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BRIEF REPORT

Are Apes Inequity Averse? New Data on the Token-Exchange Paradigm

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Recent studies have produced mixed evidence about inequity aversion in nonhuman primates. Brosnan et al. [Proceedings of the Royal Society of London. Series B. Biological Sciences 272:253–258, 2005] found inequity aversion in chimpanzees and argued that effort is crucial, if subjects are to evaluate how they are rewarded in comparison to a competitor for an identical performance. In this study we investigated inequity aversion with chimpanzees, bonobos and orangutans, using the method of Brosnan et al. [Proceedings of the Royal Society of London. Series B. Biological Sciences 272:253–258, 2005] after introducing some methodological improvements. Subjects always received a less-preferred food in exchange for a token, whereas the competitor received either the same type of food for their token (equity) or a more favored food for it (inequity). Apes did not refuse more of the less-preferred food when a competitor had received the more favored food. Thus, with an improved methodology we failed to reproduce the findings of Brosnan et al. [Proceedings of the Royal Society of London. Series B. Biological Sciences 272:253–258, 2005] that apes show inequity aversion. Am. J. Primatol. 71:175–181, 2009.

Key words: inequity aversion; social cognition; prosocial behavior; other regarding preferences; fairness

INTRODUCTION

The question of whether nonhuman primates show inequity aversion in the same way as humans [Fehr & Schmidt 1999] has triggered a lively debate [Bräuer et al., 2006; Brosnan and de Waal, 2003; Brosnan et al., 2005; Dubreuil et al., 2006; Roma et al., 2006; Wynne, 2004]. A sense of fairness is important in human cooperation, as the ability to compare payoffs enables one to detect cheaters and to punish or avoid them [Fehr & Fischbacher, 2003].

Brosnan and de Waal [2003] first addressed this question by testing capuchin monkeys who exchanged tokens for food. In their study the subject always received a cucumber for the token, however a competitor either received the same type of food (equity) or instead a more favored food for a token (inequity). It was found that subjects rejected potential exchanges for the less-preferred food when their competitors had received better food for the same token. Brosnan and de Waal [2003] concluded that these monkeys are averse to inequity, and therefore inequity aversion has an early evolutionary origin. However, these findings have been challenged on a number of empirical and methodological grounds. Wynne [2004] pointed out that as preferred food was not visible for the subjects in the equity test, it is possible that the capuchins had rejected bad food when better food was present and therefore potentially available to them. Dubreuil et al. [2006] provided experimental evidence supporting this hypothesis when the tested capuchin monkeys were found to be less motivated to initiate a session in those conditions when the preferred food was visible.

Roma et al. [2006] argued that monkeys may have shown higher rejection rates owing to the well-known frustration effect that typically occurs when subjects receive low-quality rewards after they had previously received high-quality reward for the same task [see Amsel, 1994; Amsel & Roussel, 1952; Flaherty, 1996; Tinklepaugh, 1928]. Indeed, Roma et al. [2006] provided some empirical support for the frustration effect in a group of capuchin monkeys and suggested that this frustration effect, rather than inequity aversion, may have caused the Brosnan and de Waal [2003] results.

However, as Brosnan and de Waal [2006] and Dindo and de Waal [2007] have pointed out, in both of these studies subjects were not required to

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exchange tokens for rewards; rather they received the food without any effort. They argued that for testing inequity aversion it is important that the provision of food is contingent on task performance, thus enabling subjects to compare how they and the competitor were rewarded for the same performance. Following this argument, Fontenot et al. [2007] tested capuchins monkeys in both situations: they were either required to exchange tokens for food (experiment 1) or they received the food without any required effort (experiment 2). They found no evidence that the monkeys were able to evaluate either the relative work effort of a competitor or the inequity of a food reward. However, they did not compare the two critical conditions of the original experiment [Brosnan & de Waal 2003] in which the subject exchanged a token for a less-preferred food, whereas the competitor exchanged its token either for the same type of food (equity condition) or for a more favored food (inequity condition). This was tested recently by Wolkenten et al. [2007] who replicated previous findings that subjects showed negative reactions when competitors received favored food for their token (although with weaker effects).

