

Orangutans (*Pongo pygmaeus*) Do Not Form Expectations Based on Their Partner's Outcomes

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Key Words

Orangutan · *Pongo pygmaeus* · Inequity · Expectation · Convergent evolution · Social comparison · Great apes

Abstract

Several primate species form expectations based on others' outcomes, responding negatively when their outcomes differ from their partners'. The function and evolutionary pathway of this behavior are unknown, in part because all of the species which have been tested thus far share traits related to a gregarious lifestyle, intelligence, and cooperativeness. Our goal was to test whether inequity is a homology among primates or a convergence by comparing one species known to show social comparisons, the chimpanzee, to another great ape which differs on several of these life history characteristics. Using a protocol identical to one used previously with chimpanzees, we tested whether orangutans, an intelligent but predominantly solitary species with few opportunities to cooperate, responded similarly. To allow for a strong comparison with chimpanzees (and other species), we used socially housed adults of both sexes, tested with members of their social group. Orangutans did not respond negatively to inequity, supporting previous findings and indicating that inequity responses in apes are likely a convergence based on either sociality or cooperative tendency. These results in such closely related species highlight the need for additional comparative studies to understand better the function and evolution of social behaviors. Copyright © 2011 S. Karger AG, Basel

Introduction

Many species show behavioral reactions indicating that they dislike receiving less than anticipated, a phenomenon known as the contrast effect [Reynolds, 1961]. In a study almost a century ago, Tinklepaugh [1928] hid treats under a bucket in the evening, and the following morning, he lifted the bucket and gave those treats to the monkeys (*Macaca* spp.). If, however, he surreptitiously switched the treats for a lettuce leaf, the monkeys reacted poorly in the morning, refusing those rewards. In the case of such contrast effects, the primates formed an expectation based on what they were initially offered; then reacted negatively when they did not receive it. Thus, the monkeys were comparing their outcomes with those they expected, without reference to other individuals, setting up an individual comparison (that is, a comparison with one's self). On the other hand, recent evidence indicates that expectations may also be formed based on what *others* receive, setting up a social comparison (a comparison with one's partners).

Several species of primates have been found to respond negatively when given rewards of lower value than those their partners receive [Brosnan and de Waal, 2003; Brosnan et al., 2005; Fletcher, 2008; Brosnan et al., 2010b], as do dogs [Range et al., 2008]. In the typical experimental situation for such a social comparison, the subject first observes a social partner complete a task and receive a reward, and then completes the same task to receive a reward. In some cases, the social comparison provides the same reward to both the subject and its partner, and thus expectations by the subject based on what it observed its partner receive agree with the actual reward the subject receives. In other cases, the subject may receive less desirable rewards than its partner, so the subject experiences inequity, based on the (social) comparison of its outcomes with those of its partner. Finally, the relative importance of social and individual comparisons can be evaluated by comparing reactions when both the subject and its partner receive the same reward, while better rewards are shown, but not given to either individual (see below for more discussion of this individual comparison control). If subjects are more likely to refuse the reward in the inequity condition than in the equity control, they are presumably forming an expectation about what reward they will receive based upon the reward that their partner got, hence making a social comparison. This social comparison is a violation of expectation based upon another's outcomes, and is likely the basis for the negative reaction to inequity which is seen in humans as well as other species [Brosnan, 2009].

Interestingly, although Tinklepaugh [1928] elicited individual comparisons by simply offering rewards to his monkeys, social comparisons appear to occur only in the context of a task. In no study in which subjects (and their partners) are simply handed rewards do subjects show a negative reaction. Although some of the studies differ on multiple factors [Bräuer et al., 2006; Dubreuil et al., 2006; Roma et al., 2006; Fontenot et al., 2007], it also includes studies using the same subjects that previously showed a negative reaction when a task was involved [Dindo and de Waal, 2006] and studies which included this comparison specifically as either a between-subject [Newirth et al., 2009] or within-subject [Brosnan et al., 2010b; Talbot et al., 2011] component. Thus, a task is clearly critical for eliciting inequity response in a social setting. Such a different treatment of 'earned' versus 'free' rewards is known in several paradigms [Carder and Berkowitz, 1970], and may be more salient in this case as so-

cial comparison is likely most critical when subjects are comparing their outcomes after a joint activity [Brosnan, 2006a; van Wolkenten et al., 2007].

