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Social comparison mediates chimpanzees' responses to loss, not frustration

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Abstract

Why do chimpanzees react when their partner gets a better deal than them? Do they note the inequity or do their responses reflect frustration in response to unattainable rewards? To tease apart inequity and contrast, we tested chimpanzees in a series of conditions that created loss through individual contrast, through inequity, or by both. Chimpanzees were tested in four social and two individual conditions in which they received food rewards in return for exchanging tokens with an experimenter. In conditions designed to create individual contrast, after completing an exchange, the chimpanzees were given a relatively less-preferred reward than the one they were previously shown. The chimpanzees' willingness to accept the less-preferred rewards was independent of previously offered foods in both the social and individual conditions. In conditions that created frustration through inequity, subjects were given a less-preferred reward than the one received by their partner, but not in relation to the reward they were previously offered. In a social context, females were more likely to refuse to participate when they received a less-preferred reward than their partner (disadvantageous inequity), than when they received a more-preferred

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reward (advantageous inequity). Specifically, the females' refusals were typified by refusals to exchange tokens rather than refusals to accept food rewards. Males showed no difference in their responses to inequity or individual contrast. These results support previous evidence that some chimpanzees' responses to inequity are mediated more strongly by what others receive than by frustration effects.

Keywords

Chimpanzee; Inequity; Frustration; Individual contrast; Social contrast

Introduction

Primates are extremely sensitive to available food in the environment, and become frustrated if those foods do not meet their expectations. Primates (and other species) respond to such contrast by rejecting food items if they are less than anticipated (in quantity or quality, e.g., Tinklepaugh 1928; Brosnan et al. 2010) and attempt to acquire the best food available in their environment when they are able to (Hopper et al. 2013b; Sheskin et al. 2014; van Leeuwen et al. 2013). It also appears that primates prefer an option that is not framed as a loss, even if the ultimate outcome is the same (Chen et al. 2006; although see Silberberg et al. 2008). Such aversion to losses has long been studied in the human literature under the rubric of 'loss aversion.' Humans attempt to negate personal losses, because reductions in wealth result in greater dissatisfaction as compared to the satisfaction from receiving equivalent gains (i.e., loss aversion, Rabin and Thaler 2001; Tom et al. 2007). Although studies of loss aversion with nonhuman primates are not truly comparable to loss aversion studies conducted with humans (animals in these studies risk no personal loss, as every choice results in a gain of some sort, while human studies always involve an actual loss; e.g., Tversky and Kahneman 1991), these data reinforce that primates experience frustration independent of whether their outcome represents an absolute gain. Beyond this, more recent evidence indicates that some primates are also sensitive to their partner's outcomes, at least under some circumstances (reviewed in Price and Brosnan 2012). This 'social contrast' effect indicates that, in at least some cases, primates' expectations may be formed by what they see others receive (i.e., inequity aversion, Brosnan 2013).

Previous research has explored how primates responded to social contrast (inequity) and individual contrast (frustration resulting from loss) separately, in a context in which they must work to earn rewards (e.g., with a token exchange task, Brosnan and de Waal 2003; Brosnan et al. 2010). In a typical token exchange test with nonhuman primates, the experimenter takes turns exchanging tokens with both the subject and their partner across a series of trials, but always commences with the partner, so that the subject has observed the rewards given to the partner before they participate themselves. To test for inequity, the partner is given a highly preferred food reward for each completed token exchange, while the subject receives less-preferred food rewards for doing so. If sensitive to inequity, the subject's responses are typified by refusing to continue exchanging or rejecting the food reward offered to them (Brosnan 2011). In a separate condition, designed to create frustration, and test for individual contrast, prior to each of their exchanges with the

experimenter, the partner and subject are each shown a more-preferred food reward but, after they exchange, are given a less-preferred reward. As both individuals receive the lesser-value reward, the situation is not inequitable, but the rewards they are given differ from those originally offered (and therefore, expected by both animals). This condition is essential in order to verify that in the test of inequity, any response by the subject is due to what their partner received, rather than simply the frustration arising from being shown a more-preferred food reward that is then not provided (e.g., Roma et al. 2006; Bräuer et al. 2009; Silberberg et al. 2009). For chimpanzees, whether they respond most strongly to individual contrast or inequity appears to be highly dependent on the social and environmental context (Brosnan et al. 2005, 2010; Hopper et al. 2013b; Bräuer et al. 2009).

