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Is a Sense of Inequity an Ancestral Primate Trait? Testing Social Inequity in Cotton Top Tamarins (*Saguinus oedipus*)

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To address a controversy in the literature concerning whether monkeys show an aversion to inequity, individuals of a New World monkey species, cotton top tamarins (*Saguinus oedipus*) were tested in an offering task and in a bartering task. At issue was whether the monkeys rejected rewards because of a violation of expectancy of the preferred reward, or whether they rejected rewards because of a sensitivity to socially mediated inequity. The data from both tasks indicated that the subjects were more likely to reject when preferred rewards were presented, either because of another animal eating the reward (the social condition) or because of rewards being presented but inaccessible. The bartering task led to the only behavioral indication of aversion due specifically to social inequity, which was demonstrated when tamarins' sensitivity to the difference in rewards increased with exposure to other tamarins working to receive the preferred rewards. The results suggest that social inequity aversion will be assessed by tamarins, and possibly by other primates, only under conditions of limited resources and a requirement of work, which may make the situation a bit more competitive and thus drives attention toward both social and reward evaluation.

Keywords: inequity, social, tamarins, primates, evolution

Tomasello (1999, 2003) and Hare (2007) have argued that the uniqueness of human thought emerged from evolved specialized social awareness. One such specialized ability may be the judgment of fairness and equity within a social field (Fehr & Fischbacher, 2003). Humans show a strong aversion to inequity among partners (Fehr & Schmidt, 1999), and this aversion is found in many different human societies, establishing it as a generalized universal human cognition (Heinrich et al., 2001). There is further evidence of its universal reaction among humans in that an unfair social condition activates areas in the human brain normally associated with physical disgust and negative emotional affect (Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). Establishing equity and fairness among a group of humans is valued as moral and civil in human society; thus it is intriguing to wonder from what evolutionary precursors these abilities emerged. Clearly, one would need sensitivity to notice unfair social situations and an ability to act differently when inequity is noted (de Waal, 2008), but are these abilities unique to humans?

A flurry of studies recently tested whether monkeys or apes show a sensitivity toward inequity when working among partners (Brosnan & de Waal, 2003, in capuchins [*Cebus apella*]; Roma, Silberberg, Ruggiero, & Suomi, 2006, in capuchins; Dubreuil, Gentile, & Visalberghi, 2006, in capuchins; Brauer, Call, & Tomasello, 2006; and Jensen, Call, & Tomasello, 2007, in chimpanzees [*Pan troglodytes*]). For example, Jensen et al. (2007) tested chimpanzees in an "ultimatum game" and found that the chimpanzees acted as rational decision-makers who accepted lesser rewards in unfair circumstances when a partner got more. This outcome did not match the outcome of humans who rejected the lesser amount if it was made unfair by the circumstances (i.e., a more fair option had been available). Interestingly, human participants accepted the lesser amount only if the alternative to acceptance was nothing. This suggests that unfair circumstances are considered and weighed differently by humans than they are by nonhuman apes.

Brosnan and de Waal (2003) found that 5 female capuchins, a primate species not closely related to humans within the primate classification, were less likely to exchange a token for a less preferred food if they viewed a partner who exchanged a token for a more preferred food. Moreover, the capuchins were more likely to refuse work for a less preferred food if the partner was given a more preferred food without having to exchange anything, or in other words, for no work at all. Importantly, the capuchins were also more likely to refuse to exchange tokens for the less preferred food if the more preferred food was present, a nonsocial condition involving the preferred reward. Brosnan and de Waal claimed that the results overall demonstrated an inequity aversion in capuchins. While they conceded that the nonsocial preferred reward condition generated a similar increase in rejection, they found that the rejection rates to the less preferred food decreased over trials in the nonsocial condition but did not decrease in the social condition. Thus they claimed that the addition of the social feature heightened the rejection rate by capuchins.

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According to Heinrich (2004), the capuchins' increased rejection is not predicted from a reaction that would be typical of humans, because the capuchins rejected a lesser reward in order to obtain nothing. Fontenot, Watson, Roberts, and Miller (2007) used a bartering task with capuchins and failed to find an effect of inequity or of differences in work effort in the capuchins' acceptance and consumption of a nonpreferred reward, further drawing into question the finding. The conclusions drawn by Brosnan and de Waal (2003) have been criticized by Wynne (2004), Roma et al. (2006), and Dubreuil et al. (2006), and in most cases the critics claimed that the rejections shown by capuchins may have been a result of a violation of expectancy in the food provided rather than an assessment of inequity in the social situation. To further test the alternative that the monkeys were reacting to a violation in expected food, Dubreuil et al. (2006) offered capuchins the chance to take a less preferred reward when a preferred reward was presented (i.e., shown then hidden, presented in another cage, or given to a partner), and in all cases in which the preferred reward was shown and regardless of whether a partner was involved, the capuchins were less likely to initiate a trial to choose the less preferred food. In contrast, van Wolkenten, Brosnan, and de Waal (2007) recently found that capuchins did not reject more when a preferred reward was merely presented, although they continued to reject more when their partners received a preferred reward.