It is also important to separate out when a response is due to individual comparisons (a violation of expectation based on what was offered previously) versus social comparisons (a violation of expectation based on what one's partner was offered). Monkeys are clearly sensitive to individual comparisons [Roma et al., 2006; Silberberg et al., 2009], but this alone cannot explain the primates' behavior in social comparison tests. For instance, in one comparison, chimpanzees' reactions were compared between situations in which (1) their partners received a higher-value reward while they received a lower-value one (social comparison), and (2) those in which the subjects (and their partners) were offered the (same) higher-value reward and then given the lower-value one instead (e.g. the individual comparison control from above). This latter is an individual comparison since the discrepancy is between the subject's outcomes and the earlier offer, not between the subject's and partner's outcomes, but is set in a social context and thus controls for differences in behavior due to social separation. In one group of chimpanzees, all responding subjects reacted most strongly to the social comparison condition [Brosnan et al., 2005] whereas at another facility, males responded more strongly to the social comparison condition while females responded more to individual comparison [Brosnan et al., 2010b]. Moreover, capuchins respond similarly to lower-value rewards regardless of the reward type (higher or lower) used in the previous session, showing that these results cannot be explained by individual comparisons over a longer time frame either [van Wolkenten et al., 2007]. Finally, apes do not respond to lower-value foods differently depending upon whether they received them first or second [Bräuer et al., 2006]. Note that this does not mean that individual comparisons are not important; they clearly are. However, in some contexts, social comparisons may make a stronger impact on how primates react to their outcomes than do individual comparisons.

Even in species for which reactions to social comparison are shown in some contexts, there is variability. For instance, as mentioned above, chimpanzees show highly variable responses, differing within the same study between social groups [Brosnan et al., 2005] and between males and females [Brosnan et al., 2010b]. Some studies have found no reaction at all [Bräuer et al., 2009]. Similar variability is seen in capuchins [Silberberg et al., 2009]. There is likely some effect of experimental paradigm [for a discussion, see Brosnan et al., 2010b], but clearly other social and individual factors are at play. This variability means that it is important to investigate behaviors across several groups using paradigms that are known to elicit the response in at least some contexts.

Studying inequity under conditions of social comparison is important, both to determine how this response evolved and, a related question, the function of the behavior, as well as to clarify why the context of the interaction (such as the presence of a task or the individuals' sex or social group composition) plays such a large role in shaping responses. It could represent a widespread homology, as it appears that individual comparison is widespread among animals (e.g. successive negative contrast) [Friedan et al., 2009]. However, given the data, it is also a reasonable hypothesis that it is due to convergence, based on characteristics such as cognitive ability, group living, or cooperative tendency [Fehr and Schmidt, 1999; Brosnan, 2006b]. One difficulty with the currently available data is that they all involve highly social, highly cooperative species which do well in cognitive tasks, making it difficult to

dissociate homology from convergence. Even the evidence from domestic dogs is uninformative on this measure, since domestic dogs converge on the same behavioral suite of intelligence, group living and cooperation. Thus, for the current study, we investigated social contrast in the orangutan, a primarily solitary great ape species, using a procedure that is identical to that used previously in chimpanzees and capuchin monkeys.

Orangutans are closely related to the African great apes, including chimpanzees and humans, yet have a markedly different social structure. Individuals spend much of their lives solitarily, or in pairs consisting of a mother and her unweaned offspring. Although larger assemblages are possible [Singleton et al., 2009], and orangutans are social in captivity [Edwards and Snowdon, 1980], their social system nonetheless differs widely from that of the other great apes. Thus, if sociality is one of the prerequisites for social comparison, these apes are less likely than others to show the behavior.

Orangutans also seem to be less cooperative than are chimpanzees. In captivity, orangutans learn to solve mutualistic cooperation tasks [Chalmeau et al., 1997]. Moreover, when given the chance to exchange tokens for mutual benefit, orangutans learn to do so. One pair appeared to follow a reciprocal strategy [Dufour et al., 2008], and may even have been more reciprocal than the other apes (although this may have been due to a lack of understanding of their partner's outcome) [Pelé et al., 2009]. On the other hand, there are few examples of cooperation and reciprocity in the wild, particularly in comparison to other primates. For instance, orangutans do not seem to form coalitions and alliances to the same degree as other apes [van Schaik, 2004], and food sharing is rare or nonexistent [Bard, 1992; Jaeggi et al., 2008; van Noordwijk and Van Schaik, 2009]. Thus, it may be most accurate to say that orangutans have the capacity to cooperate in some circumstances, but do not typically do so, perhaps because their less gregarious tendencies led to fewer opportunities, and hence lower selective pressure.

