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Personality influences responses to inequity and contrast in chimpanzees

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Abstract

Several species besides humans respond negatively to inequity (i.e. receiving a less preferred outcome as compared to a social partner). Among primates, the taxon for which inequity responses have been most comprehensively studied, there are large individual differences in responses that have, thus far, not been well explained by demographic features such as sex, rank and age. Recent evidence shows that individuals' personalities are important in explaining differences in behavioural outcomes in other contexts. Thus, in the current study, we explored whether personality was associated with chimpanzees' responses to both inequity and contrast (i.e. receiving less than anticipated). Chimpanzees were paired with multiple members of their social groups. These pairs alternated trading a token to receive food rewards that either differed from what their partner received (inequity condition) or from what was initially offered (contrast condition) and we compared their responses to a control in which both subjects were offered and received the same reward for trading the token. We predicted that both personality and the quality and length of the pairs' relationship would influence subjects' reactions to unequal outcomes, as measured by their refusal to exchange tokens. The quality of subjects' relationships, based on a weighted average of grooming, contact and proximity, did not correlate with refusals to exchange, whereas pairs that had lived together longer were less likely to refuse in the contrast condition than were pairs that had lived together for less time. Considering personality, some of the

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dimensions influenced responses to both inequity and contrast similarly, but the more ‘social’ personality dimensions (‘extraversion’ and ‘agreeableness’) were more strongly correlated with sensitivity to inequity. These results highlight the importance of considering individual differences, including personality, when evaluating responses in cognitive and behavioural tests.

Keywords

contrast effect; inequity; personality; social comparison; social relationship

In numerous species, if an individual gets a reward that is less preferred than the reward given to a social partner, the individual will respond negatively by refusing to (1) continue participating in the interaction or (2) accept the offered reward. Such responses have been documented in humans (Yamagishi et al., 2009) and in a number of nonhuman primate species (Brosnan, 2013; Price & Brosnan, 2012), dogs (Horowitz, 2012; Range et al., 2009, 2012) and corvids (Wascher & Bugnyar, 2013), and have been explored in fish (Raihani et al., 2012; for a review of this literature, see *Social Justice Research*, 25(2–3)). Intriguingly, however, responses to inequity are highly variable within species, as evidenced by the differences found in chimpanzees’ responses both across studies (Bräuer et al., 2009; Hopper, Lambeth, Schapiro, & Brosnan, 2013) and within the same study (Brosnan, Schiff, & de Waal, 2005; Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010; Hopper, Lambeth, Schapiro, & Brosnan, 2014). For example, inequity responses in nonhuman primates are influenced by rank, with dominant individuals typically responding more strongly when they receive less than a social partner (Bräuer et al., 2009; Brosnan et al., 2010; Takimoto & Fujita, 2011). In addition, there is some evidence that responses to inequity are influenced by age (Hopper, Lambeth, Schapiro, Bernacky, & Brosnan, 2013), sex (Brosnan et al., 2010; Hopper, Lambeth, et al., 2014) and social group (Brosnan et al., 2005), but these patterns are not consistent across studies (Price & Brosnan, 2012), nor can they explain all variation.

What other factors could affect responses to inequity? In light of the fact that responses to inequity may represent consistent individual differences in behaviour (Hopper, Lambeth, et al., 2014), one potential explanatory factor is personality, or ‘those characteristics of individuals that describe and account for consistent patterns of feeling, thinking, and behaving’ (Gosling, 2001, page 46). However, to date, no previous work has examined the impact of an individual’s personality on their response to inequity. This lack of previous work on personality’s relationship to responses to inequity is somewhat surprising given that personality has proved to be important to understanding individual differences in behavioural responses in a number of species and circumstances (Carere & Maestripieri, 2013). In particular, studies of nonhuman primate species show that they have stable, consistent personalities (Massen et al., 2013; Morton et al., 2013; for a review in nonhuman primates see Freeman & Gosling, 2010), which also correlate with their responses in behavioural experiments (e.g. Hopper, Price, et al., 2014; Massen et al., 2013). The personality dimensions that have been identified to apply to nonhuman primates include some dimensions that are more social (e.g. ‘dominance’, ‘extraversion’) and others that are more experiential (e.g. ‘openness’, ‘methodical’; Freeman, Brosnan, et al., 2013). Thus, different personality traits may influence how animals respond in different social and

nonsocial contexts (Carter et al., 2013; van Oers et al., 2005). Given this pattern, we hypothesize that personality will also influence animals' evaluations of food rewards in different contexts (i.e. social situations that create inequity compared to situations that contrast expected with received rewards).

In addition to correlating with cognitive and behavioural responses, animals' personalities also relate to their social interactions with their groupmates (Kurvers et al., 2010; Massen & Koski, 2014; Mehrabian, 1996). For example, studies investigating the relationship between chimpanzee personality ratings, collected from caregivers familiar with the individuals, and observed social behaviours, collected by a separate set of individuals at another time period, have shown that the factor of 'extraversion' correlates positively with affiliative behaviours and negatively with aggressive behaviours; similarly, the personality factor of 'dominance' correlates positively with agonistic behaviours and negatively with submissive behaviours (Freeman, Brosnan, et al., 2013; Murray, 1995; Pederson et al., 2005; Vazire et al., 2007). Furthermore, a recent study of 38 captive chimpanzees showed that subjects who spent more time sitting in contact with each other ('friends') were more similar in 'sociability' than were nonfriends (Massen & Koski, 2014). In addition, among nonkin friends, 'friendship' also correlated with 'boldness' and 'grooming equity'.

In humans, relationship quality influences decisions surrounding inequity, such that people in close relationships are less likely to respond negatively to inequity than are mere acquaintances (Clark & Grote, 2003). Work in nonhuman primates has resulted in conflicting evidence as to whether relationship quality influences responses. There is evidence that rank influences responses to inequity in primates (Bräuer et al., 2009; Brosnan et al., 2010; Takimoto & Fujita, 2011), but a study that explicitly tested relationship quality in longtailed macaques, *Macaca fascicularis*, found that relationship quality did not influence subjects' responses (Massen et al., 2012). Even in chimpanzees, one of the most-studied species in tests of inequity, evidence is mixed regarding the impact of relationship quality on responses to inequity. For example, adult chimpanzees who were housed in species-atypical arrangements (in pairs or in a recently formed social group), responded negatively to inequitable outcomes, while chimpanzees who had been housed in the same species-typical group for decades did not (Brosnan, Schiff, & de Waal, 2005). This finding points to the potential importance of relationship quality in chimpanzee responses to inequity. However, a more recent study with chimpanzees, using the same methodology but conducted at a different facility, found that group membership did not make a difference, but sex and rank did (Brosnan et al., 2010). Untangling the degree to which these reported differences are due to the impact of relationship quality or duration versus differences in the subjects' personalities requires testing these two potential influences within the same study.

Empirical considerations of inequity focus on whether individuals respond negatively to an outcome that differs from the outcome experienced by another individual, where the task implicitly involves a social comparison. However, comparisons can also be made in the absence of a social context; for example, an individual can compare the achieved outcome with their expected outcome (based on experience). This comparison is often referred to as a 'contrast effect' (Reynolds, 1961) or 'frustration' (Roma et al., 2006) and probably draws on the same cognitive mechanism as used in inequity decisions (Price & Brosnan, 2012).

Essentially, inequity decisions compare the outcome with social referents whereas contrast decisions compare the outcome with nonsocial referents (such as past experience). Most studies of inequity consider both inequity and contrast, and these studies show that there is variability both within species (e.g. there are sex differences in contrast effects in squirrel monkeys (*Saimiri* spp.); Talbot et al., 2011) and across species (e.g. while squirrel monkeys respond to contrast effects, marmosets, (*Callithrix* spp.) and owl monkeys (*Aotus* spp.) do not; Freeman, Sullivan, et al., 2013). What we do not know, however, is whether these effects are differentially influenced by social and demographic factors. For instance, features directly related to individuals' interactions with one another, such as rank and relationship quality may influence decisions with an explicitly social referent (i.e. inequity) differently than those without such a referent (i.e. contrast effects).