One critical component of previous studies of inequity that has been neglected so far is how chimpanzees respond when inequity and individual contrast co-occur. In the present study, we addressed precisely this. By creating both contrast and inequity simultaneously, our first aim was to tease apart which more strongly drives chimpanzees' responses to loss. Our second aim was to distinguish between the chimpanzees' responses to disadvantageous inequity (receiving a less-preferred reward than a social partner) compared to advantageous inequity (receiving a more-preferred reward than a social partner; Brosnan and de Waal 2012). In both humans and nonhuman primates, responses to disadvantageous inequity emerge in the first 2 years of life (Sloane et al. 2012; Hopper et al. 2013a). In contrast, responses to advantageous inequity appear not to develop in children until around 8 years of age (Blake and McAuliffe 2011; House et al. 2012). While responses to advantageous inequity have been studied in humans, far less is known about nonhuman primates' responses to receiving a more-preferred reward than their social partner (Brosnan et al. 2010), so a more detailed investigation is required. Thirdly, by also testing the chimpanzees individually, we investigated loss in an asocial context to determine the relative impact of individual contrast effects independently from any comparison with a partner.

We predicted that if chimpanzees are more sensitive to disadvantageous inequity than to frustration arising from individual contrast, they should respond more strongly to receiving a lower value reward than their partner, irrespective of whether there is a discrepancy between what the experimenter showed them initially and their final outcome. However, if they are more sensitive to individual outcomes (i.e., individual contrast), chimpanzees should respond more strongly to individual losses than to a situation in which the partner's outcome is superior (i.e., disadvantageous inequity), but there is no loss. Also, if chimpanzees are sensitive to individual outcomes, subjects should respond more strongly to a loss than to a stable outcome when tested alone. Accordingly, we included six conditions (four social, two asocial) to explore the decision making that underlies responses to such uncertain reward payoffs. Finally, by considering the chimpanzees' responses across conditions, when tested both as the subject and as the test partner, we compared their responses to advantageous inequity versus disadvantageous inequity.

Methods

Ethical statement

This study was conducted at the Michale E. Keeling Center for Comparative Medicine and Research, UT MD Anderson Cancer Center, USA. UT MD Anderson is fully accredited by the Association for the Assessment and Accreditation of Laboratory Animal Care-International and approval for the chimpanzee study was gained from the Institutional Animal Care and Use Committee (IACUC approval number: 07-92-03887) of UT MD Anderson. All the chimpanzees participated voluntarily in the study; each day the experimenter would call the chimpanzees into one of the indoor dens of their enclosure and only those animals that chose to come in for testing were studied that day. At all other times, the chimpanzees lived in social groups that had access to large, highly enriched indoor/outdoor enclosures. During test sessions, as at all other times, chimpanzees had ad libitum access to water and primate chow. Additionally, outside of test sessions, the chimpanzees were fed three meals of fresh produce every day.

Subjects

The subjects were 18 socially housed chimpanzees (eight males, ten females) who averaged 31.8 years of age (range 17–49 years). The chimpanzees were tested in nine unique pairs comprised of familiar cagemates (four female–female pairs, three male–male pairs and two male–female pairs). The 18 subjects were a subset of members of six social groups ($N_{\text{total}} = 33$ chimpanzees, average group size = 5.5 chimpanzees), such that six of the nine pairs lived in three groups (two pairs per group) and the remaining three pairs lived in the additional three groups (one pair per group). The specific subjects were selected from the total population of these six groups because they represented animals that were comfortable both being tested in a pair with their test partner and individually for their ‘solo’ tests (see the Procedure below for details of the testing conditions). Each test pair was unique, so each chimpanzee was only tested with one partner (c.f. Brosnan et al. 2010; Hopper et al. 2013b). The selected pairs were comprised of individuals who had lived with their test partner for an average of 11 years (range 1–30 years). Six of these chimpanzees (two females, four males) had been previously tested in a study of inequity and social contrast (Brosnan et al. 2010—see the electronic supplementary materials for more details about the consistency of these animal’s responses over time).