Some preliminary work indicates that orangutans do not respond to social contrast in the absence of a task [Bräuer et al., 2006], as has been seen in all other primates studied. Although they may have shown social facilitation when partners got better rewards (as has been seen in capuchins) [Dindo and De Waal, 2006], unfortunately the orangutans were not analyzed separately from the other 3 ape species, so it is difficult to say. Another study that tested 4 female orangutans found no response, but used a procedure which did not elicit responses to social comparison in chimpanzees either. In this design, the orangutans faced each other and interacted through a 1-meter-wide booth [Bräuer et al., 2009], a procedure which in chimpanzees may lead to different responses than when individuals are side by side in a shared enclosure, possibly due to a lack of attention caused by spatial separation between the participants [Brosnan et al., 2010b]. For the current study, we tested a mixed-sex sample of orangutans seated side by side in a shared enclosure, thus using the procedure which is known to elicit responses to social contrast in both chimpanzees and capuchin monkeys.

For the present study, we tested the hypothesis that the formation of social expectations is the result of a homology in primates by examining the behavior in orangutans, a great ape that differs on the dimensions of gregariousness and cooperative behavior from chimpanzees. Given the current results in the field, we predicted that orangutans would not show a response to unequal outcomes, indicating a convergence. Given that orangutans differ from chimpanzees and capuchins both

in the level of cooperation seen in the wild and the extent of gregarious social living, a failure to find the response would not be able to fully disentangle the ecological constraints which led to the convergence (and, in turn, the presence of a response would be unable to disentangle homology from similarity in cognitive ability between the 3 species). Nonetheless, the study provides a much-needed step in determining the selective pressures which led to this behavior. To do this, we tested adult orangutans, living in a socially housed environment, that had not previously been exposed to a test such as this. We replicated a previous study which investigated responses to violations of social expectations in chimpanzees, including both the same conditions and the same experimental design and procedures (e.g. side-by-side apes sharing an enclosure) [Brosnan et al., 2010b]. Due to the large number of conditions, we were able to compare responses across conditions on a variety of dimensions, including differences in reward value and level of effort, and the effect of a task.

Methods

Subjects

Subjects were 5 adult orangutans, 2 males and 3 females, housed in social groups at Zoo Atlanta, Atlanta, Ga., USA. The subject pool included a male/female pair of Bornean orangutans, which were always tested with each other, and a trio of co-housed orangutans (2 Sumatran and 1 hybrid), which were each tested with both of the others. In both groups, juveniles were present, and were allowed to stay with their mothers if they chose not to separate. Two of the Sumatran subjects had extensive experience with human testing prior to arrival at the zoo; 1 was raised in an enculturated environment where he was taught human sign language [Miles, 1990a, b; Miles et al., 1996], whereas the other was reared in an computer-enriched environment of the Georgia State University Language Research Center [Washburn et al., 2007] and participated in cognitive tasks there [Beran, 2002]. All subjects were housed in social groups with indoor/outdoor access and extensive material enrichment (climbing structures, ropes and swings, barrels, and other toys). All subjects were fed their usual diet consisting of primate chow, fruits and vegetables throughout the study. In addition, feeding enrichment was provided on a daily basis as part of the husbandry routine. At no time prior to or during testing were the subjects deprived of food or water. All subjects participated voluntarily, being called in from their social groups and tested in pairs in one of the indoor dens of their living area (in order to limit distractions). For testing, pairs shared an indoor den and were not separated from one another.

Food Preference Tests

We established food preferences of the subjects through a dichotomous-choice test between a low-value food and a high-value food [Brosnan and de Waal, 2004]. To determine which foods to use, all subjects were given a series of these choice tests for a variety of different produce and treats. For each test, subjects were given 10 successive trials in which the experimenter held up a low-value food in one hand and a high-value food in the other, approximately 30 cm apart, centered in front of the orangutan. Presentation of low- and high-value foods alternated from left to right each trial in order to control for any side biases. Subjects could indicate their choice by gesturing to it with their hand or by moving their head in front of the preferred option, and they always received the food they indicated. The chosen food was considered to be the preferred one.