Here, we explored the impact of personality and relationship quality on responses to inequity and contrast effects in chimpanzees. We selected chimpanzees because previous research has demonstrated a high degree of individual variability in their responses to tests of inequity and contrast effects (Bräuer et al., 2009; Brosnan et al., 2005, 2010; Hopper, Lambeth, et al., 2014), indicating that some as-yet unidentified factor, or factors, may be influencing their responses. To do this, we tested chimpanzees in a commonly used inequity paradigm in which they traded a token with an experimenter to receive a food reward. Sometimes this food reward was a less preferred reward than the one given to their partner (inequity condition) and sometimes both the subject and partner were shown a preferred reward but given a less preferred one (contrast condition). The chimpanzees' responses in both were compared to a control condition in which the subjects were given the same, less preferred reward as their partner (equity condition). To explore how personality influenced chimpanzees' responses, we included measures of the chimpanzees' personalities as an explanatory variable, which were collected as part of a wider study by Freeman, Brosnan, et al. (2013). We additionally explored how relationships influenced chimpanzees' responses. In most captive experiments of behaviour or cognition, partnerships are determined by the experimenter and this potentially biased assortment further limits the conclusions that can be drawn about the influence of relationship quality on these responses. In our study, we began to address this limitation by testing members of every partnership that were willing to separate briefly from their group for the study and by including (1) the quality of each pair's relationship (Sapolsky et al., 1997; Silk et al., 2003) and (2) the duration of each pair's relationship (within the same social group) as potential explanatory variables in the analysis. In addition to personality and relationship quality and duration measures, we also took into account each individual's age, sex and rank.

We hypothesized that both personality and relationship quality would influence inequity responses and contrast effects, and that these factors would influence the two types of comparisons differently. Moreover, we had several specific predictions. First, and consistent with previous findings, we predicted that chimpanzees would respond to differences in outcomes between themselves and their partners (i.e. inequity), but that there would be variability between responses, such that some individuals or partnerships would respond less strongly than others. Second, based on previous research, we predicted that more dominant individuals would respond more negatively to differences in their outcomes as compared to

their partners than subordinates (Bräuer et al., 2009; Brosnan et al., 2010). Third, we predicted that personality traits would correlate with both inequity and contrast, but given the paucity of previous research examining chimpanzee personality and cognition, we did not have specific predictions as to which factors might correlate, the direction of the relationships, or whether different factors would correlate with inequity versus contrast. Fourth, we predicted that variation in responses to inequity would correlate with their relationship quality or duration. Finally, we predicted that neither relationship quality nor duration would impact subjects' responses to individual contrast because this is not an explicitly social comparison.

METHODS

Subjects

Subjects were 24 adult chimpanzees (12 males and 12 females, average age = 26.5 years, range 15–48 years), who were the chimpanzees willing to participate in this study. The chimpanzees lived in four social groups that comprised 27 adult chimpanzees (12 males and 15 females, average age = 27.2 years; see below for details of the three females that were not tested). Six of the 27 chimpanzees were wild born and the remaining 21 were raised in captivity. All were housed at the Michale E. Keeling Center for Comparative Medicine and Research, UT MD Anderson Cancer Center, Bastrop, Texas, U.S.A. (hereafter referred to as KCCMR). These four social groups were housed such that the chimpanzees could see and hear individuals in other social groups, but they did not have the opportunity for direct physical interaction between groups. Group 1 consisted of nine chimpanzees, including four males (average age = 23.0 years) and five females (average age = 23.6 years), group 2 was composed of eight chimpanzees, including two males (average age = 32.5 years) and six females (average age = 31.3 years) and group 3 was composed of six chimpanzees, including two males (average age = 22.0 years) and four females (average age = 34.0 years). The fourth group was an all-male bachelor group of four males (average age = 24.3 years).

All subjects were housed in social groups in large enclosures with indoor/outdoor access and extensive environmental enrichment (climbing structures, ropes, swings, barrels, and other toys). All subjects had ad libitum access to primate chow and water and each group received three meals of fruits and vegetables per day, as well as additional puzzle (or occupational) enrichment multiple times per week. At no time prior to, or during, testing were the subjects deprived of food or water. All subjects participated voluntarily, coming when called to the indoor dens of their living areas to participate in the experiment. Asking subjects to come inside in this way limited distractions during the experiment. None of these subjects had previously participated in a study of inequity or contrast effects. The KCCMR is fully accredited by the Association for 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: 07-92-03888) of UT MD Anderson Cancer Center.

Subjects were paired with every partner in their social group with whom they were willing to separate. A female chimpanzee in group 1 (aged 19 years) and a female in group 3 (aged 47 years) chose not to participate in any test and a third female (aged 31 years) from group 2

was not tested because she was diabetic; therefore, the data presented herein refer to the remaining 24 chimpanzees from the four groups, described above. In addition, certain chimpanzees would partner only with select members of their group, for example due to dominance interactions (e.g. in group 3, the beta male would not consistently separate with the alpha male). In some cases, this meant that each individual was paired with every other member of their group, while in other cases subjects paired with only a single other member. To determine 'willingness to participate in the study', subjects and a partner were called inside. If they refused to come in to test for five consecutive attempts on different days, that pair was not tested. Typically, pairs willingly separated on virtually every opportunity, excluding occasions when a female was in oestrus, so this measure of willingness to separate was very conservative. Nevertheless, as group dynamics can change over time, we reattempted to pair the chimpanzees once either individual had completed a successful round of testing with another chimpanzee. In addition, in a few cases chimpanzees were moved to a new group during the course of our study (which took almost 2 years to complete), which made further pairings with these individuals impossible. In the Results section, we report data on overall differences between individuals or pairs that did separate to test and those that did not. Data were collected from October 2008 to July 2010.

To calculate the most parsimonious estimate of possible pair combinations, we excluded the three females that did not participate in any test, but included the four chimpanzees that were removed over the course of the testing period and so participated in at least one pairing. Thus, there were 78 pair combinations that could potentially have been created across these four groups (group 1 = 36 possible pairings, group 2 = 21 possible pairings, group 3 = 15 possible pairings and group 4 = 6 possible pairings), and we ultimately tested a total of 37 pairs of chimpanzees. All the possible combinations of members of group 4 were tested, 67% of possible pairs in group 2 and 47% in group 3 were tested, while in the largest group, group 1, 28% of possible pairs were tested. As both members of a pair acted as the subject, we obtained 74 complete sets of data. The 24 subjects were tested with an average of three partners (range 1–5) and subjects completed all sessions with one partner before any testing began with a new partner.

This procedure avoided possible confounds in which individuals' responses with one partner were influenced by interleaved experience with a different partner and so allowed us to assess how each chimpanzee's behaviour changed with successive partners.

Food Preference Tests

We established the food preferences of the subjects through a dichotomous-choice test between a medium-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, celery pieces). To determine food preferences, subjects were given 10 successive forced-choice trials in which the experimenter held up one food in each hand, centred on the chimpanzee. To control for any side biases, presentation of foods alternated from left to right across trials. Subjects indicated their choice by gesturing to the desired food item with their hand or by moving their head in front of their preferred option. They always received

the food they gestured towards as soon as they made their choice and the alternative food was withdrawn so that they could not take both.

To consider a food to be the high value option, each chimpanzee in the study had to select it at least 80% of the time (8 of 10 trials) in each of two consecutive sessions over the second food. Second, after the preference for the high-value food was established, each chimpanzee was given 10 consecutive pieces of the less preferred food from these tests (in a separate session) to verify that they were willing to consume all 10 pieces of the food when no other foods were available. Again, all chimpanzees being tested had to meet this criterion. It was critical that subjects ate the medium-value food in baseline conditions or their behaviour in the comparison conditions would be irrelevant. If both of these conditions were met for every chimpanzee being tested, the food pair was chosen, with the more preferred food being considered high value and the less preferred food considered medium value. For all the subjects, the preferred high-value food was a single grape and the medium-value food was a similarly sized piece of raw carrot.

Training

Prior to the study, all subjects had been trained to exchange an inedible token using positive reinforcement and shaping techniques. Tokens consisted of polyvinyl chloride (PVC) pipes 20 cm in length and 2 cm in diameter. To count as a full exchange, the chimpanzees were required to take the token from the experimenter, pull it fully into their enclosure, and then return it to the experimenter by placing it on the experimenter's outstretched palm. Upon returning the token into the experimenter's hand, the chimpanzee was given a food reward. For subjects that required training, a food not used in subsequent test sessions was used as a reinforcer, and chimpanzees were considered to have met criterion when they returned 20 tokens in a single session. Most chimpanzees learned the exchange procedure in one or two 20 min sessions and none required more than five training sessions.

Testing Conditions

All pairs remained consistent until they had completed testing with their current partner; individuals were then paired with another individual from their social group until they had either paired with each possible partner or were unwilling to form a pair with any remaining possible partners. We used both same-sex and mixed-sex pairs, and the relative rank of the two chimpanzees varied depending on the partnership in question. All testing was done in one of the indoor dens that were part of the chimpanzees' living environment and was thus familiar to them. During testing, the pair members shared the same den and thus were not separated from one another, so each could clearly see the actions of their partner, and the food rewards they received (foods were given directly to the chimpanzee so that there was no opportunity for the other chimpanzee to acquire it). No individual (and hence no pair) was tested more often than once per day, and each session, which comprised 50 trials, lasted no more than 30 min.

