

Are apes really inequity averse?

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Brosnan *et al.* (Brosnan, S. F., Schiff, H. C. & de Waal, F. B. M. 2005 Tolerance for inequity may increase with social closeness in chimpanzees. *Proc. R. Soc. B* **272**, 253–258) found that chimpanzees showed increased levels of rejection for less-preferred food when competitors received better food than themselves and postulated as an explanation inequity aversion. In the present study, we extended these findings by adding important control conditions, and we investigated whether inequity aversion could also be found in the other great ape species and whether it would be influenced by subjects' relationship with the competitor. In the present study, subjects showed a pattern of food rejection opposite to the subjects of the above study by Brosnan *et al.* (2005). Our apes ignored fewer food pieces and stayed longer in front of the experimenter when a conspecific received better food than themselves. Moreover, chimpanzees begged more vigorously when the conspecific got favoured food. The most plausible explanation for these results is the food expectation hypothesis—seeing another individual receive high-quality food creates the expectation of receiving the same food oneself—and not inequity aversion.

Keywords: inequity aversion; social cognition; joint attention

1. INTRODUCTION

Humans show strong aversion against inequity (Fehr & Schmidt 1999), and third parties that do not personally suffer from inequity will punish others for unfair behaviour—even when such punishment is costly (Fehr & Fischbacher 2004a). Moreover, humans' reactions to unfairness have detectable neural signatures in the brain (Sanfey *et al.* 2003)—unfair offers elicit activity in areas related to emotion (anterior insula) and cognition (dorsolateral prefrontal cortex). Some theorists argue that this sense of fairness may have played a key role in the evolution of cooperation in humans (Fehr & Fischbacher 2003). However, since animals cooperate with each other in certain contexts (Stevens & Gilby 2004), it is possible that they also possess some sense of fairness. It is therefore unclear whether this skill is really uniquely human.

Brosnan & de Waal (2003) addressed this question by training capuchin monkeys to exchange tokens for food. The subject always received a cucumber for the token, but a competitor received either the same type of food for a token (equity test), a more favoured food for a token (inequity test), or a more favoured food without exchanging a token (effort control). In a non-social condition, a grape was placed in the location where the competitor normally sat (food control). It was found that subjects rejected potential exchanges for the less-preferred food when a competitor received better food for the same token exchange. That is, subjects in the inequity test either did not return the token or did not accept the reward. Moreover, they rejected more frequently when the favoured food was given to the competitor without exchanging a token than when the favoured food was simply placed in an empty cage with no competitor present. The authors concluded that capuchin monkeys showed inequity aversion (Brosnan & de Waal 2003).

These results have sparked a lively debate. Leaving aside theoretical considerations for the moment (see Henrich 2004), Wynne (2004) pointed out that a major problem with this paradigm was that the preferred food was not visible to the subjects in the equity test. Thus, according to Wynne (2004), it is possible that the capuchins had rejected bad food when better food was present, and therefore potentially available. Indeed, Dubreuil *et al.* (2006) provided experimental evidence supporting this hypothesis by testing capuchin monkeys in four similar conditions. Here, subjects always received less-preferred food, and the favoured food was either not visible to the subject, was shown to the subject but then hidden, was put in another empty cage, or was given to a competitor. Results showed that monkeys were less motivated to initiate a trial in conditions when the preferred food was visible. The authors argued that the refusals were not due to inequity aversion, but due to the frustration of seeing and not obtaining the preferred food.

Roma *et al.* (2006) raised an additional concern. They argued that monkeys may have showed higher rejection rates owing to the well-known frustration effect that typically arises when subjects are initially given a high-quality reward followed by low-quality reward. Thus, rejection is a consequence of the change of food quality experienced by the subject rather than the difference between what the subject and her partner are receiving. Roma *et al.* (2006) provided some empirical support for the frustration effect in a group of capuchin monkeys and suggested that such a frustration effect, rather than inequity aversion, may have been the cause of Brosnan & de Waal (2003) results. However, Brosnan & de Waal (2006) reanalysed some of their original data and found no support for the frustration effect, although the small sample size in both studies makes it difficult to draw conclusions.