There is also mixed evidence about inequity aversion in great apes. Brosnan et al. [2005] found inequity aversion in chimpanzees when they had to exchange tokens for food using a similar setup as with the capuchin monkeys in the original Brosnan and de Waal study (and also replicating that study's confounding of condition with order). In contrast Bräuer et al. [2006] tested all four great ape species and found that the apes who witnessed a competitor receiving better food than themselves in general reacted not by refusing lower-quality food or leaving, but by staying longer, ignoring fewer food pieces, and in the case of chimpanzees, by begging for food more vigorously. Their study concluded that rather than inequity aversion it was expectation that was the best explanation for the observed behavior: seeing another individual receiving high-quality food creates the expectation of receiving the same food oneself. However, the apes in that study also did not have to exchange tokens for the food.

The aim of the this study was to investigate inequity aversion in chimpanzees, bonobos and oragutans using the token-food exchange method by Brosnan et al. [2005] after implementing some methodological changes. We compared the two critical conditions: inequity and equity. Our methods were identical to those of Brosnan et al. [2005] with two exceptions aimed at improving the original design: (1) in the equity test the favored food was visible (but not—as in the Food control—held in front of both animals before each exchange, because this would make it different from the other conditions); and (2) conditions were presented in different sequences to avoid the possible order effects that may have confounded the original study.

METHODS

Subjects

Four orangutans, five bonobos, and six chimpanzees of various ages (range: 5–34 years old) participated in this study (see Table I). There were ten females and five males. Ten subjects were mother-reared and five were nursery-reared as infants and later on integrated into existing peer or social groups. All subjects lived in groups with their conspecifics at the Wolfgang Köhler Primate Center in the Zoo of Leipzig (Germany). They participate regularly in cognitive tests (13 of the 15 subjects were also tested in the inequity aversion study of Bräuer et al. [2006]. Apes were housed in enclosures with outdoor and indoor areas, and sleeping cages for the night. Water was available ad libitum and subjects were not food deprived at any time.

The precondition for apes participating in the experiment was that they exchanged tokens in a pretest trial for a less preferred food such as a carrot and an apple in the presence of a highly preferred food (grapes). The apes had already learned to exchange objects for food in their daily routine with their keepers. The bonobos and the orangutans had also participated in another test in which they were required to exchange various objects for food [Pelé et al., 2008] for 2–4 month. The research reported here adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates and were reviewed and approved by the ethics commission of the department of Psychology of the Max Planck Institute for Evolutionary Anthropology and the Leipzig Zoo. Furthermore, this research complied with the legal requirements of Germany.

TABLE I. Subjects that Participated in Experiment 1 and 2 (See Text for Explanation of Rearing History Terms)

Subject	Species	Gender	Age in years	Rearing history
Robert	Chimpanzee	Male	32	Mother
Riet	Chimpanzee	Female	30	Nursery
Dorien	Chimpanzee	Female	27	Nursery
Sandra	Chimpanzee	Female	14	Mother
Patrick	Chimpanzee	Male	10	Mother
Tai	Chimpanzee	Female	5	Mother
Joey	Bonobo	Male	25	Nursery
Ulindi	Bonobo	Female	14	Mother
Limbuko	Bonobo	Male	12	Nursery
Kuno	Bonobo	Male	11	Nursery
Yasa	Bonobo	Female	10	Mother
Dunja	Orangutan	Female	34	Mother
Pini	Orangutan	Female	19	Mother
Dokana	Orangutan	Female	18	Mother
Padana	Orangutan	Female	10	Mother

Materials

Testing took place in testing cages (25 m^2) with one familiar experimenter (E) in 2007. The room was divided into three sections, consisting of two cages and a third area for E. A rectangular booth located between the cages allowed the two apes to look at each other. The booth had a frontal window (98 × 95 cm) and two Plexiglas panels (75 × 50 cm) on either side. Each panel had three holes through which subjects could either hand over the token or through which they could stick their fingers.