Roma et al. (2006) argued that the refusals were an expression of the frustration effect often noted in rats and pigeons when schedules of reward are changed from a preferred reward to a less preferred one (for a review, see Amsel, 1958). Using methods similar to those found in Dubreuil et al. (2006), Roma et al. found that capuchins were more likely to refuse less preferred rewards if they had previously received the more preferred rewards. In fact, Dindo and de Waal (2007) gave pairs of capuchins food trays and did not find a difference in consumption of the food; rather they found that capuchins ate the less preferred food more rapidly if their partners received preferred food, a reaction that is the opposite the rejection of the less preferred food in the 2003 study. Dindo and de Waal (2007) argued that the tasks themselves generate different types of reactions by capuchins: Offering a capuchin food items (an "offering" task) generates foraging strategies, including social facilitation of eating and scramble competition. Requiring capuchins to exchange tokens to acquire a reward (a "bartering" task) induces a comparison of costs and payoffs between capuchins and their partners and thus rejections when inequity is noticed.

The current study uses both a bartering method and an offering method to test inequity aversion in cotton top tamarins, a member of the callitrichid New World monkey subfamily taxonomy. It is important to compare the rejection rates of a single species of monkey across the two tasks (offering and bartering) to determine whether the bartering task generates a unique sensitivity to the social variables of inequity and fairness. It is imperative that a New World monkey species other than capuchins is tested, because researchers have suggested that capuchins evolved specialized social skills because of their extensive use of tools, their cooperative hunting, and published evidence of social awareness (for a review, see Parker & McKinney, 1999). Cotton top tamarins exhibit well-developed social abilities, including cooperative breeding (Kostan & Snowdon, 2002), cooperation in tasks (Cronin, Kurian, & Snowdon, 2005; Hauser, Chen, Chen, & Chuang, 2003), tolerated food sharing (Feistner & Price, 1999, 2000; McConkey, 2000; Price & Feistner, 2001), and shared visual attention (Neiworth, Burman, Basile, & Lickteig, 2002). If inequity aversion is an evolved ancestral trait present in primates, there should be evidence of it in many species of monkeys, especially those who show similar social awareness capacities.

One method, a bartering task, required the tamarins to drop a wooden token in a cup in order to acquire a less preferred reward. In another method, an offering task, a different group of tamarins was simply offered a less preferred reward. The rate of rejection of the less preferred reward was measured in a variety of social and nonsocial conditions. Subjects were exposed to different orders of conditions in both the bartering task and the offering task. This design insured that rejection rates were not a function of consistent switching from preferred to less preferred rewards in the design. In fact, each subject had to demonstrate adequate baseline performance of accepting the less preferred reward 80% of the time before each condition was conducted. Thus the difference in rejection was a true measure of the condition and not a lingering effect of switching reward types.

This study allowed a direct examination of rate of rejections in both tasks. If presence of the preferred reward generates higher rates of rejection, then subjects in both tasks should reject more often when the preferred food is present, both when a partner eats it (i.e., in food inequity conditions), and when it is present in the environment (preferred food control). If the task characteristics invoke different assessments by monkeys, the offering task should generate assessments around the food itself and thus rejection based on violations of expected rewards regardless of social or nonsocial conditions. In contrast, the bartering task should induce an assessment of payoff and fairness since more work is involved and the work is explicitly tied to the reward.

Method

Subjects

A total of 11 adult cotton top tamarins, 6 females and 5 males, ranging in age from 3 years to 14 years old, were in the study. There were 5 subjects in the bartering task, including 3 females (Fozzy, Olympia, and Ophelia) and 2 males (Zhivago and Vulture). The subjects were tested in pairs, with Olympia and Vulture, a breeding couple, tested as a pair, and Fozzy, Zhivago, and Ophelia, a nonbreeding couple and adjacent cagemate, tested in pairs via the trio. In the bartering task, 4 of the 5 monkeys were both subjects and models, taking on each of the roles for all of the conditions before being switched to the other role.[1] Each subject was exposed to the conditions of the bartering task in a different order and each was randomly selected as subject or model first. All 5 subjects had never participated in a study involving social variables other than testing for shared visual attention, and they had not been tested in any cooperative task or in any social inequity situation. All subjects except Vulture had been exposed in prior studies to mirrors and to digitized images of themselves, to digitized images of other animals, to hidden treats in cups, and to discriminations of numbers of objects and objects constructed of

[1] Ophelia was a subject in the bartering task only.

small graphic shapes, all printed in two-dimensional form on plastic cards.

There were 6 subjects in the offering task, 3 females (Quince, Encore, and Cezanne) and 3 males (Willow, Heron, and Quaker). All 6 subjects were naïve to any social inequity or cooperative situation. All subjects in the offering task had been exposed to mirrors and to discriminations of numbers of objects and objects constructed of elements, all printed in two-dimensional form on plastic cards. These subjects were also tested in pairs, formed as nonbreeding pairs Willow and Quince, and Cezanne and Quaker, and breeding pair Encore and Heron. Subjects participated as subjects and as models with order of position and order of conditions counterbalanced across the group.

The monkeys had been monkey-family reared in laboratory settings and had been socially housed in pairs or larger family groups in 0.85 × 1.50 × 2.3 m cages, with the cages visually separated by opaque sheets. The subjects were on a 12-hr light/dark cycle and had free access to water. They were maintained on a complete diet consisting of a yogurt-applesauce breakfast, a lunch of Zupreem Marmoset chow and fruits and vegetables, and an afternoon protein snack (e.g., eggs, hamburger, peanuts, cottage cheese, and mealworms) daily. The experiments were conducted between meals, in the morning between breakfast and lunch, or in the afternoon between lunch and snack. Subjects were not food deprived but were offered a less preferred fruit (grapes) or a highly preferred sugared cereal (Berry Trix™, Apple Crunchies™, or Froot Loops™) for participating.