However, some evidence suggests that chimpanzees may show a response to reward inequity that is derived from the partner receiving the reward, rather than the presence of the reward alone. Brosnan *et al.* (2005) tested

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chimpanzees in a similar design but used another control condition: a grape was held in front of the pair but not given to either individual. They found that chimpanzees rejected exchanges for less-preferred food more often when the competitor received better food than when the better food was just visible. However, the rate of rejection was low: 14 out of 20 chimpanzees refused less than 2% of the trials, and rejection only appeared in two out of three groups that were tested. To explain these differences, the authors argued that group size, social closeness of the group and group-specific traditions were likely to influence chimpanzees' tolerance for inequity.

The Brosnan *et al.* (2005) study also had some limitations. First, both the subject and the competitor were always present in the same cage, and in neither condition was the favoured food moved but not eaten by a competitor. This raises the possibility that the subjects' refusals in that study stemmed from the preferred food being moved in their presence, and not owing to the fact that the competitor ultimately ate it. In other words, subjects might not have refused to exchange because the favoured food was given to the competitor, but because it was moved and not given to them. Moreover, previous analyses have not jointly assessed the relative importance of factors, such as the presence of the competitor, the type of food received or the relationship between the subject and the competitor, that may have contributed to explaining the subjects' choices—by creating different expectations about whether they too would receive some preferred food. Second, it is unclear whether similar results can be found in other groups of chimpanzees or other paradigms can produce similar results. This is especially important because inequity aversion was shown in only one of the two groups tested by Brosnan *et al.* (2005).

The present study had three main aims. First, we tested an alternative hypothesis to inequity aversion, namely the food expectation hypothesis that apes' behaviour is mainly determined by whether they expect to get preferred food in this situation. To do this, we used a 2×2 design with two factors: the presence or absence of a competitor in a second cage; and handing over low- or high-value food. Both kinds of food were always visible to the apes, but as in the Dubreuil *et al.* (2006) and the Roma *et al.* (2006) studies, subjects did not have to exchange a token for food. Would subjects under these conditions still behave according to the predictions of the inequity aversion hypothesis, that is, would they reject more of their own food when the competitor got better food? Second, we examined social aspects more closely by investigating whether the subjects' relationship with the competitor affected the subjects' choices. Finally, we investigated whether inequity aversion was restricted to chimpanzees or it could also be found in bonobos, gorillas and orangutans using the same procedure.

2. MATERIAL AND METHODS

(a) Subjects

In this study, 7 orangutans, 6 gorillas, 4 bonobos and 13 chimpanzees of various ages (range 5–31 years old) participated. All subjects lived in groups with their conspecifics in the Wolfgang Köhler-Primate Center in Leipzig Zoo (Germany) and had participated regularly in cognitive tests. They 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.

(b) Materials

Testing took place in special testing rooms (25 m²) with a familiar experimenter. Each room was divided into two cages, with a third area for the experimenter. A rectangular booth located between the cages allowed the 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 stick their fingers.

Food preference was determined according to previous experiments. The low-value reward was usually a piece of carrot (apples for the orangutans), while the high-value reward was a grape. Food was presented on two dishes that stood on the floor of the booth. The dishes had a diameter of 12 cm. The subject and the competitor were filmed during the whole experiment from behind the experimenter.

(c) Procedure

Subjects were tested individually in one cage while the other cage was either occupied by the competitor (social conditions) or it was empty (non-social conditions). The only exceptions were the mothers with dependent offspring, which stayed together with their infants (Fraukje, Corry, Riet, Dunja, Dokana, Pini, Viringika). During all trials, the experimenter sat in front of the booth. The two dishes with the counted number of food pieces were placed in front of the experimenter so that they were visible to both apes. In addition, in the 'same' conditions, there were always eight grapes on these dishes. The trial started when the experimenter handed one piece of food to the subject. If the subject did not take the food, the experimenter put it through the hole of the panel. Then the experimenter fed the competitor in the same way (social conditions) or put the food piece through the hole (non-social conditions). The experimenter went on feeding both apes until each of them received eight pieces of food. The experimenter tried to make sure that both apes were able to get the food and she behaved identically in all conditions. A trial was over when the last of the eight food pieces was given to the competitor or put into the empty cage.

Subjects always got the low-value reward—carrots (or apples in the case of the orangutans). Competitors were either present or absent, and either low- (carrots/apples) or high-value food (grapes) was handed to them. There were four conditions, as follows.

- (i) *Social-different*. The competitor was present and was fed with grapes.
- (ii) *Social-same*. The competitor was present and was fed with carrots (apples).
- (iii) *Non-social-different*. The competitor was absent, and grapes were put in the adjacent cage.
- (iv) *Non-social-same*. The competitor was absent, and carrots (apples) were put in the adjacent cage.