Food preference was determined according to previous experiments. In general apes were tested with carrots as a low-value reward, and only when one member of a given pair refused to exchange its token for a carrot, did that pair then get tested with an apple. The high-value reward was always a grape. Plastic tubes (22 cm × 5 cm diameter) served as tokens. Food was presented in two buckets (diameter: 21 cm), one containing the low-preferred food and the other containing the highly preferred food. Subject and competitor were filmed during the entire experiment from a position behind E.

Procedure

Subjects were tested individually in one cage whereas the competitor/second subject was in the other cage (with the exception of mothers with dependent offspring). During all sessions E sat in front of the booth. The two buckets with food pieces were placed in a line in front of E in the booth, so that both were equidistant from the Plexiglas panels of the two cages. In that way both kinds of foods were always visible to the apes.

There were two experimental conditions

Inequity: The subject got the less-preferred food (carrot or apple) in exchange for a token, whereas the competitor got the preferred-food (grape) in exchange for a token.

Equity: Both apes served as subjects and got the same less-preferred food (carrot or apple) in exchange for a token.

The session started when E handed the token to the competitor (Inequity condition) or to the first subject (Equity condition). After the ape had taken the token, E opened her hand to signal that she wanted it back. When the ape returned the token, E reached into the appropriate bucket, took the food (grape in the Inequity condition, carrot/apple in the Equity condition) and handed it to the competitor/subject. Then E handed the token to the other ape, the subject (or second subject in the Equity condition) and exchanged a carrot/apple in the same way as with the first ape.

If an ape did not take the token, E put it through the hole of the panel; E got the attention of the ape by calling their name and rattling the token in the hole. If the ape did not return the token immediately, E continued to call their name and to show the 'begging' hand to attempt to elicit the exchange. In cases when apes did not return the token after 60 sec or did not return it through one of the three holes in the Plexiglas panel, the experimenter started the next exchange using another token with the other ape. If the ape did not take the food, E placed it in the hole in the Plexiglas panel while encouraging the subject verbally to eat it. Thus, food could accumulate until the ape decided to eat it or until the session was over. After encouraging the ape to eat the food in case the she did not take it immediately E shifted her attention to the other ape.

E tried to behave the same in all exchanges in both conditions. E continued exchanging tokens and food with both apes without a break until each of them had received 25 pieces of food. A session was over 5 sec after the last of the 25 food pieces was given to the subject. Subjects were only tested in one session per day, however after that they could still serve as a competitor in another pairing.

Within a species all possible combinations of animals were tested. Each subject received one session per condition with each competitor. Thus, each pair was tested in three sessions, as in the Equity condition both apes were tested simultaneously. The order of these three sessions was randomized between pairs so that each animal played its roles in different sequence (subject in the Inequity condition/competitor in the Inequity condition/subject in the Equity condition). Overall, each chimpanzee, bonobo and orangutan experienced 375, 300 and 225 opportunities to exchange, respectively.

Scoring

All sessions were scored from the videotapes (24, 40 and 60 sessions for the orangutans, bonobos and chimpanzees, respectively). We scored the following behaviors:

Overall refusals: Subjects were coded as refusing if they (a) refused the food by not eating it in view of the camera within 10 sec after having received it from the experimenter or (b) if they did not put the token through one of the three holes within 60 sec of E first offering the token.

Normal exchange: Subjects were coded as exchanging normally if they put the token through one of the three holes within 5 sec of E first offering the token.

Duration of absence: The percentage of the whole session's duration during which subjects were not present in the area in front of E where they could acquire the food.