Apparatus

A white projector cart measuring 1.17 m in height with a shelf measuring 40 × 50 cm was used in the food control condition of both tasks and in all conditions in the bartering task. Also in the food control condition in both tasks, the preferred reward was presented as several pieces of sugared cereal (Froot Loops™, Apple Crunchies™, or Berry Trix™) sealed inside a transparent plastic dome measuring 5 cm in diameter with a height of 3.8 cm, which was glued on top of a small wood base measuring 6 × 5 cm.

In the bartering task, we used as tokens colorful small magenta, yellow, and green wooden figures manufactured for parrot use and shaped as rectangles, squares, and circles measuring on average 2 × 3.5 cm with a thickness of 8 mm. Paper cups with a 5 cm base were cut down in size to measure 2 cm in height, and these were placed on the cart upright and were the mechanism by which the subjects were trained to deposit their tokens to exchange them for a reward.

Procedure

In all tasks, the tamarins were tested in their home cages. The subjects had participated in a number of studies in which an individual of the pair was called to participate at the beginning of each trial. The tamarins were quite familiar with this kind of procedure and readily came close to the experimenter when called. Both tamarins attended to the tasks while one was participating. There were a total of 5 experimenters who conducted the tasks and were all trained to copy the exact movements described here in the procedure. The interpretation of the response was very clear: either a tamarin took a reward from one's hand within a particular period of time, or a tamarin placed a token inside a cup and accepted a food item by removing it from one's hand within a particular period of time. All experimenters watched Julie J. Neiworth demonstrate this with subjects when being trained, and she monitored the experimenters on 20% of the trials within the two procedures with 100% agreement on responses by tamarins in the various tasks.

Reward Pretest

We first determined whether each pair of subjects preferred sugared cereal to the less preferred rewards, which were quartered pieces of grape. This was accomplished by placing multiple pieces of both items in a bowl and presenting the bowl to each subject for 30 s. The number of pieces eaten was counted for the first 10 s of the exposure. All 11 subjects ate all pieces of at least one type of cereal before eating grapes. Within the pairs, one type of cereal seemed preferred by the pair over the other types of cereal, but cereal was always consumed before grapes by all tamarins. The preferred cereal was defined as the preferred reward for each pair, while grapes were defined as the less preferred reward.

Bartering Task

Each subject was first shaped in successive approximations to exchange a wooden token for a quarter piece of grape. These shaping sessions consisted of 10 trials per day, each lasting 60 s. For each trial, the experimenter would call a subject down to the cart and require that the subject sit on the cart in front of the experimenter. Then the experimenter would offer the token by hand to the subject and reward the subject with a quarter grape for touching the wooden token. The next step, after subjects demonstrated accomplishing this touching response for 8 out of 10 trials, was to call the subject down and reward him or her for holding and dropping the token into a cup fortuitously positioned directly under the monkey's paws for a quarter grape. Each step required a response in 8 out of 10 trials in a session to move to the next step. Once subjects were reliably holding and dropping the token to acquire rewards, the subject was called down to the cart and the token was presented to the subject while the cup was moved by a single 5-cm increment to the left on the cart. This movement forced the subjects to hold the token for a longer period of time and to physically move and then drop the token in the cup in order to obtain a reward. Within any one trial, the subjects were given 10 s to emit the response properly, and if they missed the cup within the 10 s, they could retrieve the token and try again. After 10 s of missing the cup, no rewards were given for that trial. Once the cup could be placed at least 10 cm from the center point of the cart, and the subject had successfully dropped the token in the cup for a reward within the first 10 s of each trial on 8 out of 10 consecutive trials, the experiment began.

Five conditions were conducted in counterbalanced order such that 1 subject started in one of the different conditions described in the next sections. For each condition, subjects were tested in five daily sessions, each consisting of five 60-s trials. This rate of exposure matches Brosnan and de Waal's (2003) original study using a bartering method. In between conditions, subjects and models were required to pass a "baseline" condition in which they traded tokens in 10-trial sessions for one-quarter grape rewards until they reached the criterion of 8 out of 10 successful trades

within a session. The monkey that was randomly assigned the model position first remained the model throughout the conditions, and then the roles were reversed. The five conditions are described next.

Food equity. In the food equity condition, the model was first called down to the cart and handed a token to trade (by depositing it in a cup 10 cm away) for a quarter grape. The model was required to successfully make the trade for the grape before the trial started for the subject. Once the model demonstrated this behavior, the subject was tested on a single trial. The subject was called to the cart and was handed a token by the experimenter to deposit in the cup to acquire a quarter grape. Refusal to accept the token or refusal to take the quarter grape after making a deposit were both counted as refusals. An accept response was recorded if the subject took the token and successfully traded it for a quarter grape. After each trial for the subject, a 15-s intertrial interval (ITI) was presented, and then the model was made to demonstrate the trading behavior for the quarter grape before the next trial for the subject began. The subject was tested in 5 trials per session, and after 5 consecutive sessions, the subject and model were placed in a baseline condition of trading for grapes in 10-trial sessions until they met criterion of 8 out of 10 successful trades within a session.

Food inequity. In this condition, the model was first called down to the cart and handed a token. When the model demonstrated the appropriate trade by depositing the token in the cup, the model was given the preferred reward, a sugared cereal. Immediately following this event, a trial began for the subject. In this case, as in the conditions before, the subject was handed a token that he or she could trade for a quarter grape. The trial lasted 60 s and a successful or refusal response was noted, followed by a 15-s ITI. Then the model would trade for the preferred reward again, followed by the next trial for the subject. Each session consisted of five trials for the subject, and after five sessions, both model and subject were required to trade for quartered grapes until meeting criterion in a baseline condition.