Our criteria for food selection were that each individual had to prefer the same high-value food to the same low-value food at least 80% of the time (8 of 10 trials in 2 sessions completed on different days) to be considered the food choice pair for this study. After the preference was established, each orangutan was given 10 consecutive pieces of the low-value food (in a separate session) to verify that they were willing to consume the food when no other foods were available. This was critical, as otherwise subjects would always reject the low-value food. Ultimately,

Table 1. Description of experimental conditions and their corresponding abbreviations

Abbreviation	Condition	Exchange	Food
ETLV	Equity Test, Low Value	Both exchange	Both low value (potato)
ETHV	Equity Test, High Value	Both exchange	Both high value (cereal or grape)
IT	Inequity Test	Both exchange	Subject low value (potato) Partner high value (cereal or grape)
FC	Food Control	Both exchange	Both see high value (cereal or grape) before exchange, receive low value (potato) following exchange
DT	Delay Test	Both exchange, subject waits 10 s after exchange before receiving food	Both high value (cereal or grape)
GR	Gift Reward	No exchange	Subject low value (potato) Partner high value (cereal or grape)
DETLV	Differential Exchange Test, Low Value	Subject exchanges Partner does not exchange	Both low value (potato)
DETHV	Differential Exchange Test, High Value	Subject exchanges Partner does not exchange	Both high value (cereal or grape)

This table is derived from Brosnan et al. [2010b].

there was no single food that all subjects preferred, so we used a piece of sweetened breakfast cereal for some subjects and a grape for the others; the same food was used for both individuals within a pair, and throughout that pair's tests. The lower-value food was a small piece of white potato, which all subjects would eat when it was presented alone.

Training

Prior to the study, all subjects had been trained to barter an inedible token in exchange for a food reward (this food was not used in subsequent testing). Tokens consisted of polyvinyl chloride pipes 20 cm in length and 1.9 cm in diameter. For a barter interaction, the experimenter positioned him or herself at eye level with the subject, showed the token to the orangutan, and then gave it to the orangutan. After the orangutan took the token completely inside the mesh housing, the experimenter held his/her hand outstretched, palm up, with fingertips a few inches from the caging. Upon returning the token into the experimenter's hand, the orangutan was given a food reward.

Testing

Each subject underwent a series of 8 tests, completing two 50-trial sessions of each test. All tests involved a conspecific partner from the same social group, and partners remained the same throughout testing. In some cases, individuals were used in multiple partnerships; in these cases, subjects completed all 26 sessions with one partner before beginning any testing with the second partner. Subjects received only 1 test per day. Both reward containers (one for the low-value food and one for the high-value food) were always present, full, and in the same position, regardless of whether they were used in the session, so that the presence of either of these rewards did not cue the subject or create differences in reaction. Subjects alternated the roles of subject and partner between sessions, but kept the same role within each session.

The order of sessions was randomized for each pair. For conditions in which the actions of both individuals were the same [such as the Equity Test, Low Value (ETLV) condition, see table 1], each pair (instead of each individual) received 2 sessions of each test, and it was randomly decided which individual went first on the first session. Ultimately, each pair received a total of 26 test sessions. Each test session consisted of 50 alternating trials between the partner and subject, so that each individual received 25 trials per test session and the partner always exchanged prior to the subject on each trial. Trials were separated only by the time it took the experimenter to record the response and prepare for the next trial, i.e. approximately 5 s.

In each trial, the orangutan had up to 10 s to accept the token and then up to 30 additional seconds to complete the exchange. Exchanges were considered successful if the subject returned the token to the experimenter's hand. If the exchange was not completed, we recorded a token refusal, consisting of either sharing the token with a partner (e.g. allowing the partner to have the token, with no implication for intent), pushing the token out of the mesh (away from the experimenter's hand), or placing the token down inside the cage and ignoring it, which were not considered successful exchanges. When the token had been returned, the experimenter held it up in front of, but out of reach of, the orangutan, then lifted the correct reward from the container visible to both orangutans and gave it to the orangutan that had just completed the exchange. Subjects occasionally did not take these rewards, again either refusing to accept them, sharing them with their partner, ignoring them, or throwing them away. These results were considered a refusal to accept the reward, and analysis was based on the total number of refusals.