Each pair formed was tested in three conditions, the inequity, contrast and equity control conditions, with each member of the pair acting as the subject on different sessions (see also Brosnan et al., 2010). In most conditions, neither the subjects nor the partners were shown

what reward they would receive upon completing the exchange; the exception was the contrast condition, in which we wished to draw attention to the reward that they were not to receive (other work demonstrates that in the inequity and equity conditions, subjects' responses are the same when they are shown the reward that they will see in advance of the exchange and when they are not; Hopper, Lambeth, Schapiro, & Brosnan, 2014). All sessions consisted of a single condition.

The equity control condition was designed to investigate baseline responses to the less preferred food when both individuals received the same-value food for completing an exchange with the experimenter. In this case, the medium-value food (carrot pieces) was the reward for all subjects (although high-value rewards were also visible at all times) that returned the PVC pipe token to the experimenter within 30 s.

The inequity condition was designed to investigate subjects' responses when they were given a lower-value reward than their partner received for the same task. Subjects first watched as their partner exchanged a token with the experimenter and received a high-value reward (a grape), following which the subject was offered an opportunity to exchange. He or she then received a medium-value reward (a carrot piece) if they successfully completed the exchange. This allowed us to investigate the degree to which social contrast, or comparison with one's partner's rewards, affected the subjects' behaviour.

The contrast condition was designed to investigate subjects' responses when they were given a lower-value reward than they had earlier been shown. In this case, unlike in either of the other two conditions, the experimenter held up a high-value reward (a grape) until they had the subjects' attention, as evidenced by reaching for the food item with the hand or lips. Following this, the high-value reward was placed back in the container. The subject was then given an opportunity to exchange and, if they did so, then they were given a medium-value reward (a carrot piece). The partner followed exactly the same procedure; thus, any social comparison was identical, including both what the partner was offered and what the partner received. This procedure allowed us to investigate the degree to which individual contrast, or comparison with previously offered rewards, affected the subjects' behaviour.

There were eight test sessions per pair, four inequity tests (two with each chimpanzee in the subject role), two contrast tests, and two equity control tests. Thus, for every chimpanzee, we had data from two sessions of each condition in the role of interest. These conditions were run in a randomly assigned order that was different for each pair tested. In each test of every condition two food containers (one containing the high-value rewards and one containing the medium-value rewards) were placed in front of, but out of reach of, the chimpanzees, so that they were visible to both chimpanzees. There were always more of both foods than would be used in the course of the test. This was done to ensure that the presence of either of these rewards did not cue the subject or create differences in reactions among the different test conditions. Each test session consisted of 50 alternating trials between the partner and subject, so that each chimpanzee 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 s.

In all trials, the chimpanzee had 10 s to accept the token and 30 s more to complete the exchange (mean latency to exchange = 3.95 s, range 1.06–14.54 s). 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 not returning it within 30 s were not considered successful exchanges. When the token had been returned, the experimenter held up the appropriate reward from the container so that it was visible to both chimpanzees and gave it to the chimpanzee that had just completed the exchange. Responses were immediately recorded on data sheets by the experimenter and all test sessions were videotaped for later analysis and coding.

Personality Data Collection

Personality ratings were collected for each of the 27 chimpanzees as part of a wider assessment of the personalities of the chimpanzees housed at KCCMR (Freeman, Brosnan, et al., 2013). Full details of the combined top-down and bottom-up procedure used to generate the personality rating scale are described in Freeman, Brosnan, et al. (2013). Briefly, the questionnaire required staff members to rate chimpanzees against a list of 41 traits (adjectives with associated descriptions). The questionnaire was completed by 17 staff members who had worked directly with the chimpanzees at UT MD Anderson for a minimum of 6 months (range 6 months – 21 years). Ratings were completed at weekly meetings from 2006 to 2008, and raters were instructed not to speak to each other about the ratings during or outside of the meetings. From the responses to the personality questionnaire, factor analysis of the 41 traits revealed six dimensions of chimpanzee personality: methodical, extraversion, agreeableness, openness (to experience), reactivity/undependability and dominance. For details on which traits loaded on which dimension, see Table 1.

The personality dimensions have been validated with respect to behavioural data, recorded 2 years prior to the administration of the questionnaires. These validation data were collected on the same chimpanzees but by a separate group of individuals from those who completed the questionnaires (for full details and results, see Freeman, Brosnan, et al., 2013). To test whether any of the six personality dimensions correlated with the chimpanzees' responses in the inequity or contrast conditions, we used these previously collected dimension scores for the 27 chimpanzee subjects examined here. Note that the personality results were compiled using raters that were not part of the current study, and these ratings were not originally collected for the purpose of considering how chimpanzees' personalities relate to either inequity or contrast, so it is unlikely that rater's expectations influenced the results for the purposes of the current analysis.

Relationship Data Collection

Finally, we explored whether individuals' social relationships with each of their test partners influenced their responses to inequity and contrast. We collated data on social affiliation collected on these groups during the period that this study was conducted. Note, to ensure that all group members were present throughout the observation period, these social relationship data were collected at times that were distinct from the focal experiments.

Specifically, scans were done from October 2008 until March 2010 (range 10–20 h/group, average = 13 h). Relationship data were derived from scan samples taken during these 60 min sessions. During these sessions, data on each individuals' social interactions were recorded every 180 s (i.e. scan sampling; Altmann, 1974). For each scan, we noted the activities of each colony member in the same order. Data were entered directly on to an Excel workbook using a laptop computer. For the purposes of this study, the data of interest were (1) 'contact', defined as individuals touching while not locomoting, (2) 'proximity', defined as being close enough to reach out and touch each other with a hand or foot, and (3) 'grooming', defined as one individual using the hands or lips to manipulate the hair of another individual. Grooming was coded such that the individual who was doing the grooming was coded as the subject; in the case of mutual grooming, both individuals were coded as subjects. Coding for these behaviours was mutually exclusive, such that an individual coded as grooming was not also coded as in contact with their partner, and a pair coded as in contact was not also coded as in proximity. As grooming was directional, if A was grooming B, but not the reverse, A was coded as grooming B, and B was coded as in contact with A.

Data from these scans were used to create an association rank index that allowed us to quantify each possible dyad in the group based on the frequency of affiliation (i.e. the composite sociality index, or CSI; Silk et al., 2003). To do this, data from the scans were extracted into matrices, one for each behaviour. In the case of grooming, we were interested in grooming interactions, rather than the directionality of grooming. We then summed these matrices for each pair. From these matrices, we created an CSI (Silk et al., 2003), which is a weighted average to measure each pair's relationship as compared to the others.

There was a large degree of variation in the number of interactions both between and within groups, so we used these sums as the measure of relationship quality, rather than a measure of ordinal rank, which would have decreased our ability to distinguish between relative relationship qualities in different pairs.

Finally, other evidence indicates that subjects' responses to inequitable situations may be influenced by the length of time that members of a pair have lived in the same social group (Brosnan et al., 2005; Hopper, Lambeth, et al., 2014). However, the quality of the subjects' relationships was not assessed in either of these cases (e.g. the only measure was length of cohabitation). Therefore, we added a variable of the length of time that subjects had been co housed (number of days) as a variable in the model so that we could compare both of these measures.

Statistical Analysis

Data analysis was done using a clustered logistic regression analysis in STATA version 12. We investigated a number of variables. First, we were interested in subjects' responses to the three conditions (inequity, contrast and equity). Second, we were interested in individual effects, including sex, rank, age and personality. Third, we were interested in relationship effects, in particular whether subjects' responses changed depending on the identity of their partner and their relationship to that partner. To control for order effects, we included a variable indicating test session number (e.g. their first, their second, and so forth) and trial

number (trial order within each test session). Finally, to see whether there was consistent variation between our four study groups, we included group as a variable.

The dependent variable was dichotomous: whether or not an individual refused to accept or return a token to the experimenter or refused to accept or eat the reward. As the dependent variable was dichotomous, we created a logistic regression model for the determinants of a chimpanzee refusing to exchange in the experiment. Our data were also clustered at three levels: the subject's interactions with a given partner (e.g. repeated trials per pair); the subject's interactions with other partners; and the group in which the subject lived. To control for the first two of these, we included a variable in the model that indicated both levels for each interaction. To control for group, we included different variables in the model for each group. Note that in our model, there was low interclass correlation between differing partners or subjects, and the group variables were not a significant predictors of subjects' behaviour. The analyses based on these variables indicated that the subjects' responses were largely independent of the group in which they happened to live.