Within a species, all possible combinations of animals were tested. Each subject received one trial per condition with each competitor. One half of the subjects started with the social conditions, and the other with the non-social. A session with a given pair consisted of eight trials: the four conditions for each subject. The trials were mixed, such that each animal sometimes played the role of the subject and sometimes the role of the competitor.

(d) Scoring

All trials were scored from the videotapes. We scored the behaviours, which are as follows.

Ignored food pieces. Subjects were coded as ignoring the food if they did not touch it during the whole trial (or, in the case of mothers, if they let the infants eat it without intervening).

Duration of absence. Percentage of the whole trial's duration during which subjects were not present in the area in front of the experimenter where they could acquire the food.

Begging behaviour. Subjects were coded as begging for food if they performed one of the following behaviours: pointing (putting fingers or hand through one of the holes in the panel); begging with lips (presenting the lower lip through one of the holes—a begging behaviour in the orangutans and the bonobos); knocking (hitting the Plexiglas with hand/arm—a begging behaviour in gorillas); or rocking their body (rocking more than one time back and forth with the upper part of the body—a begging behaviour in the chimpanzees).

Rate of eating. The number of food pieces that were eaten in the view of the camera divided by the length of time the subjects were present in front of the experimenter.

For the hierarchy analysis, we only included the subjects that were clearly dominant over or subordinate to the competitor in a given dyad. Dominance was determined from former tests and observations. With respect to learning and order effects, we compared the first half of trials to the second half of trials for each condition and found no significant differences.

A coder who was unaware of the goal of the study scored 20% of the trials to assess inter-observer reliability. Inter-observer reliability was excellent for ignoring the food (Spearman's correlation $r=0.94$, $p=0.000$, $N=200$), for both duration of absence (Spearman's correlation $r=0.93$, $p=0.000$, $N=200$) and begging (Cohen's $\kappa=0.83$, $N=200$).

3. RESULTS**(a) All four species**

As the number of subjects within a species varied substantially (14 chimpanzees versus 4 bonobos), we first analysed all species together. Figure 1 presents the number of ignored food pieces in each condition. A repeated measures ANOVA on the number of ignored food pieces with the factors, competitor presence (present versus absent) and type of food (different versus same), indicated that subjects ignored fewer food pieces when the competitor was present ($F(1,29)=13.58$, $p=0.001$), and different food was handed over ($F(1,29)=4.19$, $p=0.050$). There was no significant interaction between factors.

Figure 2 shows the mean durations away from the testing station in each condition. A repeated measures ANOVA indicated that subjects were absent for longer periods (spent more time away from the area in front of the experimenter) when there was no competitor in the other cage ($F(1,29)=16.17$, $p=0.001$). In contrast, there was no effect of the type of food ($F(1,29)=0.53$, $p=0.473$). However, there was a competitor presence \times type of food interaction effect ($F(1,29)=6.31$, $p=0.018$). Planned pairwise comparisons indicated that apes were less likely to be absent in the social-different condition compared to all the other conditions (social-same: $t(29)=3.03$, $p=0.005$; non-social-different: $t(29)=4.09$, $p=0.000$; non-social-same: $t(29)=3.94$,

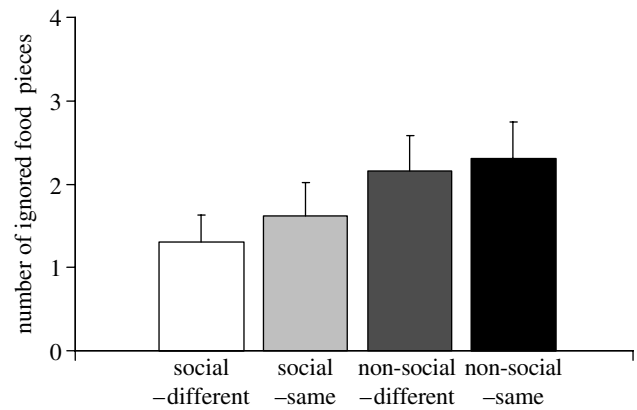


Figure 1. Mean number (+s.e.) of ignored food pieces of all subjects in the four conditions.