Work inequity. Each trial started with the model being handed [1/4] a quarter grape without the requirement of trading a token first. Once the model obtained the quarter grape, the subject was called down and was offered a token to trade (by depositing into the cup) for a quarter grape. Again there were five trials per session, with each trial for the subject preceded by the model demonstration. After five consecutive sessions, the subject and model were placed in the baseline trading condition until criterion was met.

Food + work inequity. In this condition, the model was handed a preferred reward of sugared cereal without the requirement of trading at the beginning of each trial. Then the subject was tested in the bartering task, again for a quarter grape. Before each of the five trials per session, the model was handed the preferred reward and then the trial for the subject began. There were 5 consecutive sessions of 5 trials per session, and then both subject and model were placed in baseline training in10-trial sessions until they traded for grapes in 8 of 10 trials within a single session.

Food control. This is the only condition that did not involve a model at all. Instead, before each trial was initiated for the subject, a plastic dome-covered wood base containing the preferred reward, sugared cereals, was placed on the cart. Then the subject was called down to the cart and was offered a token to deposit in the cup for a quarter grape. The subject was given 60 s to make the trade, and then the trial ended with a 15-s ITI, during which time the preferred food was removed from the cart. At the beginning of the next trial, the food inside the domed container was placed again on the cart, and the monkey was called down to start the next trial. After five consecutive sessions consisting of five trials per session, the subject and model were put in the baseline condition of trading for grapes to meet criterion.

Offering Task

This task required that subjects approach the closed hand of the experimenter when the experimenter called his or her name. Then the experimenter would open the hand, palm up, to reveal the reward that was offered for a 60-s period. If the subject took the reward offered within the 60 s, the response was recorded as an accept; otherwise the lack of response was recorded as a reject. There was a 15-s ITI that separated trials. Subjects readily took items from experimenters when the items were handed to them with a thumb and finger grasp by the experimenter. Thus there was some pretraining involved in inducing subjects to approach a closed fist and take items from an open palm. Once subject and model could accomplish taking items in 8 out of 10 consecutive trials in a session, the experiment began. In this task, three conditions were conducted in counterbalanced order across subjects. There were 2 subjects out of the 6 that started in one of the three conditions described. The monkey randomly assigned the model position first remained the model throughout the conditions for the subject, and then the roles were reversed.

Food equity. Each trial was preceded by the model being offered a quarter grape in an open palm. Once the model took the grape, the trial for the subject began. The subject was called down while the experimenter offered a closed fist high in the branches of the home cage. Once the subject was near, the experimenter opened the fist to reveal the palm containing a quarter grape. The subject was allowed 60 s of time to take or refuse the reward. Sessions consisted of 10 trials, which better matched other studies that used an offering methodology (i.e., Roma et al., 2006), and each trial was preceded by the model behavior. After five consecutive sessions, the subject and model were placed in 10-trial baseline sessions in which they were alternately offered quartered grapes until both took them in 8 out of 10 trials within a single session.

Food inequity. In this condition, the model was called down first to a closed fist that was opened to reveal the preferred reward that he or she could take. Once the model accepted the reward, the trial began for the subject, who was called down to a closed fist and then offered a quarter grape in the open palm. The same number of trials, sessions, and follow-up baseline conditions were used.

Food control. The model was not involved in this condition; rather the cart was placed in the home cage for each 10-trial session, and each trial began with a presentation of the domed container containing the preferred cereal. The subject was then called down toward a closed fist, which opened to reveal a quarter grape in the open palm. The same number of trials, sessions, and baseline conditions were used.

Results

The trading response in the bartering task took an average of 63 sessions (range = 43–121 sessions) until subjects could reliably meet the criterion of 8 successful trades out of 10 consecutive

trials. The accept response to an open palm in the offering task was acquired on average in 9 sessions (range = 3 to 16 sessions). An interesting outcome noted immediately was that subjects in the bartering task who were required to trade with tokens for a reward rejected far less overall than did the group in the offering task, which simply accepted or rejected food in an open palm, independent samples $t(9) = -5.49$, $p < .01$. The mean rate of rejection across all the experimental conditions (not including the baseline scores) in the bartering task was 13.92%, while the mean rate of rejections in the experimental conditions in the offering task was 50.00%. Next, we examined when the rejections occurred within each of the tasks.

Bartering Task

A mixed-model analysis of variance (ANOVA) was conducted comparing each subject's average rejection rate for each of six conditions (baseline, food equity, work inequity, food inequity, food + work inequity, and food control) by the subject's status first as model or as subject. There was a significant condition effect, $F(5, 15) = 3.56$, $p = .03$, with a large effect size ($\eta^2 = 0.54$). There was no difference found for subject status, $F(1, 3) = 0.19$, $p = .69$, nor for an interaction between subject status and condition, $F(5, 15) = 0.32$, $p = .89$. Figure 1 shows the rejection rates averaged across subjects for each of the conditions.