Procedure

Following Brosnan et al. (2010), the chimpanzees exchanged a PVC token with the experimenter in order to gain a food reward. The food rewards given were either high or medium value. Value had been previously determined using forced-choice food preference tests run with all chimpanzees prior to the testing (described next). In every condition, prior to each exchange, each chimpanzee was first shown, but not given, a food reward of either high or medium value (depending on the condition). All testing took place in the chimpanzees’ familiar indoor home enclosures. Moreover, when chimpanzees were tested in the paired conditions, both chimpanzees were tested in the same den with no barrier between them, such that they were positioned side-by-side next to one another, both facing the experimenter, and could easily see the food offered to one another, as well as their partner’s

responses. At the beginning of a test session, the chimpanzees were called into one of their inside dens by the experimenter, with whom they were familiar and had a positive relationship. Only if the chimpanzees voluntarily came in would a test session be run; if not, the experimenter tried again the following day. During tests, these pairs did not have visual access to the rest of their group. Each test lasted no more than 25 min, and immediately after a test was completed, the chimpanzees returned to their social group. No pair was ever tested more than once per day.

Food preference tests

To determine which foods should be used as the high- and medium-value rewards, a series of forced-choice procedures were conducted prior to testing. Chimpanzees were presented with two pieces of food and allowed to select one item. Once they made their selection, by reaching for the food with either their hand or lips, they were given that food and the other item was withdrawn. The chimpanzees were each required to make ten such selections on 1 day and a second set of ten choices the next day. If the chimpanzee selected the same food for 80 % or more of the trials on each day, then that food was considered to be a high-value reward (HR). On a third day, ten pieces of the alternative food item were then offered to the chimpanzee to ensure that the less-preferred food was still desirable, albeit less so than when given the opportunity to obtain the HR. If this was the case, this food was determined to be the medium-value reward (MR). Note, we did not use a low-value food, as it is essential that both rewards are desirable to the chimpanzees. For all 18 chimpanzees, grapes were determined to be the HR and grape-sized pieces of carrot were the MR.

Procedure

Each chimpanzee was tested as the subject in six conditions. Each condition was repeated twice so that each chimpanzee acted as the subject on two occasions for each condition (Table 1). Within each pair, each chimpanzee acted as both the subject and the partner, and all conditions were run in a counterbalanced manner. In four of the conditions, the subject was tested with a partner but, in order to determine their reactions to loss separate from a social partner's outcome, in two additional conditions, the chimpanzees were tested individually (with no partner, Table 1). Following this schedule, each chimpanzee was tested on 18 occasions (each test was run on a separate day). Of these 18 tests, in 14 they were tested with a social partner and in four they were tested individually.

In each condition, the chimpanzee had to make 20 exchanges with the experimenter for food rewards and, in the conditions where there was a partner, the exchanges alternated between the subject and partner (who also received 20 exchanges), with the partner always making the first exchange in the session. For every condition, prior to offering the chimpanzee the token to exchange, the experimenter showed the chimpanzee a food reward that was then placed in a small plastic pot in plain sight of both the subject and partner. Once the chimpanzee completed the token exchange with the experimenter, depending on the condition, the experimenter either gave the chimpanzee the visible reward that was in the pot, or in certain conditions (e.g., Loss Inequity condition, Table 1), the reward was placed back in the appropriate food reward container and the alternative reward was given to the

chimpanzee. Both foods used in the study were present and visible at all times, even if they were not used in the condition being tested.

Dependent variables and analyses

We used behavioral measures to assess the responses of the primates in both the inequity and individual contrast conditions; we recorded the number of refusals made by the subject and by the partner. Specifically, for every trial in which a token was offered to the chimpanzee, a completed 'exchange' required the chimpanzee to accept and return the token to the experimenter within 30 s and then eat the food reward they were offered by the experimenter, also within 30 s of receiving it. However, if the chimpanzee refused to exchange the token, by not accepting it or not returning it to the experimenter within 30 s, their response was coded as a 'refusal.' Furthermore, even if a chimpanzee exchanged the token, if they then refused the food reward (by not taking it, or accepting it but not eating it within 30 s) their response was also coded as a 'refusal'.