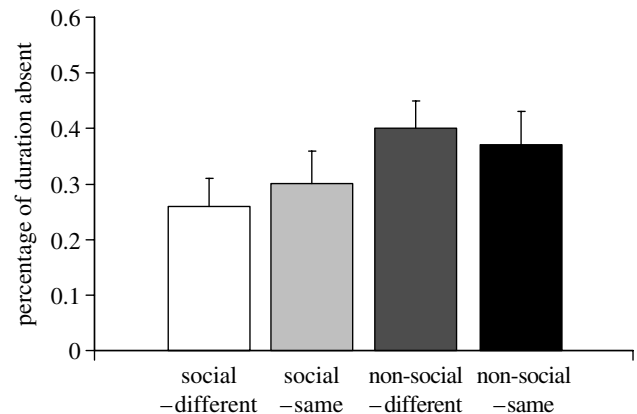


Figure 2. Mean percentage (+s.e.) of trial duration for which subjects were absent in the four conditions.

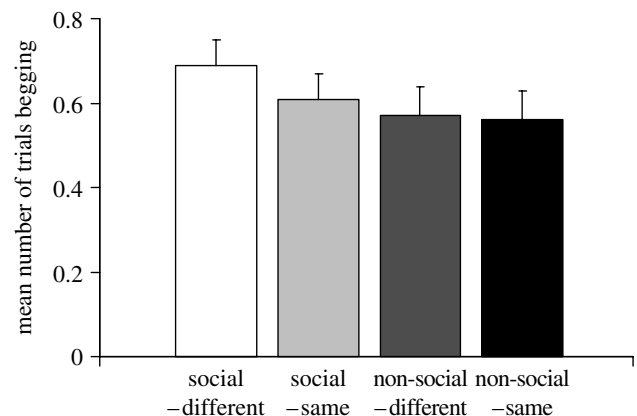


Figure 3. Mean number (+s.e.) of trials when subjects engaged in begging behaviour in the four conditions.

$p=0.000$). Moreover, they were absent for shorter periods of time in the social-same condition compared to both non-social conditions (non-social-different: $t(29)=3.20$, $p=0.003$; non-social-same: $t(29)=2.96$, $p=0.006$).

Figure 3 presents the mean number of trials when the subject engaged in begging behaviour. A repeated measures ANOVA revealed that apes begged more when the competitor was present ($F(1,29)=10.21$, $p=0.003$), independent of the type of food ($F(1,29)=1.79$, $p=0.191$). There was no interaction effect. Subjects ate the food pieces at the same rate in all conditions (competitor presence: $F(1,29)=0.16$, $p=0.697$; food type: $F(1,29)=0.15$, $p=0.700$).

(b) The frustration hypothesis

In order to test the frustration hypothesis, we compared the behaviour of those subjects in their first session of the social conditions that had received high-quality food in their first interaction followed by low-quality food in the second interaction with those that had received low-quality food on both occasions. A frustration effect predicts that subjects in the degraded condition would be more likely to reject food than those in the constant condition. We only used those subjects for whom we had information in both their very first and second test rounds. Subjects did not behave differently when they received high-value food first compared to low-value food second (number of ignored food pieces: $t(17)=0.30$, $p=0.768$; duration of absence: $t(17)=0.02$, $p=0.987$; begging behaviour: $t(17)=0.43$, $p=0.676$, frequency of eating: $t(17)=0.29$, $p=0.774$).

(c) Hierarchy

In this analysis, we compared the behaviour of subjects when they were dominant or subordinate to the competitor in the social conditions. We used three repeated measures ANOVAs for each of the measures with the factor food (different versus same) and the factor dominance (subject being dominant versus subject being subordinate). Subjects ignored more food pieces when they were dominant over the competitor ($F(1,18)=4.53$, $p=0.047$) independent of the type of food ($F(1,18)=3.43$, $p=0.081$).

For the measure of absence duration, there was a significant effect of food ($F(1,18)=4.74$, $p=0.043$), but not of dominance ($F(1,18)=2.46$, $p=0.135$). However, there was a significant food \times dominance effect ($F(1,18)=5.29$, $p=0.031$). Subjects were absent for longer periods when they were dominant over the competitor that got the same food compared to all the other combinations (dominant/social-different condition: $t(18)=2.36$, $p=0.030$; subordinate/social-different condition: $t(18)=-2.27$, $p=0.036$; subordinate/social-same condition: $t(18)=-2.24$, $p=0.038$). We found no significant effect for the begging behaviour.