To determine whether personality interacted with exposure to inequality or contrast, we examined the six personality dimensions (methodical, extraversion, agreeableness, openness (to experience), reactivity/undependability and dominance; Freeman, Brosnan, et al., 2013). We also included dichotomous measures of the treatments (contrast and inequity), while the omitted base category was the equity control. To determine whether chimpanzees higher in certain personality dimensions reacted differently in the inequity or contrast conditions, the models included a multiplicative interaction between these treatments (i.e. the experimental conditions) and the personality factors.

We analysed the data using two sets of models; the first set explored how these factors influenced whether or not subjects completed the interaction (e.g. returned the token and accepted the food reward) and the second looked at how the variables that were significant in the first model differentially influenced responses in the inequity and contrast conditions, each as compared to the equity condition. This step was taken because there were so many potential variables that the model with interactions would have been uninterpretable had we used all of them; so the first set of models allowed us to narrow down to those that had an influence. In all cases, the dependent variable was whether the subject participated in a trial (i.e. completed an exchange and ate the reward). The fixed effects were the pair's relationship scores (CSI and length of time cohabiting) and the individual's personality. The random effects were the subjects' sex, age, and rank. The dependent variable was coded such that if the coefficient (b) was positive, then refusals (to exchange the token or eat the reward) were increasing as the fixed and random effects increased, whereas if it was negative, refusals decreased.

The first set of models only looked at each condition and factor's effect on refusal rate and did not explore whether these factors differentially influenced exchange rates in the different conditions (e.g. inequity versus Control or contrast versus Control). This first set included three models, a basic model including demographic features and the CSI variable (see Results, Table 2, model 2.1), a second adding personality to this model (model 2.2), and a third adding the duration of the relationship to the first model (model 2.3). From this set of

models we established which of our relationship and personality variables influenced refusal rates, and then created two additional models that explored how the relevant relationship (see Results, Table 3) and personality (see Results, Table 4) variables interacted with the relative refusal rates in contrast as compared to control (models 3.1 and 4.1) and inequity as compared to the control condition (models 3.2 and 4.2).

RESULTS

Comparison of Pairs Tested and Pairs Not Tested

Across the four groups combined, we were able to test 37 unique pairs (derived from testing 24 chimpanzees, each with a variable number of partners; see above for details on how we attempted to test each pair). To determine whether the sample of pairs tested was a representative sample of the potential pairs, we compared characteristics of those pairs tested to those pairs not tested. For this analysis, we included the two females that never chose to participate, because this refusal may have been due to an aspect of their relationships with other group members. We did, however, exclude the diabetic female in group 2 who was not given the opportunity to participate. Excluding her, there were 78 possible pairs that could have been formed among the four social groups. Twenty-four chimpanzees were ultimately paired to create 37 unique dyads comprising nine male–male pairs, 15 female–female pairs and 13 male–female pairs. Including the two females that never chose to participate, there were 41 potential unique pairs that were never tested (five male–male pairs, 12 female–female pairs and 24 male–female pairs). Although the majority of untested pairs represented mixed-sex pairs, there was no significant difference in the number of same-sex versus mixed-sex pairs tested and not tested (chi-square test: $\chi^2_1 = 3.38$, $P = 0.07$), although given that this result is close to significant, this pattern is worth examining in future research.

In addition to the demographic characteristics of the pairs tested versus potential pairs that were not tested, we were also interested in whether the quality of the relationship between individuals would make them more or less likely to be tested together. To ascertain this, we first compared the raw CSI scores for those pairs that were willing to separate to test (average CSI = 0.94) and those potential pairs that were not (average CSI = 1.09); we found no difference between the two (Mann–Whitney U test: $U = 759.0$, $N_{\text{tested}} = 37$, $N_{\text{not tested}} = 41$, $P = 0.996$). We then compared the number of days that the pair had lived together for those pairs that were willing to separate to test together (average time together = 2170.51 days, range 354–9441 days) and those potential pairs that were not (average time together = 2011.61 days, range 127–15793 days) and found that pairs that were willing to separate together had been living together longer ($U = 1102.00$, $N_{\text{tested}} = 37$, $N_{\text{not tested}} = 41$, $P = 0.001$). Therefore, while relationship quality, as measured by the CSI did not influence willingness to test, relationship duration did, although we note that the difference was a very small percentage of the average time living together, and that the range of pairs not tested completely overlapped with the range of pairs tested.

Overall Refusal Rates

We first looked at how the factors we included in the model (individual, relationship, order effects; see Statistical Analysis, above) influenced the chimpanzees' likelihood to refuse to exchange, independent of whether they influenced contrast or inequity differentially (Table 2). First, we found a testing order effect that influenced the chimpanzees' responses across trials within a session and across overall number of sessions differently. Within a session, as the trials progressed, the likelihood of refusal increased, such that subjects refused to exchange tokens and accept food rewards more often in later trials than in earlier ones ($b = 0.023$, $P < 0.001$). However, refusals decreased across sessions ($b = -0.095$, $P < 0.001$). We found a sex difference only in the third model (including time living together), indicating that this was not a strong effect. In this case, males refused more often than females ($b = 0.508$, $P < 0.001$). As has been found previously, the rate of refusals increased as subject rank increased ($P < 0.001$ in all models; rank was coded so that 1 = highest rank and 3 = lowest rank). Refusals also decreased in older chimpanzees as compared to younger ones ($P < 0.001$ in all models).

Considering the main variables of interest, we first consider relationship quality. While the CSI was a significant predictor in model 2.1 (pairs that spent more time engaged in grooming, contact and proximity also refused more often; $b = 0.152$, $P = 0.015$), when the number of days that the subjects had lived together was added in model 2.3, the CSI was no longer significant ($b = -0.005$, $P = 0.343$), while the number of days a chimpanzee had lived together with its test partner was significant; the longer individuals had lived with their test partner, the less likely they were to refuse to participate ($b = -0.00015$, $P = 0.053$; note that this small coefficient is due to the fact that the variable, number of days, extended from 354 to 9441, whereas for all of the other variables, the range was much smaller, typically less than 5). Therefore, when considering the interactions between the relationship and personality variables and condition, we included only the time together as the measure of relationship, and not the CSI.

Considering the personality variables in model 2.2, five out of the six dimensions also had significant effects. The coefficients for openness, agreeableness, reactivity and dominance were negative ($P < 0.001$), indicating that individuals that were rated more highly in these factors were less likely to refuse (to exchange tokens or eat the food rewards). The coefficient for extraversion was positive ($P = 0.002$), such that as chimpanzees' ratings in extraversion increased, so did their refusals. The only personality dimension that did not correlate with refusals was methodical ($P = 0.087$, negative coefficient). However, methodical comprised only two traits and is the least well-validated dimension (Freeman, Brosnan, et al., 2013). Because each of the other dimensions was significant and methodical showed a tendency ($P = 0.087$), and because personality dimensions are established relative to one another, we included all six personality dimensions in our interaction model.

Effects of Inequity and Contrast

Contrary to our predictions, when considering the entire data set, we found no differences in subjects' reactions based on the experimental condition (e.g. comparing the inequity condition to the equity control condition or comparing the contrast condition to the equity

control condition; see Table 2). However, previous studies have shown a great deal of variability in chimpanzees' responses in such tests, without much consistency. Therefore, in the present study we sought to determine whether individual differences might be explained by our interaction models.

Relationship Interactions with Social and Individual Comparisons

Because of the significant influence of the number of days that a chimpanzee had lived with its test partner on its refusal rates overall, we further explored how this relationship variable interacted with subjects' responses to inequity and contrast as compared to the equity control condition (Table 3; Fig. 1). We found no effect of number of days that chimpanzees had lived with their test partners on their responses to inequity (as compared to the equity control condition; $b = -0.00004$, $P = 0.356$). However, contrary to our prediction that relationships would influence responses to the inequity condition but not the contrast condition, the longer subjects had lived with their test partner, the less likely they were to refuse in the contrast condition, compared to in the equity control condition ($b = -0.0001$, $P = 0.003$).