If the chimpanzee refused to exchange the token or accept/eat the food reward, the experimenter recorded the refusal in real time directly on to a score sheet. These data were later transcribed into Excel. Additionally, and also in real time, the experimenter used a stopwatch to record how long it took the chimpanzee to return the token to the experimenter for successful exchanges (note that if they took longer than 30 s to return the token, this was counted as a refusal and they were not given a reward for such a delayed exchange, nor was this counted as part of their latency measurement) and how long it took for the chimpanzee to eat the reward after accepting it (again, because if they did not eat the reward within 30 s, it was classed as a refusal).

To compare the chimpanzees' responses across conditions, average refusals were calculated from responses in the two sessions for each of the six conditions. Given that our previous research demonstrated that male and female chimpanzees may respond differently to both inequity and individual contrast (Brosnan et al. 2010), we analyzed the responses of our subjects by sex. To compare average refusals across conditions, repeated measures ANOVA tests were used and, for each, if the Mauchly's test indicated that the assumption of sphericity was violated, we report the Greenhouse–Geisser corrected tests. *T* tests were run to test pairwise comparisons. To correlate the chimpanzees' responses against the length of time that they had lived with their test partner, Pearson's correlations were used. All *P* values were two-tailed. All analyses were run in IBM SPSS version 20.

Results

Latency to exchange

For each completed exchange, subjects took, on average, 1.7 s (range 0.6–7.7 s) to return a token to the experimenter. There was no difference in the time taken by subjects across the six conditions (females: $X^2(5) = 1.266$, $P = 0.938$; males: $X^2(5) = 9.207$, $P = 0.101$).

Social conditions

There was no difference across conditions in the number of refusals made by the chimpanzees repeated measures ANOVA, $F(2, 33.87) = 0.591, P = 0.559$). However, when analyzed separately by sex, the females, but not males, showed significant differences in the number of refusals (i.e., incomplete exchanges or refused rewards) across the four social conditions (Fig. 1).

The females' total refusals were significantly different across the four social conditions (repeated measures ANOVA: $F(3, 6.96) = 3.04, P = 0.046$). This difference across conditions was driven by the females' refusal to complete exchanges, rather than their refusal to accept or eat the food rewards. There was a significant difference in the female chimpanzees' token refusals across the four conditions ($F(3, 5.51) = 3.47, P = 0.030$), but no difference across conditions in the number of food rewards that the females refused ($F(2, 1.49) = 0.605, P = 0.511$). The females refused to exchange tokens with the experimenter more in conditions that created disadvantageous inequity than in those that created loss (i.e., individual contrast, Fig. 1). Thus, females refused more token exchanges in the Loss Inequity compared to the high-value rewards condition ($t(9) = 2.43, P = 0.038$) and in the Same Inequity condition compared to the Loss Equity condition ($t(9) = 2.33, P = 0.045$).

In contrast to the females, the males' total refusals did not differ across the four social conditions (repeated measures ANOVA: $F(3, 21.0) = 2.17, P = 0.122$). This held true when the refusals to exchange tokens and accept food rewards were considered separately (token refusals: $F(3, 21.0) = 2.41, P = 0.095$, food refusals: $F(1, 9.9) = 2.13, P = 0.332$).

Individual conditions

There was no difference in the subjects' refusals between the two individual conditions (Solo Same vs. Solo Loss, $t(17) = -1.05, P = 0.310$). This held true when the data were analyzed by sex (females $t(9) = -0.91, P = 0.389$; males $t(7) = -0.48, P = 0.647$).