(d) Chimpanzees

In a second step, we reanalysed the data for chimpanzees alone to compare the results with previous studies. Chimpanzees ignored fewer food pieces when the competitor was present ($F(1,12)=19.53$, $p=0.001$), and different food was handed over ($F(1,12)=9.70$, $p=0.009$). There was no significant interaction between factors. For the duration of absence measure, there was a significant effect for competitor presence ($F(1,12)=18.68$, $p=0.001$), food type ($F(1,12)=19.09$, $p=0.001$), and competitor presence \times food type ($F(1,12)=5.36$, $p=0.039$). Planned pairwise comparisons revealed that chimpanzees were significantly absent for shorter periods in the social-different condition compared to the other conditions (social-same: $t(12)=4.83$, $p=0.000$; non-social-different: $t(12)=4.27$, $p=0.001$; non-social-same: $t(12)=5.11$, $p=0.000$). Moreover, they were absent for shorter periods in the social-same condition compared to both non-social conditions (non-social-different: $t(12)=3.14$, $p=0.008$; non-social-same: $t(12)=3.82$, $p=0.002$). Finally, chimpanzees begged more in the presence of the competitor ($F(1,12)=11.14$, $p=0.006$), and when different food was handed over ($F(1,12)=26.83$, $p=0.000$).

4. DISCUSSION

Apes ignored fewer food pieces and stayed longer at the testing station when a conspecific got favoured food. Moreover, the subject begged more when the competitor was present than when she was absent, and chimpanzees, in particular, also begged more when the conspecific got favoured food. These results are exactly the opposite to that of Brosnan *et al.* (2005), as subjects ignored the least food (not the most, as it was the case in Brosnan *et al.* 2005) when the competitor received food of higher quality than themselves. Thus, if food refusals are the key to infer inequity aversion, the apes in the present study were not inequity averse.

However, Henrich (2004) argued that inequity aversion would be shown not by refusals to accept low-quality food, but on the contrary, by a greater willingness to accept lower-quality food as an attempt to offset the higher-quality food received by their partners. If subjects were averse to inequity, rejecting food does not solve the problem, but it exacerbates it because subjects are getting even less food. Henrich (2004) has argued that humans would not reject unfair offers unless this affected the others' pay-off, although note that Fehr & Fischbacher (2004b) showed that humans even punish when that does not change the pay-off difference between the punished and the punishing individual. Henrich (2004) argued that accepting low-quality offers would help subjects in reducing the inequality between partners. Apparently, this is what the apes in the present study did. In fact, chimpanzees actively begged to obtain more food in those conditions of social inequality. This difference cannot be attributed to the presence of grapes in some conditions but not others, because grapes were present in all conditions, or to the manipulation and the transfer of grapes in the social-different condition, because this was also present in the non-social-different condition.

Do our results constitute evidence of inequity aversion? Before accepting such a possibility, we need to consider at least three other alternative hypotheses. First, there is social facilitation, defined as an increase in the frequency of a behaviour already in animals' repertoire when in the presence of others engaged in the same behaviour (Galloway *et al.* 2005). Social facilitation would explain why subjects rejected less food, stayed longer and begged more insistently in the social conditions. However, the social facilitation hypothesis does not explain why they ignored food least when the competitor received the preferred food and they did not. One could argue that the competitor probably ate more of the grapes in the social-different condition than she ate carrots in the social-same condition. This might have facilitated the subject to ignore least when the competitor got grapes. However, social facilitation of eating behaviour could not be found in the same group of chimpanzees (Adessi & Visalberghi 2006). More importantly, in the present study, the subject's eating rate was the same in all conditions. The differences in the numbers of ignored food pieces arose because subjects stayed longer in the social conditions, especially when the preferred food was manipulated. Thus, the social facilitation hypothesis does not seem to fully explain the data.

Second, Roma *et al.* (2006) proposed that subjects may have ignored more food owing to a frustration effect that typically occurs when subjects are initially fed high-quality

rewards followed by low-quality rewards. Numerous studies had previously shown that various species show less willingness to accept the lower-quality food under those circumstances (Tinklepaugh 1928; Amsel & Rousell 1952; Amsel 1994; Flaherty 1996). Moreover, Roma *et al.* (2006) presented data supporting the operation of the frustration effect in capuchin monkeys. Thus, the decrease in food quality experienced by the subjects rather than what their partners received could have been the cause of their decreased willingness to accept lower-quality food. This criticism, however, does not apply to our study because subjects increased rather than decreased their willingness to accept low-quality food. Moreover, our counterbalanced design across subjects controlled for this possibility. Indeed, our analyses detected no evidence of a frustration effect when we compared subjects that received high-quality food first followed by low-quality food (degraded diet) with those that received only low-quality food (constant diet). Thus, the frustration effect hypothesis cannot explain the data from the present study. Let us now turn our attention to the food expectation hypothesis.