Begging behavior: Subjects were coded as begging for food if they performed one of the following behaviors: pointing (putting fingers or a hand through one of the holes in the panel); begging with lips (presenting the lower lip through one of the

holes); knocking (hitting the Plexiglas with their hand/arm); or rocking their body (rocking back and forth more than once with the upper part of the body).

Orangutans and bonobos were coded by JB. Another coder IK naïve to the goal of the study scored the chimpanzees, and 20% of all sessions to assess inter-observer reliability. Inter-observer reliability was significant for refusals to accept the reward (Spearman correlation $r = 0.89$, $P < 0.001$, $N = 25$); refusal to return the token (Spearman correlation $r = 0.87$, $P < 0.001$, $N = 25$); normal exchanges (Spearman correlation $r = 0.87$, $P < 0.001$, $N = 25$); duration of absence (Spearman correlation $r = 0.94$, $P < 0.000$, $N = 25$) and for begging (Cohen's $\kappa = 0.82$, N = 25). In addition JB coded 20% of the chimpanzees to check for inter-observer reliability also for that species. It was significant for: refusals to accept the reward (Spearman correlation $r = 0.63$, $P = 0.027$, $N = 12$); refusal to return the token (Spearman correlation $r = 1.00$, $P < 0.001$, $N = 12$); normal exchanges (Spearman correlation $r = 0.94$, $P < 0.001$, $N = 12$); duration of absence (Spearman correlation $r = 0.99$, $P < 0.000$, $N = 12$) and for begging (Cohen's $\kappa = 1.00$, $N = 12$).

We conducted one main analysis considering the whole data set and two supporting analyses considering a subsample of the data. The first supporting analyses focused exclusively on those pairs with short-term relations because Brosnan et al. [2005] found that subjects in the short-term groups refused more than in the long-term groups. Thus, we considered as short-term all pairs in which members have been living together in the group for 6 years (when the Wolfgang Köhler Primate Center opened) or less. The second supporting analysis focused exclusively on the first exposure that each subject had to each of the conditions. We did this because Brosnan et al. [2005] tested one subject only within one pair, which means that each subject only received 25 trials (1 session) per condition. In contrast our subjects received many more trials than those tested by Brosnan et al. owing to our use of multiple pairs per subject. Thus, we looked at 14 subjects in seven pairs (one bonobo had to be left out because of the uneven number of bonobos). We only considered the subject's first partner independently of when the session with the other condition occurred, which owing to the counterbalancing method may have taken place a few days after the subject had already interacted with other subjects.

RESULTS

All possible pairs

Figure 1 presents the mean percentage of overall refusals to exchange of all subjects and the individuals of the three species divided into refusals to return the token or refusals to accept the reward.

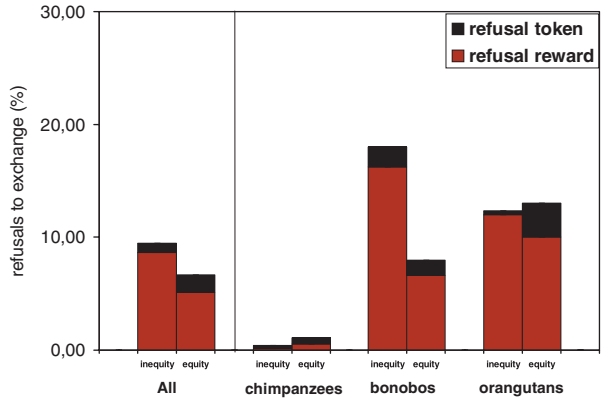

Fig. 1. Mean percentage of overall refusals to exchange of all subjects, and individuals of the three species in the two conditions; black bars indicate refusal to return the token, red bars indicate refusals to accept the reward.