It is important to note that rejection rates in this task were very low. Still, a few significant differences in rejection rates emerged. Specifically, by using paired sample *t* tests on average rejections per subject, there was a significant difference between rejections in the baseline condition ($M = 3.16\%$, $SE = 1.19$) and the food control condition ($M = 23\%$, $SE = 6.37$), $t(4) = -3.54$, $p = .02$, and between rejections in the food equity condition ($M = 3.3\%$, $SE = 0.86$) and the food control condition, $t(4) = -3.87$, $p = .02$. This indicated that there were significantly more rejections in the food control condition when a preferred reward was present but unavailable than in conditions in which less preferred rewards were offered equitably (e.g., in baseline and in food equity). There was a nonsignificant trend difference between baseline and the work inequity condition ($M = 9.0\%$ rejection, $SE = 2.69$), $t(4) = -2.38$, $p = .076$, and a difference between the food equity condition and the work inequity condition, which also revealed a weak trend, $t(4) = 2.18$, $p = .10$. It is important to note that there were no differences found between any of the inequity conditions with each other (either work- or food-related), nor between any of the inequity conditions and the food control condition (when preferred food was presented either to a model or in a domed container). Thus the only real significant finding was that the rejection rates were much higher in the food control condition in which preferred food was presented but less preferred food was given. The finding that work inequity generated a trend difference suggests that the tamarins may note the difference between having to trade for a less preferred reward and getting the less preferred reward for free, although that difference did not reach the level of significance.

A final analysis compared rejection rates by session to reveal whether the socially mediated conditions produced different rejections over time than did the nonsocial preferred food control condition (see Figure 2 for rejections over sessions). A repeated-measures ANOVA first tested for differences in the last session only across the three conditions involving preferred food: the food control condition, the food inequity condition, and the food + work inequity condition. This ANOVA produced a nonsignificant effect for condition, $F(1, 4) = 0.19$, $p = .69$, indicating no final session differences among these three conditions. Moreover, a repeated-measures ANOVA revealed a nonsignificant difference in the first sessions between condition, $F(1, 4) = 1.61$, $p = .48$. Paired-sample *t* tests of the rejection rates within each of the three conditions compared the first session to the last session and revealed a significant difference in the food inequity condition, $t(4) = -5.715$, $p < .01$, but not in any other condition: food control, $t(4) = -0.232$, $p = .83$; food + work inequity, $t(4) = -0.302$, $p = .78$. Specifically, rejection rates were significantly

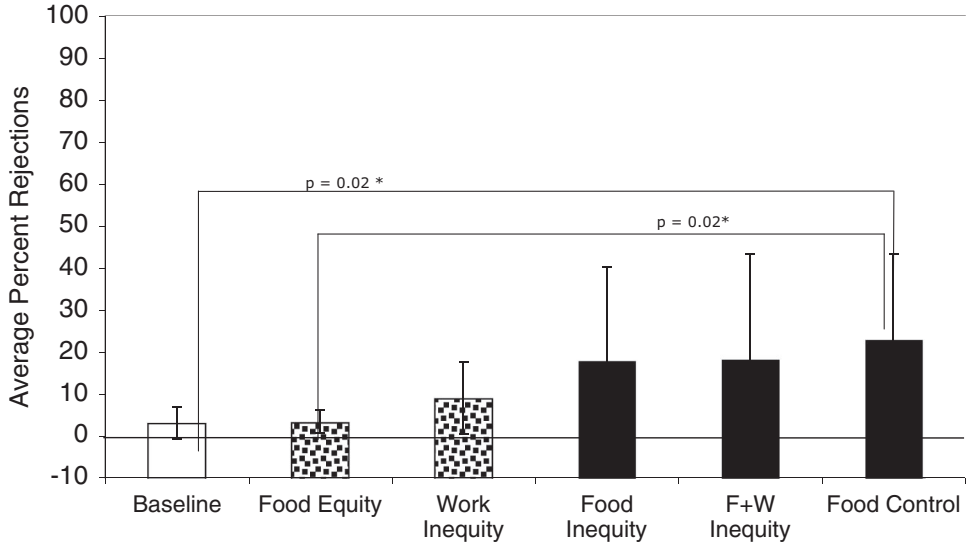

Figure 1. Averaged rejection rates to all the conditions during the bartering task, with 95% confidence intervals plotted.

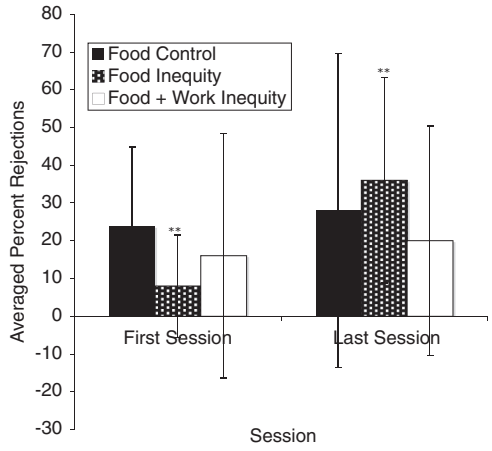

Figure 2. Averaged rejection rates for the first and last sessions for all conditions involving the presentation of preferred rewards (either under social conditions or not) before the exchange in the bartering task. The double asterisk denotes that the first and last session of that condition are significantly different from each other at $p < .01$.

higher in the last session of the food inequity condition (M = 36.0%) than they were in the first session of this condition (M = 8.0%). This was not attributable to low first-session results, because the first sessions of all three conditions were not different statistically from each other. This indicated that the subjects rejected the less preferred reward in the food inequity condition significantly more as the test went on. Still, the food + work inequity condition, which was another socially mediated condition involving preferred food, did not generate a significant difference in rejection rates in the last session in comparison with the first session.