Personality Interactions with Social and Individual Comparisons

Because of the significant influence of personality on refusal rates overall (i.e. regardless of condition), we further explored how an individual's personality dimension ratings interacted with their responses in the inequity and contrast conditions, as compared to the equity control condition (Table 4). We found that the chimpanzees' personality dimension ratings showed differential effects on their responses in the inequity condition (i.e. to social comparison; Fig. 2). Chimpanzees that rated higher in openness were more likely to refuse in the inequity condition than in the equity control condition ($b = 1.737$, $P < 0.001$), whereas chimpanzees that rated higher in methodical were less likely to refuse in the inequity condition ($b = -1.323$, $P = 0.004$). Subjects that rated lower in agreeableness were less likely to refuse in the inequity condition than in the control condition ($b = -1.426$, $P < 0.001$). There was also a marginally significant tendency for chimpanzees that rated higher in extraversion to refuse more often in the inequity condition ($b = 0.439$, $P = 0.061$).

Considering the contrast condition (e.g. individual comparison), chimpanzees that rated higher in openness were more likely to refuse in the contrast condition, in which they (and their partners) were shown the high-value reward prior to receiving the lower-value one, as compared to the equity control ($b = 2.785$, $P < 0.001$). In contrast, chimpanzees that rated higher in methodical and Reactivity were less likely to refuse in the contrast condition as compared to the equity control condition (methodical: $b = -2.300$, $P < 0.001$; reactivity: $b = -1.239$, $P = 0.001$). There was no significant interaction between the chimpanzees' ratings in the dominance dimension and their refusals in the contrast or inequity conditions compared to the equity control.

DISCUSSION

Our study was designed to explore how chimpanzees' personality ratings and their relationships with their social partners influenced their responses to both inequitable outcomes (those in which their rewards compared unfavourably to their social partner's) and

situations of contrast (those in which their rewards compared unfavourably to their own previous offers). Personality was associated with reactions to both inequity and contrast; chimpanzees that were rated higher in the extraversion dimension and lower in the agreeableness dimension were more likely to respond to inequity, while those that were rated lower in the reactivity dimension were more likely to respond to contrast. Chimpanzees that were rated higher in the openness dimension and lower in the methodical dimension responded strongly in both the inequity and contrast conditions. Contrary to our prediction, relationship quality did not influence which chimpanzees chose to participate in the tests together or the strength of individuals' responses to the inequity condition, nor did it influence subjects' reactions to the inequity and contrast conditions differently. However, the number of days that a chimpanzee had lived with his or her test partner (i.e. the duration of their relationship) did influence their willingness to be tested together, as well as their responses in the contrast condition such that as their relationship tenure increased, their likelihood of refusing when faced with contrast effects decreased. Finally, we found that the overall frequency with which chimpanzees refused rewards (independent of condition) was influenced by demographic factors (their sex, rank and age) and their test experience (i.e. number of trials and sessions completed), but that these factors did not differ across the experimental manipulations.

We found that some of the chimpanzees' personality dimensions were associated with responses in both conditions, whereas others were specific to just one condition. Specifically, chimpanzees that were rated higher in the openness dimension and lower in the methodical dimension were more likely to refuse in both the inequity and contrast conditions. Openness includes traits such as 'human-oriented', 'inquisitive' and 'intelligent' (see Table 1), and thus, chimpanzees that were rated higher in openness might have refused more often because they were more reactive to being 'deceived' by the human experimenter in both conditions (it was the human who distributed and delivered the rewards). The finding related to the methodical dimension is more difficult to interpret, in part because the methodical dimension has only two adjectives (self-caring, methodical) that load onto it (Freeman, Brosnan, et al., 2013). The fact that chimpanzees that were scored highly on methodical were less likely to refuse in these conditions might imply that they were methodical and persistent in attempting to 'solve' the task, despite the frustration arising from receiving a less preferred reward. Indeed, a recent study, conducted at the same facility, found that male chimpanzees that rated highly on the methodical dimension showed greater persistence when presented with novel foraging tasks (Hopper, Price, et al., 2014).

More interesting are the personality dimensions that influenced chimpanzees in one condition but not the other. Specifically, when faced with inequity, chimpanzees that were rated higher on the extraversion dimension (this was only marginally significant; $P = 0.06$) and lower on the agreeableness dimension refused to exchange tokens and accept food rewards in the test more often than did other subjects. The chimpanzee personality dimension extraversion is positively correlated with behaviours such as begging and contact aggression and traits including 'active' and 'playful' but negatively correlated with the trait 'solitary,' indicating a socially oriented chimpanzee (Freeman, Brosnan, et al., 2013). Thus, chimpanzees with higher extraversion scores may be more sensitive to interindividual

interactions, which, in turn, may have made them more sensitive to the inequitable outcomes between themselves and a social partner. Conversely, the agreeableness dimension is positively correlated with affiliative behaviours but negatively correlated with ‘displace’, and is also positively correlated with the traits ‘protectiveness’ and ‘consideration’. We propose that chimpanzees with higher agreeableness scores are also socially oriented, but they are more interested in maintaining positive social relationships than they are in interindividual interactions in general, which may be why they are less reactive to inequity.

Chimpanzees that were scored higher on the reactivity/undependability dimension were less likely to refuse in the contrast condition than were individuals that scored lower on this dimension. In this condition, both the subject and its partner received a lower-value reward after both were shown a high-value reward. The chimpanzee dimension reactivity/undependability includes a suite of traits such as ‘excitable’, ‘impulsive’, ‘aggressive’ and ‘irritable’, and is negatively correlated with ‘calm’. A high rating on the reactivity/undependability dimension is also positively correlated with aggressive behaviours and negatively correlated with affiliative behaviours. Although it might be thought that these reactive individuals would be more likely to respond negatively to contrast effects, it could be that these chimpanzees’ impulsivity caused them to complete exchanges without considering the other rewards available to them. Alternatively, it might simply be that the reactivity/undependability dimension describes the behaviour of chimpanzees in a social behavioural context and is less suited to describing their behaviour in tests of individual cognition (cf. Hopper, Price, et al., 2014). More research is required to determine the predictive nature of these personality factors in a suite of different contexts.

Different personality dimensions correlated differentially with responses in the inequity and contrast conditions, indicating that the chimpanzees did view these two situations differently, despite the presence of the same social partner and the same foods in both conditions and an almost identical experimental procedure. We believe that responses to both are underpinned by the same cognitive mechanism, but the fact that this small tweak alters responses supports the notion that social and individual comparisons are viewed differently by the chimpanzees. There is a long history of research into personality, temperament and behavioural syndromes in nonhuman animals, all of which indicates that nonhuman species, like humans, show long-term, consistent patterns of behaviour that are independent of specific contexts (Budaev & Brown, 2011; Gosling, 2001; Sih et al., 2004). More recently, work in nonhuman primates has begun to link personality to behaviour and cognition (Hopper, Price, et al., 2014; Massen et al., 2013; van Oers, 2007), and our study extends this trend, emphasizing the need to consider personality when evaluating subjects’ behaviour and cognition in both social and nonsocial contexts. The variability in personality ratings and the typically limited sample pool for nonhuman primate research will make this task challenging, but, whenever possible, personality should be included as a between-subjects variable. We do note, however, the importance of ensuring that the traits being utilized are comparable to previously established traits. Differences in terminology or definitions in the literature may lead to inaccurate results, as would the application of one species’ personality dimensions to another species (Freeman & Gosling, 2010).

Considering subjects' relationships to one another, contrary to our prediction we found no influence of the quality of the interindividual relationship on the chimpanzees' responses to inequity, even when controlling for personality. Based on previous results in humans (Clark & Grote, 2003) and chimpanzees (Brosnan et al., 2005), we anticipated that subjects in closer relationships would respond less strongly to inequity than when paired with a chimpanzee with whom they had a less close relationship. Moreover, we expected that any failure of relationship quality to influence inequity would be due to those pairs with less strong or less positive relationships refusing to participate at all. This is not what we found. This finding was surprising given that relationship quality influences behaviour in other contexts (Cheney, 1999; Horner et al., 2010; Silk et al., 2013; Watts, 2002), and tolerance predicts whether chimpanzees will work together in a cooperative task (Melis et al., 2006a, 2006b). Furthermore, our measure of relationship quality, which was based on the composite sociality index measure developed for baboons (Silk, Alberts, & Altmann, 2003, 2006; Silk, Altmann, & Alberts, 2006), has been shown to predict the influence of relationships on food sharing in the same population of chimpanzees that we examined here (Silk et al., 2013).