Overall, subjects did not refuse to exchange any more in the Inequity condition than in the Equity condition. A repeated measures Analysis of variance (ANOVA) with the factors condition and species showed a significant effect for species ($F(2, 12) = 4.172$, $P = 0.042$, $\eta^2 = 0.410$) but no significant effect for condition ($F(1, 12) = 1.701$, $P = 0.217$, $\eta^2 = 0.124$) or condition × species ($F(2, 12) = 6.079$, $P = 0.092$, $\eta^2 = 0.329$). Although we did not find a significant interaction effect, we took a closer look at each species separately. In terms of absolute numbers, none of the chimpanzees, two (of four) orangutans, but five (of five) bonobos showed increased refusal in the Inequity condition than in the Equity condition. Subjects also did not show significant differences in their normal exchange rate. A repeated measures ANOVA with the factors condition and species showed no significant effect of species ($F(2, 12) = 3.188$, $P = 0.078$, $\eta^2 = 0.347$), condition ($F(1, 12) = 0.547$, $P = 0.474$, $\eta^2 = 0.044$), or condition × species ($F(2, 12) = 4.729$, $P = 0.138$, $\eta^2 = 0.281$).

Regarding the behavioral differences subjects were present longer (i.e. absent shorter) in the inequity condition. A repeated measures ANOVA with the factors condition and species showed a significant effect for condition ($F(1, 12) = 4.905$, $P = 0.047$ $\eta^2 = 0.290$), no interaction effect (condition × species $F(2, 12) = 3.650$, $P = 0.058$, $\eta^2 = 0.378$) and no effect for species ($F(2, 12) = 0.150$, $P = 0.862$, $\eta^2 = 0.024$). There was only a tendency for the interaction effect, nevertheless we took a closer look at each species. In none of the three species did we find a significant difference between conditions. However, five (of six) chimpanzees, four (of four) orangutans but only two (of five) bonobos remained present longer in the Inequity than in the Equity condition. Finally, subjects did not show differences in their begging behavior. A repeated measures ANOVA with the factors condition and

species showed no significant effects: (condition $F(1, 12) = 0.902$, $P = 0.361$, $\eta^2 = 0.070$ condition × species $F(2, 12) = 0.275$, $P = 0.765$, $\eta^2 = 0.044$ species $F(2, 12) = 3.284$, $P = 0.073$, $\eta^2 = 0.354$).

Short-term relationship

We found very similar results to the overall analysis: Subjects in short term relationships did not refuse to exchange any more in the Inequity condition than in the Equity condition. A repeated measures ANOVA with the factors condition and species showed no significant effect (condition $F(2,12) = 1.152$, $P = 0.304$, $\eta^2 = 0.088$; species $F(1, 12) = 3.275$, $P = 0.073$, $\eta^2 = 0.353$; condition × species $F(2, 12) = 1.122$, $P = 0.357$, $\eta^2 = 0.158$). Subjects also did not show significant differences in their normal exchange rate. A repeated measures ANOVA showed no significant effect (condition $F(2, 12) = 0.402$, $P = 0{,}538$, $\eta^2 = 0.032$; species $F(1, 12) = 3.512$, $P = 0.063$, $\eta^2 = 0.369$; condition × species $F(2, 12) = 1.096$, $P = 0.366$, $\eta^2 = 0.154$). There were also no differences for the duration of absence (ANOVA condition $F(1, 12) = 1.399$, $P = 0.260$, $\eta^2 = 0.104$; species $F(2,12) = 0.460$, $P = 0.636$, $\eta^2 = 0.073$; condition × species ($F(2, 12) = 1.353$, $P = 0.295$, $\eta^2 = 0.184$) and begging behavior (ANOVA condition $F(1, 12) = 0.031$, $P = 0.862$, $\eta^2 = 0.003$; species $F(2, 12) = 1.840$, $P = 0.201$, $\eta^2 = 0.235$; condition × species ($F(2, 12) = 0.032$, $P = 0.968$, $\eta^2 = 0.005$).