Offering Task

A mixed-model ANOVA examined differences in subjects' averaged rejection rates to the conditions of the task (baseline, food equity, food inequity, and food control) as well as the between-subjects variable of status (model first or subject first). There was a significant condition effect, $F(3, 12) = 16.804$, $p < .01$ with a large effect size ($\eta^2 = 0.81$) but no effect of status, $F(1, 4) = .034$, $p = .86$, nor of an interaction, $F(3, 12) = 0.24$, $p = .87$. Figure 3 depicts the averaged rejection rates by condition. Pairwise comparisons between conditions revealed that both the baseline and equity conditions were not different from each other, $t(5) = 0.28$, $p = .79$, but each was significantly different from the food inequity condition, $t(5) = -4.88$, $p = .01$, and $t(5) = -6.42$, $p < .01$, respectively, and each was significantly different from the food control condition, $t(5) = -5.73$, $p < .01$; $t(5) = 5.53$, $p = <0.01$, respectively. Thus the equity conditions produced less rejection overall (Ms = 23.89% and 22%) than did the conditions in which a preferred reward was present, either in the case when a partner took it in the inequity condition (M = 65.67%) or when it was present but unavailable in the food control condition (M = 50.33%). There was no difference statistically between the food control condition and the food inequity condition, $t(5) = -1.96$, $p = .11$.

The rejection rates were analyzed by session to note any accumulating differences that emerged as a function of participating in the different conditions involving preferred rewards. Specifically, Figure 4 reveals the pattern of rejection rates to the food control condition and the food inequity condition. Paired sample t tests revealed a trend difference between the last session under food control (M = 48.33%) and the last session of the food inequity condition (73.33%), $t(5) = -2.03$, $p = .10$. This trend indicated that the subjects' rate of rejection was somewhat higher in the last session of the food inequity condition when the partner was offered preferred rewards than in the last session of the food control when the preferred reward remained present in an inaccessible container. There were no significant differences found within each condition between rejections on the first session in comparison with rejections on the last session: first–last food control, $t(5) = -0.38$, $p = .72$, first–last food inequity, $t(5) = -0.51$, $p = .63$. Nor were there significant differences between the first sessions across the two conditions: first control versus first inequity, $t(5) = -1.9$, $p = .12$.

Discussion

All the conditions in both the bartering task and the offering task posed the same basic problem for the tamarin subjects: whether to accept or reject a quarter grape. The conditions presented different events to the tamarins preceding the choice, and these events caused some significant changes in the monkeys' patterns of rejections. Clearly, the monkeys rejected more often in some conditions than in others. But what is the mediating cause of the differential rejections?

Across both tasks, the consistent finding was that subjects rejected the quarter grape significantly more in the food control condition when preferred food was presented in an unattainable way. This indicates that the presence of a preferred but unattainable reward caused the monkeys to reject the less preferred but

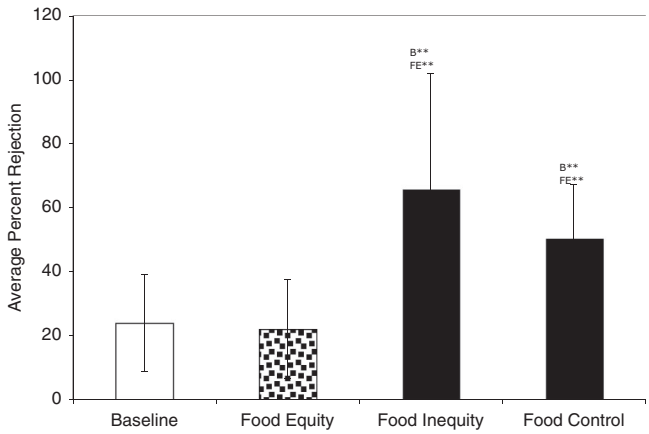

Figure 3. Averaged rejection rates to all the conditions in the offering task, with 95% confidence intervals plotted. Solid bars indicate that preferred food was available. Dotted bars and the open bar indicate that quartered grapes were the only food item perceived. In all cases, subjects' rate of rejecting quartered grapes is plotted. B^{**} indicates that condition was significantly different from baseline at $p < .01$. FE^{**} indicates that condition was significantly different from food equity at $p < .01$.

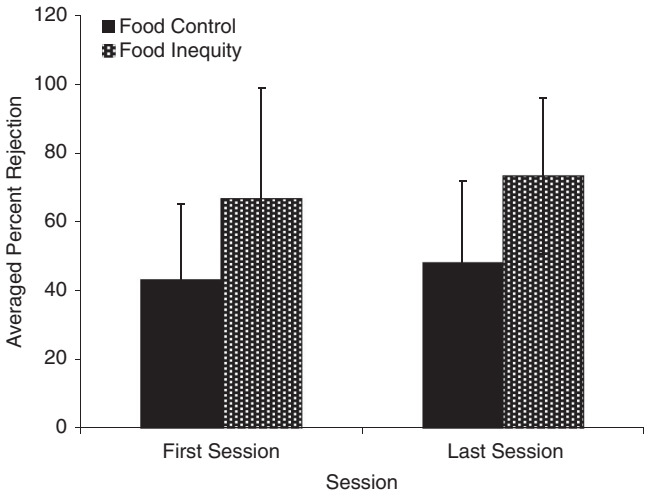

Figure 4. Averaged rejection rates for the first and last sessions for the conditions involving the presentation of preferred rewards in the offering task.

attainable food more. There were conditions in both tasks in which a social variable was added to this problem: A partner received a more preferred food before the subject was given the opportunity to accept or reject. In the bartering task, the socially mediated conditions that are related to preferred rewards (food inequity and food + work inequity) did not produce rejections significantly greater than did the preferred food control condition. In the offering task, the socially mediated food inequity condition generated significantly more rejections than did the equity conditions (both baseline and food equity) but no difference between rejections to it and the food control condition. In terms of the various predictions set out at the beginning of this article, the results more closely match rejection based on a violation of expected reward, because the social cues did not cause a significant difference in rejections beyond that caused by preferred food being presented.