We did, however, find that chimpanzees that had lived with their partners longer were (1) more likely to be willing to test together and (2) less reactive to individual contrast effects, but this did not influence their responses to inequity. The former result may indicate that they were more comfortable with individuals they had known longer. The latter is harder to explain as we predicted the opposite, that subjects' relationships would influence inequity, which is a social comparison, more than contrast, which is not. Perhaps when paired with a subject with whom they were comfortable they were more accepting of lower-than-anticipated outcomes (contrast condition) and less attentive or responsive to their partner's better outcome (inequity condition). Additionally, while our measure of relationship duration has been implicated in responses to inequity in other contexts (Brosnan et al., 2005; Hopper et al., 2004), in neither case were all possible explanations controlled for, therefore it may be that these results were influenced by another factor, such as the chimpanzees' personalities. Clearly more work needs to be done to determine whether relationship quality or tenure influences responses to inequity in chimpanzees, as has been observed in chimpanzees in other contexts (Bonnie & de Waal, 2005; Kutsukake, 2006).

The focus of this study was on the differential effects of inequity and individual contrast on subjects' reactions to working for food rewards. However, we also found that the overall rate of refusals (across all three conditions) varied across demographics and contexts, independent of the condition (e.g. inequity or contrast). These findings are worth additional consideration because they highlight how these demographic factors influence cognitive and behavioural testing in nonhuman primates even when they do not differentially influence the dependent variables. We found a sex difference, with males being more likely to refuse to complete the task in all three conditions than females. However, this effect only showed up in some of the models, which is consistent with earlier findings of inconsistent or absent sex differences in inequity responses (Brosnan et al., 2005, 2010; Hopper, Lambeth, et al., 2014). As has been found previously, higher-ranking subjects were also more likely to refuse to exchange tokens and accept food rewards than were lower-ranking ones (Bräuer et al., 2009; Brosnan et al., 2010), and refusals decreased among older chimpanzees, perhaps related to cognitive changes seen in older chimpanzees (Lacreuse et al., 2014). There was

also a strong test order effect that was independent of partnership or session. All subjects were more likely to refuse as the number of trials progressed within a session but less likely to refuse as the period of testing progressed across sessions. These results may indicate that within a session, subjects became more frustrated by the continual violation of their expectations, or more sated, but across sessions, which covered an extended period, the chimpanzees grew accustomed to their lack of control over the situation and so reacted less often when faced with rewards that were less valuable than anticipated (e.g. learned helplessness; Seligman & Maier, 1967). The variability we see across demographic factors and testing conditions highlights the importance of considering demographic variables and comparing results from earlier trials and sessions to those from later trials and sessions when interpreting results in cognitive and behavioural tests.

In conclusion, a number of factors influenced subjects' responses. Counter to our hypothesis, factors related to relationship duration were correlated with refusals in the contrast condition but not in the inequity condition. Supporting the fact that contrast and inequity were treated differently by the chimpanzees, several personality factors were correlated with one but not the other. These results join a growing body of literature highlighting the importance of considering subjects' personalities when assessing the responses of animals in behavioural and cognitive studies.

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References

- Altmann J. Observational study of behavior: sampling methods. *Behaviour*. 1974; 49:227–267. [PubMed: 4597405]
- Bonnie KE, de Waal FBM. Affiliation promotes the transmission of a social custom: handclasp grooming among captive chimpanzees. *Primates*. 2005; 47:27–34. [PubMed: 16142425]
- Bräuer J, Call J, Tomasello M. Are apes inequity averse? New data on the token-exchange paradigm. *American Journal of Primatology*. 2009; 71:175–181. [PubMed: 19021260]
- Brosnan SF. Justice and fairness related behaviors in non-human primates. *Proceedings of the National Academy of Sciences of the United States of America*. 2013; 110:10416–10423. [PubMed: 23754407]
- Brosnan SF, de Waal FBM. A concept of value during experimental exchange in brown capuchin monkeys. *Folia Primatologica*. 2004; 75:317–330.
- Brosnan SF, Schiff HC, de Waal FBM. Tolerance for inequity may increase with social closeness in chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*. 2005; 272:253–258.
- Brosnan SF, Talbot C, Ahlgren M, Lambeth SP, Schapiro SJ. Mechanisms underlying responses to inequitable outcomes in chimpanzees. *Pan troglodytes*. *Animal Behaviour*. 2010; 79:1229–1237.
- Budaev, S.; Brown, C. Personality traits and behaviour. In: Brown, C.; Laland, K.; Fish, J Krause, editors. *Cognition and behaviour*. Cambridge, UK: Blackwell; 2011. p. 135–165.
- Carere, C.; Maestripieri, D. *Animal personalities: behavior, physiology and evolution*. Chicago, IL: University of Chicago Press; 2013.
- Carter AJ, Marshall HH, Heinsohn R, Cowlishaw G. Personality predicts decision making only when information is unreliable. *Animal Behaviour*. 2013; 86:633–639.

- Cheney DL. Recognition of other individuals' social relationships by female baboons. *Animal Behaviour*. 1999; 58:67–75. [PubMed: 10413542]
- Clark, MS.; Grote, NK. Close relationships. In: Millon, T.; Lerner, MJ.; Weiner, IB., editors. *Handbook of psychology: Personality and social psychology*. New York, NY: John Wiley; 2003. p. 447–461.
- Freeman HD, Brosnan SF, Hopper LM, Lambeth SP, Schapiro SJ, Gosling SD. Developing a comprehensive and comparative questionnaire for measuring personality in chimpanzees using a simultaneous top–down/bottom–up design: chimpanzee personality. *American Journal of Primatology*. 2013; 75:1042–1053. [PubMed: 23733359]
- Freeman HD, Gosling SD. Personality in nonhuman primates: a review and evaluation of past research. *American Journal of Primatology*. 2010; 72:653–671. [PubMed: 20568079]
- Freeman HD, Sullivan J, Hopper LM, Talbot CF, Holmes AN, Schultz-Darken N, et al. Different responses to reward comparisons by three primate species. *PLoS One*. 2013; 8:e76297. [PubMed: 24130767]
- Gosling SD. From mice to men: what can we learn about personality from animal research? *Psychological Bulletin*. 2001; 127:45–86. [PubMed: 11271756]
- Hopper LM, Lambeth SP, Schapiro SJ, Bernacky BJ, Brosnan SF. The ontogeny of social comparisons in rhesus macaques (*Macaca mulatta*). *Journal of Primatology*. 2013; 2:109.
- Hopper LM, Lambeth SP, Schapiro SJ, Brosnan SF. When given the opportunity, chimpanzees maximize personal gain rather than 'level the playing field'. *PeerJ*. 2013; 1:e165. [PubMed: 24109550]
- Hopper LM, Lambeth SP, Schapiro SJ, Brosnan SF. Social comparison mediates chimpanzees' responses to loss, not frustration. *Animal Cognition*. 2014; 17:1303–1311. [PubMed: 24880642]
- Hopper LM, Price SA, Freeman HD, Lambeth SP, Schapiro SJ, Kendal RL. Influence of personality, age, sex, and estrous state on chimpanzee problem-solving success. *Animal Cognition*. 2014; 17:835–847. [PubMed: 24322874]
- Horner V, Proctor D, Bonnie KE, Whiten A, de Waal FBM. Prestige affects cultural learning in chimpanzees. *PLoS One*. 2010; 5:e10625. [PubMed: 20502702]
- Horowitz A. Fair is fine, but more is better: limits to inequity aversion in the domestic dog. *Social Justice Research*. 2012; 25:195–212.
- Kurvers RHJM, van Oers K, Nolet BA, Jonker RM, van Wieren SE, Prins HHT, et al. Personality predicts the use of social information. *Ecology Letters*. 2010; 13:829–837. [PubMed: 20482585]
- Kutsukake N. The context and quality of social relationships affect vigilance behaviour in wild chimpanzees. *Ethology*. 2006; 112:581–591.
- Lacreuse A, Russell JL, Hopkins WD, Hearndon JG. Cognitive and motor aging in female chimpanzees. *Neurobiology of Aging*. 2014; 35:623–632. [PubMed: 24112794]
- Massen JJM, Antonides A, Arnold A-MK, Bionda T, Koski S. A behavioral view on chimpanzee personality: exploration tendency, persistence, boldness, and tool-orientation measured with group experiments. *American Journal of Primatology*. 2013; 9:947–958. [PubMed: 23649750]
- Massen JJM, Koski SE. Chimps of a feather sit together: chimpanzee friendships are based on homophily in personality. *Evolution and Human Behavior*. 2014; 35:1–8.
- Massen JJM, van den Berg LM, Spruijt BM, Sterck EHM. Inequity aversion in relation to effort and relationship quality in long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology*. 2012; 74:145–156. [PubMed: 22038902]
- Mehrabian A. Pleasure–arousal–dominance: a general framework for describing and measuring individual differences in temperament. *Current Psychology*. 1996; 14:261–292.
- Melis AP, Hare B, Tomasello M. Chimpanzees recruit the best collaborators. *Science*. 2006a; 311:1297–1300. [PubMed: 16513985]
- Melis AP, Hare B, Tomasello M. Engineering cooperation in chimpanzees: tolerance constraints on cooperation. *Animal Behaviour*. 2006b; 72:275–286.
- Morton FB, Lee PC, Buchanan-Smith HM, Brosnan SF, Thierry B, Paukner A, et al. Personality structure in brown capuchin monkeys (*Sapajus apella*): comparisons with chimpanzees (*Pan troglodytes*), orangutans (*Pongo* spp.), and rhesus macaques (*Macaca mulatta*). *Journal of Comparative Psychology*. 2013; 127:282–298. [PubMed: 23668695]