First exposure

Six out of 14 subjects refused no exchanges, whereas eight refused at least one exchange (one chimpanzee, three bonobos, four orangutans). Six subjects refused more in the Inequity than the Equity condition (Riet 1:0, Yasa 20:2, Joey 2:0, Kuno 24:0 Pini 2:1, Dokana 2:0), whereas two subjects showed the reverse pattern (Dunja 0:4, Padana 0:1). Similarly, six subjects showed the same normal exchange rate in both conditions, six subjects showed normal exchanges more often in the Equity condition and two subjects more in the Inequity condition. There was no difference in the duration of absence and in begging behavior.

DISCUSSION

We found no conclusive evidence that apes show aversion to inequity in a token-food exchange paradigm. More specifically, subjects who saw their partners exchange a token for food of higher quality to the one that they had received for exchanging the same token did not lead subjects to refuse further exchanges, particularly when compared with the case in which both the subject and the partner exchanged the token for the same low-quality reward. Thus, we failed to reproduce the findings of Brosnan et al. [2005] on inequity aversion. Next we explore the possible methodological, statistical and interpretative reasons for this discrepancy.

It is conceivable that our procedural changes (aimed at removing the potential confounds of the original study) could explain the difference between studies. One methodological difference was that in this study the favored food was also visible for the subject in the Equity condition, but it was not held in front of both animals before each exchange. As Wynne [2004] and Dubreuil et al. [2006] have emphasized, the favored food has to be visible to allow a correct comparison because otherwise subjects might not exchange for inferior food just because the better food is present in the Inequity condition. But if the food is held in front of the two animals while both have to exchange for the less-preferred food [as in the Food control of Brosnan et al. 2005], another variable is added and it is not comparable to the Inequity condition where no food is held in front of the animals. Moreover, it is even possible that this procedure might have created an expectation in the subject in the food control so that they were more willing to exchange because a grape was shown to them before each exchange. Note that this also applies to the study of Wolkenten et al. [2007] who found inequity aversion in capuchin monkeys. Thus, it is possible that in both studies in which inequity aversion was found in primates, it was owing to this methodological problem.

The second major methodological difference to the original study was that we avoided possible order effects, as did Wolkenten et al. [2007]. In the Brosnan et al. [2005] study subjects received first the Equity condition (where preferred food was not presented), then the Inequity condition, then the Effort control (where the competitor got the preferred food without having to exchange for it) and finally the Food control. It is thus, possible, that subjects started to reject in the Inequity condition because they saw the grapes, that they continued to do so in the Effort control, and later stopped refusing in the Food control. There are other methodological differences such as using two cages (instead of one) that may have influenced the results. It is impossible to say whether this difference is responsible for the discrepancy between studies but given that capuchins are commonly tested in two cages, with positive results, this may not represent a serious problem.

Another possibility is that we failed to reproduce Brosnan et al's results because of statistical reasons. Testing subjects in multiple pairs meant that we obtained a denser data set than Brosnan et al. [2005]. Namely, subjects in this study received about five to six times more trials than in the original study, which means that we were able to obtain a better estimate of each subject's preferences. This is true unless one postulates that repeated exposure to both conditions with multiple partners may wash out the

differences between conditions. However, analyzing the subset of initial trials to make the two studies more comparable did not alter the main results. Bonobos were the species that showed high refusal rates in the Inequity compared with the Equity conditions, whereas chimpanzees rarely refused in any condition (there was only a single chimpanzee that refused once in the Inequity condition) and orangutans showed mixed results.

Yet, it is conceivable that we failed to reproduce Brosnan et al's results because of a lack of statistical power. Although this could very well be the case for the bonobo data, which go in the same direction as the data reported by Brosnan et al. [2005], statistical power cannot explain the result for the chimpanzees (or the orangutans) because our results go slightly in the opposite direction to those that would be expected based on Brosnan et al. data (see Fig. 1). In other words, if statistical power were the problem, we would expect that increasing the sample size would make our results converge with those of Brosnan et al. In reality, increasing statistical power would have the opposite effect—it would make them significantly different from those of Brosnan et al. because, we repeat, they go in the opposite direction to what Brosnan et al. found.