But were there any noticeable effects of the social variables on rejection rates? One subtle finding that suggested social awareness in the tasks was uncovered by analyzing the subjects' reactions across sessions. In the bartering task, the food inequity condition, which offered preferred rewards to partners and thus added a social component to the preferred food, led to rejection rates in subjects that increased significantly from the first to the last session (bartering task). This tendency was noted in the offering task as well, although it did not reach the level of significance in the food inequity condition. More importantly, the presence of preferred rewards in the food control condition did not generate a cumulative increase in rejections in either task.

As Brosnan and de Waal (2003) found in their original study, the addition of a social being consuming the preferred reward induced a stronger cumulative rejection over time. This cumulative effect was attributed by Brosnan and de Waal to an increasing aversion to the perceived inequity between partner and subject. Social facilitation of eating, by which an animal is more likely to approach and eat the same food after observing another animal doing so, has been well-established in mammals and birds (for a historical review, see Crawford, 1939). Perhaps when food is readily available, eating facilitates eating, as has been documented historically and repeated by Dindo and de Waal (2007) in capuchins. But under conditions of restriction in which food limits occur within an event and in which there is greater effort expended to obtain the limited resource, the social facilitation caused by another subject eating a preferred reward is considered differently: It does not generate the "grab-and-go" competition that occurs when food is more freely available; rather it produces increased rejection of the food-getting situation, and this effect has been found in this study and by Brosnan and de Waal (2003) and Dindo and de Waal (2007).

There remains an inconsistent finding in this study regarding the increased rejection induced by socially mediated inequity in the bartering task. Specifically, the food + work inequity condition presented a partner with a preferred food for no work, and this condition did not increase rejection rates over time, while the food inequity condition in which both partner and subject had to trade tokens for food induced a significant increased rejection rate over time. Why, under the most unfair conditions presented—unfair rewards and unfair work comparison—did the tamarins not assess the situation and reject more with increased exposure? Here again the results suggest that the constraints within the task induce different types of assessment by the tamarins. In the case of food + work inequity, the partner is simply handed the preferred item while the subject has to work to trade a token for the less preferred food. Here, as in the food control condition in which the preferred food is simply presented, the preferred food handed to a partner has a similar noncumulative effect on subjects' rejections. The effect of a partner eating a preferred food or a preferred food being presented is the same. But if a partner works and obtains a preferred reward while the subject has to work to obtain a less preferred one, the task characteristics are of limited resources and effort for rewards for both partner and subject. Under these conditions, the rejection rates increase over time, and the aversion to the situation grows. It is likely then that subjects can habituate more easily to preferred foods being present or being eaten by partners. However, when partners are acting to acquire the preferred reward, the work of the partner and the reward are not easily ignored, and under this condition, the subjects show increased rates of aversion noted by increased rates of rejection with exposure.

A final difference that requires an explanation involves the type of work and the difference in rejections induced across the tasks and conditions. Clearly the 5 monkeys randomly placed in the bartering task accepted significantly more often the less preferred reward overall than did the 6 other monkeys in the offering task. The most notable difference between the two tasks is the amount of work put in before obtaining the less preferred reward, and the results suggest that monkeys prize a less preferred reward more if they have worked for it. This phenomenon is very similar to the within-trial contrast first suggested by Zentall (2005), in which pigeons demonstrated a preference for a stimulus associated with more effort, a delay, or the absence of reward. Zentall argued that such a contrast effect could explain many human social phenomena, including cognitive dissonance and the justification of effort effects, both contradictory outcomes in which humans seem to prefer an outcome paired with more work, effort, or contrast. When this is applied here, the monkeys seem to discriminate in the same way and show an overall preference for accepting the less preferred food if they have had to work for it.

The tamarins in this study clearly demonstrated rejections reliably across all tasks as a function of the difference between expected and obtained reward, and this difference was not made more striking by adding a social partner to the assessment. But the tamarins were more willing to accept less preferred rewards when they worked for them, and they also demonstrated a sensitivity to others obtaining the preferred rewards through work, which induced a heightened rejection reaction with exposure. The sensitivity to the combination of work, others, and food quality only effected the tamarins' behavior in the bartering task during which food was limited and effort was required. It is likely that these assessments do not come together in a whole social assessment for tamarins unless the constraints on work and differential foods are put in place. Under more open foraging circumstances, as when tamarins are handed different types of food, they seem to assess only the difference between expected and obtained rewards and reject more when those do not match. Under those conditions, whether or not the difference is defined socially is irrelevant to the behavior.

To return to the question posed by the title, this research suggests that inequity assessment is a trait shared among primates with particular characteristics and in particular circumstances: (a) They are socially tolerant enough to observe each other working for particular types of food, (b) they can differentiate quality of food and have food preferences, and (c) the circumstance demands that they exert effort to obtain food. If we speculate further, primate species that show social tolerance through cooperative breeding and food sharing are the species most likely to be in a position to assess equity among their group members. These would include capuchins and tamarins among the New World monkeys, and humans, chimpanzees, and bonobos (*Pan paniscus*) among the apes. It seems likely that under circumstances in which resources are more limited, social assessments and evaluations can play a much stronger role in behavior. Others have suggested similar pressures for cooperation to emerge under competitive circumstances among particular species of primates, including humans (i.e., Hare, 2007).