Absolute versus relative reward values

In the Loss Inequity, Loss Equity and Same Inequity conditions, when tested as the partner, the chimpanzees never experienced loss or disadvantageous inequity (Table 1). However, in the Loss Equity condition partners were shown and received carrot pieces for every exchange, while in the Loss Inequity and Same Inequity conditions, partners were shown and received grapes for every exchange. Therefore, by analyzing the responses of the chimpanzees when tested in the role of the partner in these three conditions, we could determine whether differences in reward value alone were enough to induce refusals (i.e., if they refused more when receiving the less-preferred rewards, regardless of what they had been offered or what their test partner was offered). When tested in the role of the partner, the chimpanzees' responses did not vary across the Loss Inequity, Loss Equity and Same Inequity conditions (females: $F(2, 18.0) = 0.52, P = 0.604$; males: $F(1, 7.61) = 3.47, P = 0.100$). This suggests that simply being shown and receiving the less-preferred reward was not sufficient to stimulate the chimpanzees, either females or males, to refuse to participate.

Disadvantageous versus advantageous inequity

In both the Loss Inequity and Same Inequity conditions, the partner experienced advantageous inequity, but not individual contrast (the partner was shown, and offered, the more-preferred grapes while the subject received carrot pieces, Table 1). When tested as the subject in both of these conditions, chimpanzees experienced disadvantageous inequity and, in the Loss Inequity condition, subjects also experienced individual contrast. In both conditions, female chimpanzees refused more when tested as the subject than when they were the partner (Loss Inequity: $t(9) = -2.60$, $P = 0.029$; Same Inequity: $t(9) = -3.22$, $P = 0.011$, Fig. 2), presumably reflecting a reaction to the disadvantageous inequity that arose in both conditions, rather than individual contrast that they only experienced in the Loss Inequity condition. Supporting this, in the Loss Equity condition, female subjects, who experienced individual contrast without disadvantageous inequity, did not refuse more than when tested as the partner and experienced neither individual contrast nor inequity ($t(9) = -1.03$, $P = 0.328$, Fig. 2). Experiencing individual contrast effects alone, without disadvantageous inequity, was not sufficient to cause the females to refuse more when in the role of the subject compared to when they were tested as the partner (Fig. 2).

This pattern of refusals by females *within* a condition (but across roles) also reflects their responses *across* conditions when tested as the subject (i.e., their refusals were driven by inequity, not individual contrast). This also suggests that females responded more strongly to disadvantageous, rather than advantageous, inequity, as they refused more frequently in disadvantageous conditions than they did in advantageous ones. For the males, no such differences in refusals were found across conditions when tested as the subject compared to the partner (Loss Inequity: $t(7) = -1.75$, $P = 0.123$; Same Inequity: $t(7) = -1.55$, $P = 0.164$; Loss Equity: $t(7) = -0.87$, $P = 0.413$), suggesting that they were not sensitive to advantageous or disadvantageous inequity.

Tenure of relationship and responses to disadvantageous inequity

As previous studies have indicated that the length of time chimpanzees live together may influence their responses to inequity (e.g., Brosnan et al. 2005), we correlated the number of refusals that subjects made in each of the four social conditions against the number of days that they had been living with their social partner at the start of testing (range 398–10,847 days, average: 4,137 days). Although none of the correlations were significant (Table 2), there were some interesting trends in the correlations between the number of refusals and the length of time chimpanzees had lived with their social partner in the condition in which they experienced disadvantageous inequity (i.e., the Loss Inequity condition). Females seemed less likely to refuse the longer they had lived with their partner (Pearson's correlation, females: $r = -0.602$, $N = 10$, $P = 0.065$), while males' refusals increased with increasing relationship tenure ($r = 0.691$, $N = 8$, $P = 0.058$). For females, this response appeared to be driven by their token refusals, as in their other responses ($r = -0.614$, $N = 10$, $P = 0.059$), whereas for males it appeared to be driven by food refusals ($r = 0.701$, $N = 8$, $P = 0.053$, Table 2).