This hypothesis postulates that subjects have an expectation to receive the preferred food in some conditions but not others. Seeing the experimenter give favoured food to a conspecific, not just being placed into an empty cage, may have created the *expectation* that they will get some of the favoured food soon. Moreover, the ape caretakers at our facility routinely feed the apes first the less-favoured food, and later the better one. Such an expectation would explain why the apes in the present study stayed longer in front of the experimenter. However, it is less clear why chimpanzees also begged for the food more vigorously, unless they had a stronger expectation of getting access to those grapes. They perceived the situation as 'it is grape feeding time' and so they expected to get grapes. This would also explain why they stayed longer in front of the experimenter. Call *et al.* (2004) also found that chimpanzees were more likely to stay with an experimenter that they perceived as unable as opposed to unwilling to give them food. However, the increase in begging behaviour is still difficult to explain, as chimpanzees in that study begged more from an experimenter who was unwilling rather than unable to give them food.

To summarize, if one accepts Henrich's (2004) increase in low-quality food consumption as valid evidence for inequity aversion, the expectation hypothesis and the inequity aversion hypothesis explain our data best. Nevertheless, it is still unclear why our results differed so markedly from Brosnan *et al.* (2005). One possibility is that subjects and competitors in the present study simply received food, whereas in the earlier study subjects had to exchange tokens to receive food. Brosnan & de Waal (2006) have insisted that this is a key difference between their studies and those of others (e.g. Roma *et al.* 2006). Exchanging a token and receiving a worse reward than a competitor who trades in the same kind of token might enhance the subject's annoyance. This, however, would not explain why subjects in the present study behaved in the opposite way to those in the Brosnan *et al.* (2005) study. Moreover, omitting the token exchange does not seem to reduce the rejection rate of 'unfair' offers. On the contrary, capuchin monkeys rejected unfair offers (no effort condition, Brosnan & de Waal 2003) more often

when no tokens were involved. Therefore, if the capuchin data can be extrapolated to the ape data, refusals in the present study should have been accentuated, not eliminated. Although in economics it is assumed that defining prices in terms of responses per reinforcer is equivalent to defining price in terms of tokens per reinforcer (Hursh 1984; Roma *et al.* 2006), the different procedure could create different results.

Another possibility is that the operationalization of relevant behaviours is at the core of the discrepancies between studies. Brosnan *et al.* (2005) scored a refusal when subjects refused the reward or did not even return the token, whereas we scored refusals as ignored rewards. In our case, it was not possible to code food rejections because it was often impossible to see whether the subject intentionally threw the food back, or whether they accidentally dropped it. Interestingly, if one focuses just on the number of the refusals to return the token, the results of Brosnan *et al.* (2005) showed the same pattern as the present study: subjects refused fewer token exchanges when the competitor received better food.

This study allowed us to investigate the effect that social variables such as dominance rank had on the subject's behaviour. Overall, apes ignored more food pieces when they were dominant over their competitor than when they were subordinate. This result may stem from the asymmetry between subordinates and dominants. Subordinates may be more predisposed to accept any kind of food because they would always be displaced from monopolizable food in competition with a dominant individual.

Although the reduced sample size for some species prevented us from comparing them directly, a comparison of the results based on the chimpanzees alone with those based on all apes indicated that all species displayed a similar pattern of results except for begging behaviour, which chimpanzees deployed more often when conspecifics got favoured food. Thus, it appears that, in general, all great ape species reacted in similar ways when conspecifics received better food than themselves.

In conclusion, great apes witnessing a competitor getting 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, begging for food more vigorously. Dominant individuals were less likely to accept low-quality food when subordinate partners were getting high-quality food. Unless one postulates that subjects are willing to accept lower-quality food in an attempt to offset the higher-quality food received by their partners (Henrich 2004), the inequity aversion hypothesis is not supported by our data. Moreover, subjects waiting longer and begging more vigorously is consistent with having an increased expectation to receive high-quality food. In other words, seeing another individual receive high-quality food creates the expectation to receive the same food. At present, it is unclear which one of these two hypotheses is correct, but the fact that chimpanzees do not prevent others from getting food that they are not getting (Jensen *et al.* 2006) suggests that non-human apes may not be deeply inequity averse.

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