Note, however, that our argument against statistical power rests on the assumption that our chimpanzee (and orangutan) data faithfully represents the population values. If they do not, then the problem is not about statistical power but about how representative our sample is in relation to the population. Future studies are necessary to determine whether this is the case. Moreover future studies should investigate the variability between populations as it is conceivable that different populations of chimpanzees (and other species) differ in their propensity for displaying aversion to inequity. Indeed, one thing that has become apparent in the last few decades is the greater variability that exists between chimpanzee individuals and populations both at the behavioral and cognitive levels [Call & Tomasello, 1996; Whiten et al., 2001]. Future studies should be devoted first to document the differences and second investigate the factors promoting those differences. In fact, Brosnan et al. [2005] indicated that pairs with short-term relationships were more likely to display inequity aversion. Although we were unable to confirm this hypothesis with our sample, it is conceivable that other variables that could explain potential differences.

Once we have reached this point we also have to consider the possibility that the difference between our findings and those of Brosnan et al. are not a result of methodological differences or statistical artifacts. We have already alluded to the real possibility that different populations of the same species may behave differently but we must also point out that our findings are consistent with evidence from other studies in captivity that chimpanzees are not other-regarding when food is involved. When they are allowed to provide themselves and conspecifics with food, they basically show no regard for the outcomes of others [Jensen et al., 2006; Silk et al., 2005]. They also behave like rational maximizers in an ultimatum game, accepting every offer above zero independent of what the proposer gets [Jensen et al., 2007]. Although seeing another individual getting preferred food can create an expectation to get the same kind of food [Bräuer et al., 2006], this study suggests that apes do not refuse to exchange for inferior food in relation to what others are receiving. Note that taken together these studies involved at least three different populations and three different methods all of which producing analogous results.

Unlike Bräuer et al. [2006] who found no interspecific differences in other regarding preferences in the great apes, this study found differences in the refusal rate (bonobos and orangutans were more likely to reject offers (both ''fair'' and ''unfair'') than chimpanzees) and hinted at possible species differences in aversion to inequity. In particular, all five bonobos refused more often in the inequity than the equity condition. In contrast, none of the chimpanzees rejected more in the Inequity than in the Equity condition. However, we urge caution when interpreting these data because this difference could not be confirmed statistically, perhaps owing to our low statistical power (see above). Nevertheless, we offer some speculation about the reason for this putative difference, while at the same time calling for future studies to try to confirm this result.

Perhaps the most striking difference involves chimpanzees and bonobos. Although closely related and similar in a number of ways, chimpanzees and bonobos are also different in their ecology, anatomy, temperament and social behavior [Heilbronner et al., 2008; Wrangham & Peterson, 1996, but see Stanford, 1998]. Bonobos have been characterized as less dominance driven, more tolerant and less competitive than chimpanzees [de Waal, 1989]. This may not only lead to co-feeding and a more successful cooperation [Hare et al., 2007] but also to more sensitivity to what others are getting. In other words, with their more egalitarian relationships, bonobos might expect equity in general and a violation of equity is more acutely perceived by bonobos than by chimpanzees.

In conclusion, we failed to reproduce the findings of Brosnan et al. [2005]. We end by suggesting two lines for future research. First, all studies on inequity aversion have used food as the currency. It would be important to substitute food for other currencies because the great food appeal may mask the expression of other regarding preferences. Second, future studies should investigate more closely the potential differences between species. Based on the available data, bonobos seem a serious candidate for inequity aversion. Additionally, some

research attention should be devoted to the study of the potential differences between populations of the same species as well as the factors that may generate those differences.

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