- Murray, L. Personality and individual differences in captive African apes. Cambridge, UK: University of Cambridge; 1995.
- Pederson A, King J, Landau VI. Chimpanzee (*Pan troglodytes*) personality predicts behavior. *Journal of Research in Personality*. 2005; 39:534–549.
- Price SA, Brosnan SF. To each according to his need? Variability in the responses to inequity in non-human primates. *Social Justice Research*. 2012; 25:140–169.
- Raihani NJ, McAuliffe K, Brosnan SF, Bshary R. Are cleaner fish, *Labroides dimidiatus* inequity averse? *Animal Behaviour*. 2012; 84:665–674.
- Range F, Horn L, Viranyi Z, Huber L. The absence of reward induces inequity aversion in dogs. *Proceedings of the National Academy of Sciences of the United States of America*. 2009; 106:340–345. [PubMed: 19064923]
- Range F, Leitner K, Virányi Z. The Influence of the relationship and motivation on inequity aversion in dogs. *Social Justice Research*. 2012; 25:170–194.
- Reynolds GS. Behavioral contrast. *Journal of the Experimental Analysis of Behavior*. 1961; 4:441–466.
- Roma PG, Silberberg A, Ruggiero AM, Suomi SJ. Capuchin monkeys, inequity aversion, and the frustration effect. *Journal of Comparative Psychology*. 2006; 120:67–73. [PubMed: 16551166]
- Sapolsky R, Alberts SC, Altmann J. Hypercortisolism associated with social subordination or social isolation among wild baboons. *Archives of General Psychiatry*. 1997; 54:1137–1143. [PubMed: 9400351]
- Seligman M, Maier S. Failure to escape traumatic shock. *Journal of Experimental Psychology*. 1967; 74:1–9. [PubMed: 6032570]
- Sih A, Bell A, Johnson JC. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*. 2004; 19:372–378. [PubMed: 16701288]
- Silk JB, Alberts SC, Altmann J. Social bonds of female baboons enhance infant survival. *Science*. 2003; 302:1231–1234. [PubMed: 14615543]
- Silk JB, Alberts SC, Altmann J. Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology*. 2006; 61:197–204.
- Silk JB, Altmann J, Alberts SC. Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology*. 2006; 61:183–195.
- Silk JB, Brosnan SF, Henrich J, Lambeth SP, Shapiro S. Chimpanzees share food for many reasons: the role of kinship, reciprocity, social bonds and harassment on food transfers. *Animal Behaviour*. 2013; 85:941–947. [PubMed: 25264374]
- Takimoto A, Fujita K. I acknowledge your help: capuchin monkeys' sensitivity to others' labor. *Animal Cognition*. 2011; 5:715–725. [PubMed: 21519900]
- Talbot CF, Freeman HD, Williams LE, Brosnan SF. Squirrel monkeys' response to inequitable outcomes indicates a behavioural convergence within the primates. *Biology Letters*. 2011; 7:680–682. [PubMed: 21508022]
- van Oers K. The need for interdisciplinary research in personality studies: invited commentary. *European Journal of Personality*. 2007; 21:635–637.
- van Oers K, Klunder M, Drent PJ. Context dependence of personalities: risk-taking behavior in a social and a nonsocial situation. *Behavioral Ecology*. 2005; 16:716–723.
- Vazire, S.; Gosling, SD.; Dickey, A.; Schapiro, S. Measuring personality in non-human animals. In: Robins, R.; Fraley, RC.; Krueger, R., editors. *Handbook of research methods in personality psychology*. New York, NY: Guilford Press; 2007. p. 190–206.
- Wascher CAF, Bugnyar T. Behavioral responses to inequity in reward distribution and working effort in crows and ravens. *PLoS One*. 2013; 8:e56885. [PubMed: 23437262]
- Watts DP. Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour*. 2002; 139:343–370.

Yamagishi T, Horita Y, Takagishi H, Shinada M, Tanida S, Cook KS. The private rejection of unfair offers and emotional commitment. *Proceedings of the National Academy of Sciences of the United States of America*. 2009; 106:11520–11523. [PubMed: 19564602]

Highlights

- We examined the effects of personality on chimpanzees' responses to inequity and contrast.
- Extraversion and agreeableness were correlated with sensitivity to inequity.
- The quality of the pairs' relationship did not explain variation in responses to inequity.
- Longer-term associates were less likely to refuse in the contrast condition.
- Personality is important when evaluating subjects' responses in cognitive and behavioural tests.

Figure 1.

Frequency of subject refusals across conditions (equity, contrast, inequity) for the number of days that subjects were housed together. Graphs compare subjects that had lived together for an extended period (>1 SD above the mean = 'High number of days') relative to other subjects ('Low number of days'). Note that in the GLLAMM analysis, relationship duration was coded continuously.

Figure 2.

Frequency of subject refusals across conditions (equity, contrast, inequity) for the six personality dimensions described by Freeman, Brosnan, et al. (2013): (a) agreeableness; (b) openness; (c) methodical; (d) extraversion; (e) dominance; (f) reactivity. Graphs compare subjects that were rated highly (>1 SD above the mean = 'High') on each dimension relative to other subjects ('Low'). Note that in the GLLAMM analysis, personality dimensions were coded continuously.

Table 1

Each of the six chimpanzee personality (varimax-rotated) factors identified by Freeman, Brosnan, et al. (2013) showing the traits that loaded onto each and the correlations found with observed behaviours collected 2 years previously

	Reactivity/undependability	Dominance	Extraversion	Openness	Agreeableness	Methodical ^a
Traits	(-) Calm Irritable Autistic Deceptive Impulsive Defiant Mischievous Jealous Manipulative Stingy Bullying Aggressive Eccentric Socially inept Excitable Temperamental/moody	(-) Fearful (-) Timid (-) Cautious (-) Dependent (-) Anxious Bold Relaxed Dominant	(-) Solitary (-) Depressed Active Playful Sexual Affiliative	Human oriented Persistent Inventive Intelligent Affectionate/friendly Inquisitive/curious	Protective Considerate	Self-caring Methodical
Behaviours (positive correlation)	Aggressive (intervene, sexual behaviour)	Aggressive (contact aggression, display, intervene, noncontact aggression, sexual behaviour)	Aggressive (contact aggression)	Submissive (submissive)	Affiliatory (affiliation)	
Behaviours (negative correlation)	Affiliatory (postconflict affiliation)	Affiliatory (proximity) Submissive (submissive)	Submissive (begging) Affiliatory (play)	Affiliatory (play) Affiliatory (proximity)	Aggressive (displace)	

A trait associated with '(-)' indicates that the trait was negatively correlated with that factor. Each behaviour correlation provides the category of behaviour followed by the specific behavioural codes in parentheses.

^aMethodical was not correlated with any of the chimpanzees' observed behaviours.