Discussion

Our results provide further support to data that show that some chimpanzees respond negatively to inequity due to comparisons with their social partner, rather than to their own previously offered outcomes; however, this response varies greatly across individuals (Brosnan et al. 2005, 2010; Hopper et al. 2013b). In this study, responses of female chimpanzees were driven by what they received in relation to what their test partner received, rather than by what they were shown previously (or what the partner was shown), or even, the absolute value of the reward itself. Importantly, our current results emphasize that this negative response to disadvantageous inequity is distinct from frustration effects caused by loss, which have been proposed by some as the underlying mechanism of inequity responses (e.g., Bräuer et al. 2009; Wynne 2004). Previous work explored responses to individual contrast and inequity across different sessions (Brosnan et al. 2005, 2010), but our current study explored responses when inequity and individual contrast competed against one another within the same trial. This was critical, as earlier work showed variability in how chimpanzees responded to these two comparisons; while some chimpanzees responded more strongly to inequity than contrast, others showed the opposite pattern (Brosnan et al. 2010).

The chimpanzees' behavior was not driven by contrast effects when they were tested by themselves, either. When tested without a social partner, both female and male chimpanzees were equally likely to accept a medium-value carrot reward, whether the experimenter had previously shown them a piece of carrot or a more-preferred grape. This implies that outside of the social context, both sexes' willingness to accept carrot pieces is independent of the better foods potentially available to them in their environment. In this study then, individual loss did not appear to induce frustration. Furthermore, it appears that the absolute values of the food items do not influence the chimpanzees' responses. When tested as the partner in social conditions in which they were shown and received carrot pieces, the chimpanzees made no more refusals than when in conditions in which they were shown and received grapes for each exchange (e.g., when tested as the partner in Loss Inequity vs. Loss Equity conditions).

Comparing the responses of the chimpanzees when tested in the role of the subject versus the role of the partner revealed that the females' refusals to social contrast, or inequity, were specific to situations in which they were underbenefited; that is, they refused when they got less than the other chimpanzee (disadvantageous inequity; here in their role as a subject), but not when they got more than the other chimpanzee (advantageous inequity; here in their role as partner). This is not necessarily unexpected, as even in humans, responses to advantageous inequity emerge much later in development than do responses to disadvantageous inequity, suggesting that these are related but distinct processes (Blake and McAuliffe 2011; House et al. 2012). However, highlighting the variability in chimpanzees' inequity responses, in other contexts, chimpanzees have shown increased refusals for the same, highly valued, food item when their partner got a less-preferred reward instead of the more-preferred option (Brosnan et al. 2010, see also the online supplementary material for a discussion about inter-individual differences but intra-individual consistency in the chimpanzees' responses).

In the short term, refusals in the face of inequitable outcomes actually compound the inequity; by refusing rewards, the subject increases the differential between what they receive (nothing, if they refuse) and what their partner receives (the high-value reward, Henrich 2004). Although perhaps not logical, refusing rewards that are less preferred than those offered to a partner occurs regularly among both nonhuman primates (Brosnan 2011) and humans (Yamagishi et al. 2009; McAuliffe et al. 2013). In the current study, however, by teasing apart the female chimpanzees' refusal types—between refusals to exchange tokens or accept rewards—we found that the females' refusals were not typified by refusals to accept the offered rewards, but, rather, were more often refusals to exchange tokens. In this way, the females were not refusing food items offered to them; instead, they refused to 'work' for the 'unfair pay.'

This study joins a growing body of research indicating that primates' responses to inequity and individual contrast are strongly influenced by a number of individual and social factors, including social grouping (Brosnan et al. 2005), dominance (Brosnan et al. 2010; Bräuer et al. 2009), sex (Brosnan et al. 2010; Talbot et al. 2011) and age (Hopper et al. 2013a). Previous studies have also shown that the specific test conditions—such as the presence of a task or the orientation of subjects with respect to one another (Bräuer et al. 2006; Brosnan et al. 2010; Neiworth et al. 2009; Talbot et al. 2011, 2013)—also affect the responses of primates in tests of inequity. In our study, not only did the chimpanzees' sex influence their responses, but we also found an indication that the chimpanzees' relationship with their test partner (as measured by the length of time living together) may have influenced their responses to disadvantageous inequity. Although the correlations were not statistically significant, it is interesting to note that males and females showed opposite patterns. Females were less likely to respond to disadvantageous inequity the longer they had lived with their test partner, while males responded more strongly the longer they lived with their partner. The pattern of females' responses provides tentative support for those of a previous study that reported that chimpanzees that had lived together longer (for more than 30 years) responded less strongly to inequity than those subjects who had lived with their test partners for a shorter period (around 8 years, Brosnan et al. 2005). Perhaps the utility of 'length of time living with a social partner' as a proxy for 'relationship strength' differs for males and females, or across different contexts, and we encourage future studies to incorporate other measures of relationship strength when considering chimpanzees' responses to inequity and other socially mediated interactions.