Responses were immediately recorded on data sheets by the experimenter and all test sessions were videotaped for later interobserver reliability coding. Seventy-three percent of the data were recoded from the videotapes by coders blinded to the hypotheses to verify the experimenter data. Agreement was quite high (99.1%), although Cohen's kappa was somewhat lower (Cohen's $\kappa = 0.66$). Because testing was done in the orangutan's home enclosures, it was impossible to capture the entire area in the frame of the video camera, and their responses were at times obscured. Because of the better visibility experienced by the experimenter, we used only experimenter-coded data for analyses. Eight sessions were missing experimenter data which could not be accurately obtained from the videotapes, so those sessions were left out of the analysis (in all cases, each subject had at least 1 session of each condition with each partner).

Test Conditions

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

Inequitable versus Equitable Rewards

To test whether or not the orangutans responded when the other received a different reward, we included 3 conditions: an Inequity Test (IT) and 2 same-reward controls. There were no procedural differences between these tests; all individuals exchanged in every trial. For the IT, both orangutans completed an exchange; however, the subject received a low-value potato and the partner received a high-value cereal or grape. In the ETLV, both orangutans completed an exchange and received the low-value potato. The Equity Test, High Value (ETHV) condition was the same, except both orangutans received a high-value food. To test how subjects responded when their partner got a better reward, we compared subjects' reactions in the IT to their reactions in the ETLV. To compare how partners responded when the subject got a less desirable reward, we compared partners' reactions in the IT to their reactions in the ETHV.

Control for Individual Expectations

To compare social and individual expectations, we included a test which was identical to the ETLV, except that the subjects both saw the high-value food prior to every exchange. In this test, the Food Control (FC), the experimenter held up a high-value reward until the orangutan gestured toward it, either by extending their fingers or their lips through the mesh towards the food (some apes have been trained to accept food with their lips). However, after completing the exchange, the ape received a low-value potato piece. Note that the FC differs from the ETLV only in the way the orangutans' attention was drawn to the high-value food; the high-value food was present in the same location for every test, including the ETLV.

Effort and Task Controls

To compare the 2 previous methodologies, we compared the IT to the Gift Reward (GR) test, in which the subject received a potato and the partner the high-value food, but both individuals received their respective reward for 'free', without having to exchange a token beforehand. Although the GR and IT differ on 2 parameters (the presence of a task and the length of the interaction), they are appropriate for comparing the 2 differing methodologies that are found in the literature (which also vary on these 2 parameters). Note also that the results from the Delay Test (DT; 10-second delay) indicate that a delay is not sufficient, alone, to cause a response, indicating that the presence of the extra delay alone is not sufficient to change behavior.

The Role of Effort

Finally, we examined the effects of effort and procedure. In the DT, both individuals exchanged and received the high-value food (as in the ETHV); however, the subject was given a 10-second delay between returning the token and receiving their reward. The subjects' behavior in the DT could be compared to their behavior in the ETHV to see whether the addition of a delay caused changes in their response. It is also possible that a delay is not sufficient to trigger a response, but that a difference in the level of effort is. To investigate this, we used 2 tests, the Differential Exchange, Low Value (DETLV) test, in which both orangutans received a piece of potato, but the subject received it for free, while the partner had to complete an exchange, and the Differential Exchange, High Value (DETHV) test, which was identical, except that both orangutans received the high-value food. Both of these tests could be compared to the Equity Tests (e.g. compare DETLV and ETLV and compare DETHV and ETHV) to see whether the presence of an exchange caused a difference in response. These latter comparisons also differ on 2 parameters: there is an exchange present in some conditions, and these conditions will last somewhat longer. However, again, the results of the DT rule out the effect of a delay alone on the orangutans' responses.

Dependent Variables

For all conditions, the variables of interest were behavioral measures of responses to the food and the token (if present). As discussed above, this measure consisted of 2 components: subjects could refuse to accept the token or the reward. Subjects who refused the token or did not complete the exchange were not given a food reward and, therefore, had no opportunity to refuse to accept the reward. In conditions in which exchange was not used, only subjects' interactions with the food were included in this refusal measure.

Statistics

In order to determine whether there was variation between the conditions, omnibus Friedman's tests (nonparametric) were run; p values reported for Wilcoxon signed-rank statistics are all exact [Mundry and Fischer, 1998]. In the case of the Wilcoxon tests, 'n' sometimes differs due to the presence of ties. Although we have a specific hypothesis, it predicts different outcomes. Thus, we chose to use 2-tailed p values in all cases. If a result would have been significant with a 1-tailed test (e.g. $p < 0.1$), we note the presence of a nonsignificant trend.