Table 2

Influence of model factors on dependent variable, independent of test condition ^a

	Model 1 (CSI only)			Model 2 (with personality)			Model 3 (with no. of days)		
	<i>b</i>	CI	<i>P</i>	<i>b</i>	CI	<i>P</i>	<i>b</i>	CI	<i>P</i>
No. of level 1 units	5548			5548			5548		
No. of level 2 units	37			37			37		
No. of level 3 units	18			18			18		
Condition number	268.31039			4141.8136			402484.92		
Log likelihood	-2441.3684			-2437.9689			-2432.5761		
No. of days together									
CSI	0.152	0.029, 0.276	0.015	0.257	0.114, 0.399	<0.001	0.00015	-0.0003, 2.08e-06	0.053
Sex	0.508	0.242, 0.774	<0.001	-0.29	-1.510, 0.930	0.641	-0.005	-0.170, 0.059	0.343
Age	-0.052	0.242, 0.774	<0.001	-0.108	-0.144, -0.072	<0.001	0.325	0.040, 0.609	0.025
Subject's rank	-0.917	-1.059, -0.775	<0.001	-1.335	-1.795, -0.876	<0.001	-0.063	-0.081, 0.044	<0.001
Session	-0.095	-0.137, -0.053	<0.001	-0.095	-0.137, -0.053	<0.001	-0.456	-0.593, -0.320	<0.001
Trial	0.023	0.013, 0.033	<0.001	0.023	0.013, 0.033	<0.001	-0.094	-0.136, -0.052	<0.001
Equity control	0.327	0.150, 0.504	<0.001	0.327	0.151, 0.503	<0.001	0.023	0.013, 0.033	<0.001
Inequity	0.347	0.170, 0.523	<0.001	0.350	0.174, 0.526	<0.001	0.324	0.148, 0.501	<0.001
Agreeableness				-2.089	-3.048, -1.131	<0.001	0.344	0.168, 0.521	<0.001
Openness				-0.997	-1.727, -0.266	<0.001			
Methodical				-0.77	-1.653, 0.113	0.087			
Extraversion				1.865	0.668, 3.062	0.002			
Dominance				-1.435	-2.127, -0.744	<0.001			
Reactivity				-3.152	-4.279, -2.025	<0.001			
Group 2	0.716	0.326, 1.105	<0.001	0.801	0.133, 1.468	0.019	0.573	-0.245, 0.901	0.001
Group 3	2.107	1.790, 2.425	<0.001	2.261	1.129, 3.393	<0.001	2.788	1.736, 3.840	<0.001
Group 4	-0.151	-0.834, 0.367	0.397	-0.658	-1.157, -0.158	0.010	0.403	-0.014, 0.821	0.058
Intercept level 1	-0.234	-0.834, 0.367	0.445	29.705	19.772, 39.637	<0.001	0.947	0.358, 1.536	0.002
Intercept partner level	0.492		<0.001	1.045	0.893, 1.196	<0.001	0.664		<0.001
Intercept subject level	2.107		<0.001	0.518	0.397, 0.639	<0.001	0.669		<0.001

CSI: composite sociability index.

^dThis GLLMM model considers the influence of our model factors on the dependent variable, refusal rate, independently from the test condition (inequity or contrast). Model 1 considers how the factors influence the dependent variable independent of personality traits, model 2 considers the influence of personality traits with those factors included in model 1, and model 3 includes the time subjects had lived together (in days) with those factors included in model 1. All variables except subject's rank were coded as continuous variables (subject's rank was categorical). Our data were clustered at three levels: the subject's interactions with a given partner (e.g. repeated trials per pair), the subject's interactions with other partners, and the group in which the subject lived. To control for the first two of these, we included variables in the model that indicated both levels for each interaction (intercept subject level and intercept partner level, respectively). To control for group, we included different variables in the model for each group (group 2, group 3, group 4). The personality dimensions are derived from Freeman, Brosnan, et al. (2013). See Table 3 for the model including the test condition. Significant *P* values are shown in bold

Table 3

Relationship interactions with social and individual comparison ^a

	Contrast vs equity model			Inequity vs equity model		
No. of level 1 units	3698			3700		
No. of level 2 units	37			37		
No. of level 3 units	18			18		
Condition number	66654.111			56834.365		
Log likelihood	-1571.3621			-1509.0148		
	<i>b</i>	CI	<i>P</i>	<i>b</i>	CI	<i>P</i>
Days together*inequity						
Days together*contrast	-0.00011	-0.00019, -0.00004	0.003	-0.0000375	-0.000117, 0.000042	0.356
Days together	-0.0003	-0.00057, -0.00005	0.016	-0.001	-0.00084, -0.00042	<0.001
CSI	-0.050	-0.180, 0.079	0.444	0.300	0.146, 0.452	<0.001
Sex	-0.396	-0.823, 0.031	0.069	0.316	-0.841, 0.716	0.122
Age	-0.002	-0.025, 0.020	0.851	-0.089	-0.117, -0.061	<0.001
Subject rank	-0.819	-1.048, -0.033	<0.001	-0.296	-0.521, -0.071	0.010
Session	-0.090	-0.148, -0.033	0.002	-0.132	-0.0188, -0.077	<0.001
Trial	0.029	0.0116, 0.041	<0.001	0.020	0.001, 0.033	0.002
Control	0.582	0.342, 0.822	<0.001			
Inequality				0.447	0.194, 0.700	0.001
Group 2	0.362	-0.100, 0.824	0.124	1.159	0.682, 1.635	<0.001
Group 3	3.973	2.299, 5.648	<0.001	6.229	4.835, 7.623	<0.001
Group 4	0.948	0.340, 1.557	0.002	1.989	1.366, 2.610	<0.001
Intercept level 1	-0.124	-0.821, 0.572	0.726	0.262	-0.762, 1.286	0.616
Intercept partner level	1.083		<0.001	0.829		<0.001
Intercept subject level	1.219		<0.001	0.913		<0.001

CSI: composite sociality index.

^aThe number of days that members of the pair had lived together influenced subjects' behavioural responses, so we separately considered whether this factor interacted differently with contrast (contrast vs equity model) and inequity (inequity vs equity model). Significant *P* values are shown in bold.

Table 4

Personality interactions with social and individual comparisons ^a

	Contrast vs equity model				Inequity vs equity model			
	<i>b</i>	CI	<i>P</i>		<i>b</i>	CI	<i>P</i>	
No. of level 1 units	3698				3700			
No. of level 2 units	37				37			
No. of level 3 units	18				18			
Condition number	433423.62				419329.46			
Log likelihood	-1537.197				-1474.0018			
Agreeableness*contrast	-0.423	-0.965, 0.119	0.126					
Openness*contrast	2.785	2.042, 3.526	<0.001					
Methodical*contrast	-2.300	-3.109, -1.491	<0.001					
Extraversion*contrast	-0.079	-0.535, 0.377	0.734					
Dominance*contrast	0.008	-0.481, 0.497	0.975					
Reactivity*contrast	-1.239	-1.964, -0.514	0.001					
Agreeableness*inequity					-1.426	0.984, 2.489	<0.001	
Openness*inequity					1.737	-2.034, -0.818	<0.001	
Methodical*inequity					-1.323	-2.228, -0.418	0.004	
Extraversion*inequity					0.439	-0.020, 0.898	0.061	
Dominance*inequity					0.328	-0.199, 0.855	0.223	
Reactivity*inequity					-0.685	-1.506, 0.137	0.102	
Agreeableness	-2.553	-3.662, -1.445	<0.001		-0.484	-2.192, 1.225	0.579	
Openness	-2.716	-3.584, -1.848	<0.001		-2.931	-3.728, -2.134	<0.001	
Methodical	-0.331	-1.418, 0.757	0.551		1.565	0.143, 2.988	0.031	
Extraversion	3.151	1.862, 4.441	<0.001		0.434	-1.660, 2.527	0.685	
Dominance	-1.636	-2.595, -0.677	0.001		-1.497	-2.293, -0.700	<0.001	
Reactivity	-3.155	-4.763, -1.548	<0.001		-2.976	-4.492, -1.461	<0.001	
Number of days together	0.0003	0.00003, 0.00060	0.029		-0.0004	-0.0007, -0.0002	<0.001	
CSI	0.136	-0.036, 0.308	0.120		0.430	0.280, -0.579	<0.001	
Sex	-1.182	-2.228, -0.136	0.027		0.953	-1.187, 3.093	0.383	
Age	-0.117	-0.160, -0.075	<0.001		-0.148	-0.188, -0.108	<0.001	

	Contrast vs equity model		Inequity vs equity model			
Subject rank	-1.321	-1.827, -0.815	<0.001	-2.005	-2.621, -1.389	<0.001
Session	-0.105	-0.164, 0.046	<0.001	-0.158	-0.217, -0.100	<0.001
Trial	0.030	0.017, 0.042	<0.001	0.020	0.008, 0.033	0.002
contrast	4.572	-1.871, 11.014	0.164			
Inequality				3.564	-3.671, 10.798	0.334
Group 2	2.769	1.935, 3.603	<0.001	0.457	-0.609, 1.523	0.401
Group 3	0.318	-2.195, 2.832	0.804	5.606	2.880, 8.331	<0.001
Group 4	-0.718	-1.430, -0.006	0.048	-0.026	-0.658, 0.606	0.936
Intercept level 1	32.472	17.802, 47.143	<0.001	30.016	17.611, 42.420	<0.001
Intercept partner level	1.310		<0.001	2.483		<0.001
Intercept subject level	0.344		<0.001	0.633		<0.001

CSI: composite sociality index.

^aPersonality influenced subjects' behavioural responses, so we separately considered whether these personality factors interacted differently with contrast (contrast vs equity model) and inequity (inequity vs equity model). Significant *P* values are shown in bold.