamamoto, S. & Tanaka, M. (2009). How did altruism and reciprocity evolve in
182 humans?: perspectives from experiments on chimpanzees (*Pan troglodytes*).
183 *Journal of Interaction Studies* 10(2): 150-182.
- 184 Zizzo, D. J., & Oswald, A. (2001). Are people willing to pay to reduce other's incomes?
185 *Annales d'Economie et de Statistique*, 63-64, 39-62.