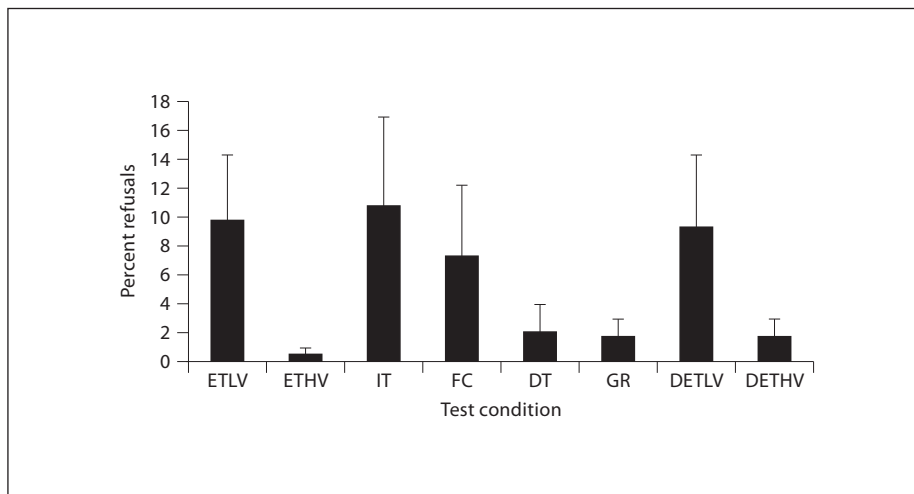


Fig. 1. The percent refusals (mean \pm SEM) by the orangutans across each of the 8 testing conditions. The refusal rate includes refusals to complete the exchange and refusals to accept the food (there is no token involved in the GR task). Orangutans' behavior did not differ across the 8 conditions. See table 1 for abbreviations.

Results

Overall Refusals

There was no overall variation among the different conditions [considering total refusals: Friedman's test: $\chi^2 = 11.287$, d.f. = 7, $p = 0.127$; considering only token refusals (which is out of 7 conditions due to the GR): Friedman's test: $\chi^2 = 8.525$, d.f. = 6, $p = 0.202$; considering only food refusals: Friedman's test: $\chi^2 = 5.751$, d.f. = 7, $p = 0.569$; fig. 1]. Despite this, we did some additional direct comparisons to test our other major hypotheses. Subjects did not respond to inequity; that is, they refused at the same rate whether the partner received the same, lower-value reward or a better reward (IT vs. ETLV: $T+ = 8$, $n = 6$, $p = 0.596$), and when they saw the higher-value reward (IT vs. FC: $T+ = 4$, $n = 4$, $p = 0.715$). They did not respond to individual contrast either (FC vs. ETLV: $T+ = 3$, $n = 6$, $p = 0.600$).

One of the refusal types, sharing, potentially varies from the others in that it results in the partner obtaining the item (food or token). Although rates of food sharing are quite low across primates [e.g. Jaeggi et al., 2010], it is possible that this outcome is treated differently by the apes, since the partner obtained the item (note that we are considering only outcomes, and make no assumptions as to the primates' motivations). Thus, we repeated the analysis considering only those refusals due to 'sharing', which made up 14% of the refusals overall. We find that behavior does not change; orangutans do not vary their behavior across conditions when considering only sharing instances (overall: Friedman's test: $\chi^2 = 11.975$, d.f. = 7, $p = 0.101$; considering only token refusals: Friedman's test: $\chi^2 = 6.8$, d.f. = 6, $p = 0.340$; considering only food refusals: Friedman's test: $\chi^2 = 7.988$, d.f. = 7, $p = 0.334$).

Effect of a Task

Subjects were not affected by whether or not there was a task. We first considered only food refusals, since there was no opportunity to refuse to return the token in the GR, and found that orangutans were equally likely to refuse to participate whether they exchanged for their rewards or got them for free (IT vs. GR: $T+ = 0$, $n = 2$, $p = 0.180$). However, since apes that refused tokens in the IT had no opportunity to refuse the foods, we also considered the total refusal rate, and still found no effect of effort (IT vs. GR: $T+ = 0$, $n = 4$, $p = 0.068$; fig. 1), despite there being a non-significant trend to respond more often when a task was present.