In a social context, female chimpanzees were far more likely to refuse to exchange tokens for carrot pieces when their test partner got the better grape, irrespective of which food item (grape or carrot) they, or the partner, were proffered initially. The responses of the female chimpanzees in the present study highlight the vigilance that they maintained, both to which rewards they received and to which rewards their test partner received. It appears that female chimpanzees were able to 'tune out' the environmental 'noise' of food items that were merely proffered but never delivered to another chimpanzee, while simultaneously monitoring what their social partner ultimately received. This is perhaps not surprising, given their sensitivity to both social and nonsocial cues in other contexts, including social learning (Bonnie et al. 2007; Hopper et al. 2008), monitoring available food rewards (e.g.,

Hopper et al. 2013b; van Leeuwen et al. 2013) or the outcome of cooperative activities, such as group hunting (Gilby and Connor 2010).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Fig. 1. Percentage of trials, and standard error of the mean for each, in which the female (*black*) and male (*gray*) chimpanzees refused to accept or exchange the token with experimenter in each of the four social conditions. The horizontal lines represent significant differences between conditions, where $P < 0.05$

Fig. 2.

Percentage of trials in which the female chimpanzees refused when tested as both the subject and partner. *Error bars* show the standard error of the mean for each. The horizontal lines across roles indicate significant differences, where $P < 0.05$

Table 1

Experimental conditions outlining the reward values, both shown and given, to the subject and their partner

Condition	Subject		Partner	
	Shown prior to exchanging	Offered after exchanging	Shown prior to exchanging	Offered after exchanging
Loss Inequity	GRAPE	carrot	GRAPE	GRAPE
Loss Equity	GRAPE	carrot	carrot	carrot
Same Inequity	carrot	carrot	GRAPE	GRAPE
HR Control	GRAPE	carrot	GRAPE	carrot
Solo Same	carrot	carrot	Partner Absent	
Solo Loss	GRAPE	carrot	Partner Absent	

The high-value reward was a grape while the medium-value reward was a small piece of carrot equivalent in size to a grape

Table 2

Correlations between the number of days that a subject had lived with their test partner and the number of total refusals (tokens and food rewards) they made in each condition

Refusal type	Condition	Males	Females
All refusals	Loss Inequity	$r = 0.691, N = 8, P = 0.058$	$r = -0.602, N = 10, P = 0.065$
	Loss Equity	$r = 0.492, N = 8, P = 0.215$	$r = -0.321, N = 10, P = 0.366$
	Same Inequity	$r = 0.239, N = 8, P = 0.569$	$r = -0.285, N = 10, P = 0.424$
	HR Control	$r = 0.639, N = 8, P = 0.088$	$r = -0.267, N = 10, P = 0.455$
Token refusals	Loss Inequity	$r = 0.647, N = 8, P = 0.083$	$r = -0.614, N = 10, P = 0.059$
	Loss Equity	$r = 0.424, N = 8, P = 0.295$	$r = -0.359, N = 10, P = 0.309$
	Same Inequity	$r = 0.345, N = 8, P = 0.403$	$r = -0.205, N = 10, P = 0.486$
	HR Control	$r = 0.560, N = 8, P = 0.149$	$r = -0.233, N = 10, P = 0.518$
Food refusals	Loss Inequity	$r = 0.701, N = 8, P = 0.053$	$r = -0.396, N = 10, P = 0.257$
	Loss Equity	$r = 0.521, N = 8, P = 0.185$	$r = -0.084, N = 10, P = 0.817$
	Same Inequity	$r = -0.526, N = 8, P = 0.541$	$r = -0.293, N = 10, P = 0.411$
	HR Control	$r = 0.352, N = 8, P = 0.393$	$r = -0.311, N = 10, P = 0.382$