References

Amsel, A. (1958). The role of frustrative nonreward in noncontinuous reward situations. *Psychological Bulletin, 55,* 102–109.

Brauer, J., Call, J., & Tomasello, M. (2006). Are apes really inequity averse? *Proceedings of the Royal Society of London, Series B: Biological Sciences, 273,* 3123–3128.

Brosnan, S. F., & de Waal, F. B. M. (2003). Monkeys reject unequal pay. *Nature, 425,* 297–299.

Brosnan, S. F., & de Waal, F. B. M. (2006). Partial support from a nonreplication: Comment on Roma, Silberberg, Ruggiero, and Suomi (2006). *Journal of Comparative Psychology, 120,* 74–75.

Crawford, M. P. (1939). The social psychology of the vertebrates. *Psychological Bulletin, 36,* 407–446.

Cronin, K. A., Kurian, A. V., & Snowdon, C. T. (2005). Cooperative problem solving in a cooperatively breeding primate (*Saguinus oedipus*). *Animal Behaviour, 69,* 133–142.

de Waal, F. B. M. (2008). Putting the altruism back into altruism: The evolution of empathy. *Annual Review of Psychology, 59,* 279–300.

Dindo, M., & de Waal, F. B. M. (2007). Partner effects on food consumption in brown capuchin monkeys. *American Journal of Primatology, 69,* 1–9.

Dubreuil, D., Gentile, M. S., & Visalberghi, E. (2006). Are capuchin monkeys (*Cebus apella*) inequity averse? *Proceedings of the Royal Society of London, Series B: Biological Sciences, 273,* 1223–1228.

Fehr, E., & Schmidt, K. M. (1999). A theory of fairness, competition and cooperation. *Quarterly Journal of Economics, 114,* 817–868.

Feistner, A. T. C., & Price, E. C. (1999). Cross-generic food sharing in tamarins. *International Journal of Primatology, 20,* 231–236.

Feistner, A. T. C., & Price, E. C. (2000). Food sharing in black lion tamarins (*Leontopithecus chrysopygus*). *American Journal of Primatology, 52,* 47–54.

Fontenot, M. B., Watson, S. L., Roberts, K. A., & Miller, R. W. (2007). Effects of food preferences on token exchange and behavioral responses to inequality in tufted capuchin monkeys, *Cebus apella. Animal Behaviour, 74,* 487–496.

Hare, B. (2007). From nonhuman to human mind: What changed and why? *Current Directions in Psychological Science, 16,* 60–64.

Hauser, M. D., Chen, M. K., Chen, F., & Chuang, E. (2003). Give unto others: Genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proceedings of the Royal Society of London, Series B: Biological Sciences, 270,* 2363–2370.

Heinrich, J. (2004). Inequity aversion in capuchins? *Nature, 428,* 139.

Heinrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., et al. (2001). Cooperation, reciprocity and punishment in fifteen small-scale societies. *American Economic Review, 91,* 73–78.

Jensen, K., Call, J., & Tomasello, M. (2007). Chimpanzees are rational maximizers in an ultimatum game. *Science, 318,* 107–109.

Kostan, K. M., & Snowdon, C. T. (2002). Attachment and social preferences in cooperatively-reared cotton-top tamarins. *American Journal of Primatology, 57,* 131–139.

McConkey, K. R. (2000). Food sharing in black lion tamarins (*Leontopithecus chrysopygus*). *American Journal of Primatology, 52,* 47–54.

Neiworth, J. J., Burman, M. A., Basile, B. M., & Lickteig, M. T. (2002). Use of experimenter-given cues in visual co-orienting and in an object-choice task by a new world monkey species, cotton top tamarins (*Saguinus oedipus*). *Journal of Comparative Psychology, 116,* 3–11.

Parker, S. T., & McKinney, M. L. (1999). Origins of Intelligence: The Evolution of Cognitive Development in Monkeys, Apes, and Humans. Baltimore, MD: Johns Hopkins University.

Price, E. C., & Feistner, A. T. C. (2001). Food sharing in pied pare-faced tamarins (*Saguinus bicolor bicolor*). *International Journal of Primatology, 22,* 231–242.

Roma, P. G., Silberberg, A., Ruggiero, A. M., & Suomi, S. J. (2006). Capuchin monkeys, inequity aversion, and the frustration effect. *Journal of Comparative Psychology, 120,* 67–73.

Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2003). The neural basis of economic decision-making in the ultimatum game. *Science, 300,* 1755–1758.

Tomasello, M. (1999). *The cultural origins of human cognition.* Cambridge, MA: Harvard University Press.

Tomasello, M. (2003). The key is social cognition. In D. Gentner & S. Goldin-Meadow (Eds.), *Language in mind: Advances in the study of language and thought* (pp. 47–57). Cambridge, MA: MIT Press.

van Wolkenten, M., Brosnan, S. F., & de Waal, F. B. M. (2007). Inequity responses of monkeys modified by effort. *Proceedings of the National Academy of Sciences, 104,* 18854–18859.

Wynne, C. D. L. (2004). Fair refusal by capuchin monkeys. *Nature, 428,* 140.

Zentall, T. R. (2005). A within-trial contrast effect and its implications for several social psychological phenomena. *International Journal of Comparative Psychology, 67,* 405–415.

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