Effect of Effort

The orangutans did not respond to differences in effort. Subjects were just as likely to complete the interaction if their partner got a reward for 'free' as when the partner also exchanged, whether they both received lower- or higher-value rewards (ETLV vs. DETLV: $T+ = 15$, $n = 7$, $p = 0.865$; ETHV vs. DETHV: $T+ = 3$, $n = 2$, $p = 0.180$). Moreover, subjects did not change their behavior when a delay period of 10 s was introduced in to the exchange (DT vs. ETHV: $T+ = 1$, $n = 1$, $p = 0.317$).

Overcompensation

Subjects did not respond to being overcompensated, or receiving a greater reward than their partner. No subject ever refused the higher-value reward when their partner got the lower-value one (partner role in the IT). Although there was no difference in the response rate between the condition in which the ape got the higher-value versus lower-value reward (e.g. the partner vs. subject roles in the IT: $T+ = 0$, $n = 4$, $p = 0.068$), the trend was in the direction of refusing more often when receiving the lower-value reward than the higher one. The subjects were no more likely to refuse the higher-value reward when their partners got the lower reward than when they got the higher reward (IT vs. ETHV: $T+ = 0$, $n = 1$, $p = 0.317$).

Discussion

Orangutans do not show a behavioral response to receiving a less valued reward than a conspecific partner. The apes showed no variation between the conditions in their willingness to participate in the task. The orangutans also failed to respond differently depending upon whether or not a task was required, although there was a trend towards more refusals in the context of a task, which reflects behavior seen in other species (summarized in Brosnan et al. [2010b]). This is interesting as several other species have responded more strongly in the context of a task, even when they did not actually respond negatively to inequity [Neiworth et al., 2009; Talbot et al., 2011], indicating that the act of completing a task may alter expectations. As in other studies, subjects did not increase refusals in the individual contrast condition (the FC), likely due to the attention paid to the other individual, who also gets shown a higher-value reward before receiving a lower-value one, which reduces the salience of the mismatch (female chimpanzees at one facility are the only exceptions to this) [Brosnan et al., 2010b].

This response is in stark contrast to results in gregarious, cooperative species. Although there is variability in the responses of these other species, both chimpan-

zees and capuchin monkeys are known to respond to inequity in some contexts [Brosnan and de Waal, 2003; Brosnan et al., 2005; Fletcher, 2008; Brosnan et al., 2010b], as do humans [Yamagishi et al., 2009]. Moreover, previous evidence regarding bonobos indicates that they, too, may respond negatively to inequity; although the sample size was quite small, precluding significant results, the bonobos refused twice as often in the inequity than equity conditions [Bräuer et al., 2009]. On the other hand, these data support a previous finding in orangutans [Bräuer et al., 2006, 2009], indicating that despite differences in experimental procedure that have proved important in chimpanzees [Brosnan et al., 2010b], orangutans' failure to respond is a robust finding. Thus, while the current sample, as well as those in the studies of Bräuer and colleagues [2006, 2009], are quite small, making it difficult for any one study to reach statistical significance, taken as a whole these results are compelling. Moreover, significant differences between conditions have been found in equally small groups of capuchin monkeys [Brosnan and de Waal, 2003].

The present results also cannot be explained by other potentially confounding variables. First, these subjects were all socially housed at Zoo Atlanta, and were tested with conspecifics from these groups. Thus, these results are not an artifact of social incompetence due to solitary housing or other suboptimal living conditions. These results cannot be explained by a difference in intelligence between the species either. First, orangutans share many cognitive skills with other great apes [Russon, 1998], or even exceed them [Shumaker et al., 2001], and more specifically, these particular orangutans engage in cognitive testing and perform at high levels [Stoinski and Whiten, 2003; Dindo et al., in preparation]. Third, orangutans did refuse rewards as often as 10% of the time, indicating that this outcome cannot be explained by a generalized unwillingness to refuse food rewards. Finally, these results cannot be explained by a lack of interest or a lack of understanding on the part of the orangutans. The same group of orangutans was recently tested to evaluate a cognitive bias, the endowment effect, using an exchange task identical to the one used previously with chimpanzees [Brosnan et al., 2007], and they showed the same behavior as the chimpanzees [Flemming et al., in revision]. Thus, there is no evidence that they fail to understand exchange interactions or that they are indifferent to their personal outcomes.

For such a phylogenetic comparison, these orangutan data are most appropriately compared with chimpanzee and human data, as these species share a taxonomic Parvorder (Hominidae), thus increasing the likelihood of homology. These results indicate that the response to inequity seen in the other apes (and capuchin monkeys) is not due to a homology in the primate lineage (or beyond) but instead is due to convergence. Two major characteristics emerge as likely candidates: the species' typical level of gregariousness and cooperation. It seems unlikely that species which are primarily solitary would have a need for, and hence have evolved, any form of social comparison. With respect to cooperation, it has been hypothesized that social comparison is a mechanism for maintaining cooperation, thus in species which are less cooperative there may not be a need for the behavior [Fehr and Schmidt, 1999; Brosnan, 2006b]. We address each of these possibilities in turn.

First, orangutans are notable for their more solitary social organization as compared to the other great apes [van Schaik and van Hooff, 1996]. Although there is variation between different populations of orangutans [van Schaik et al., 2009], with orangutans in some geographic locations gathering in larger numbers [e.g. at Suaq

Bambling, Singleton and van Schaik, 2002], and though they do socialize in captive settings [Edwards and Snowdon, 1980], they are in general far less gregarious. Of course, this does not mean that they are not social. Individuals do come together into larger groups and relationships exist among the apes which inhabit an area [van Schaik and van Hooff, 1996], particularly among clusters of females who may be related to one another [Singleton et al., 2009].

Second, orangutans appear to be less cooperative than chimpanzees. They are capable of cooperating in captivity [Chalmeau et al., 1997], and also engage in more active giving and begging [Pelé et al., 2009] than the other great apes. One pair has even engaged in behavior that appears to be reciprocal [Dufour et al., 2008]. On the other hand, sharing in the wild does not occur amongst adults [van Noordwijk and Van Schaik, 2009] and occurs only rarely amongst infants [Bard, 1992; Jaeggi et al., 2008; for active sharing rates among primates, including orangutans, see also Jaeggi et al., 2010, suppl. table 1]. Moreover, in the wild, coalitions, which are a form of cooperative behavior, are not observed, and cooperation seems to be maintained despite unequal outcomes between the participants [Chalmeau et al., 1997], an outcome which is in contrast to chimpanzees [Melis et al., 2006] and capuchins [Brosnan et al., 2006; Brosnan et al., 2010a]. It may be that orangutans are capable of cooperation, but do not normally choose to do so, possibly a secondary feature derived from their far less gregarious social organization.

Difference in gregariousness and in cooperation are both candidates for the difference in response between chimpanzees and orangutans, and with a single comparison it is difficult to determine which is the more likely cause of this convergence. However, other data in New World monkeys (Parvorder Platyrrhini) show that squirrel monkeys, a gregarious but noncooperative monkey, fail to respond negatively to inequity [Talbot et al., 2011] while capuchins, a cooperative monkey, do [Brosnan and de Waal, 2003; van Wolkenten et al., 2007; Fletcher, 2008]. This indicates that cooperation may be more important in the evolution of social comparisons than the species' level of gregariousness.

Of course, there may be multiple factors involved, and the implication of cooperation does not rule out gregariousness as another contributing factor. In this respect, it is particularly intriguing that in one study, female chimpanzees failed to respond to inequity while male chimpanzees did [Brosnan et al., 2010b]. Given that female chimpanzees spend much of their time ranging solitarily, while males are typically in groups [Goodall, 1986; although see also Stumpf, 2007], it seems possible that the level and intensity of cooperation (e.g. coalition formation) may be less relevant for females than for males, which may reduce the need for the building of social expectations among females. Thus, orangutan behavior may converge with that of female chimpanzees due to their social organization. The most likely hypothesis, then, is that social contrast emerges in situations in which individuals frequently interact and routinely cooperate with others in their social group; in this situation, natural selection will strongly favor individuals who care how their outcomes relate to those of their social partners. Thus, an overtly comparative approach to primate behavior helps to provide an understanding not only of the phylogeny of the behavior, but also of potential functional explanations. The field will be enhanced by a broadly comparative approach which spans multiple taxonomic groups in an effort to uncover the origins and function of different social behaviors.

Acknowledgements

We thank Christine Watts, Shelley Blumrick, and Latorya Dopson for help with data coding and Rebecca Antworth for assistance with data collection. S.F.B was funded by a National Science Foundation Human and Social Dynamics grant (NSF SES 0729244). The research was approved by Georgia State University IACUC No. A07011 and the Zoo Atlanta Scientific Review Committee. We thank the animal care and husbandry staff at Zoo Atlanta for maintaining the health and well-being of the orangutans and making this research possible.

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