

Competing demands of prosociality and equity in monkeys

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Abstract

Prosocial decisions may lead to unequal payoffs among group members. Although an aversion to inequity has been found in empirical studies of both human and nonhuman primates, the contexts previously studied typically do not involve a trade-off between prosociality and inequity. Here we investigate the apparent coexistence of these two factors, specifically the competing demands of prosociality and equity. We directly compare the responses of brown capuchin monkeys (*Cebus apella*) among situations where prosocial preferences conflict with equality, using a paradigm comparable to other studies of cooperation and inequity in this species. By choosing to pull a tray towards themselves, subjects rewarded themselves and/or another in conditions in which the partner either received the same or different rewards, or the subject received no reward. In unequal payoff conditions, subjects could obtain equality by choosing not to pull in the tray, so that neither individual was rewarded. The monkeys showed prosocial preferences even in situations of moderate disadvantageous inequity, preferring to pull in the tray more often when a partner was present than absent. However, when the discrepancy between rewards increased, prosocial behavior ceased.

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1. Introduction

Prosocial preferences have recently gained status as a potential motivational mechanism underlying complex cooperation in human societies, and the long-term mutual benefits associated with it (Fehr & Fischbacher, 2003). However, this motivation may result in actions that produce inequity between the performer and recipient (Engelmann & Strobel, 2004; Fehr, et al., 2006; Xiao & Bicchieri, forthcoming), so how does it overcome aversion for inequity (Dawes, Fowler, Johnson, McElreath, & Smirnov, 2007; Fehr & Schmidt, 1999)? In natural environments, it

is hard to maintain perfect equity in every interaction, making prosocial behavior hard to maintain without some degree of inequality tolerance. Indeed, the evolution of human society and economic growth are often accompanied by inequality (Aghion, Caroli, & Garcia-Penalosa, 1999), leaving open the possibility that prosocial impulses must entail inequity tolerance if they are to result in extensive cooperation.

Although human cooperation has been argued to be fundamentally different from that of other animals (Silk, 2005), two key factors which relate to cooperation have recently been demonstrated in some situations in nonhuman primates, in particular capuchin monkeys (*Cebus apella*): prosociality (de Waal, Leimgruber, & Greenberg, 2008; Lakshminarayanan & Santos, 2008; Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Warneken & Tomasello, 2006) and an aversion to inequity (Brosnan & de Waal, 2003; Brosnan, Schiff, & de Waal, 2005; Fletcher, 2008; van Wolkenten, Brosnan, & de Waal, 2007). First

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considering prosocial behavior, there is evidence that capuchin monkeys make decisions which bring rewards to their partners. Notably, when given a choice between an option that rewards only themselves and an option which rewards both them and a conspecific partner, capuchin monkeys make decisions which reward their partners, choosing options which brought food to their partners much more often when a partner was present than absent (Lakshminarayanan & Santos, 2008). These monkeys are also sensitive to relationships, more often showing prosocial behavior towards kin and close social partners than to strangers (de Waal et al., 2008).

This pattern of prosocial tendency is less consistent in other species. In a series of studies which preceded those with capuchins, experiments involving three different groups of chimpanzees have failed to find evidence that chimpanzees are willing to choose options which bring food to their partners (Jensen, Hare, Call, & Tomasello, 2006; Silk et al., 2005). In a follow-up study designed to investigate whether chimpanzees were distracted by the presence of a food reward for themselves, chimpanzees generally failed to bring rewards to their partners after they had already selected an (identical) reward for themselves (Vonk et al., 2008). Finally, chimpanzees failed to select the option which rewarded their partner even in a reciprocal situation, in which alternation of prosocial behavior would have benefited both individuals (Brosnan et al., 2009). Callitrichids show a mixed response to the original paradigm, with marmosets choosing to bring food rewards to their partners (Burkart, Fehr, Efferson, & van Schaik, 2007), but not tamarins (Cronin, Schroeder, Rothwell, Silk, & Snowdon, *in press*).

However, it may be that the presence of food rewards overshadows any prosocial tendencies in chimpanzees, who do show helping behavior towards both human experimenters and conspecifics in situations which do not involve food rewards (Warneken et al., 2007; Warneken & Tomasello, 2006). Warneken et al. have proposed that chimpanzees are more competitive in food situations, limiting prosocial behavior. If so, this may be true in other species as well. Aside from prosocial behavior, capuchins do show helping behavior (although they seem to be motivated more by food rewards; Barnes, Hill, Langer, Martinez, & Santos, 2008). Thus, for the current study, we include a non-food treatment, using tokens, to directly test this hypothesis.

Regarding the second social preference, inequity, evidence for a reaction to inequity has, thus far, been found in three different non-human species: capuchins, chimpanzees, and domestic dogs (Brosnan & de Waal, 2003; Brosnan et al., 2005; Fletcher, 2008; Range, Horn, Viranyi, & Huber, 2008; van Wolkenten et al., 2007). In these studies, individuals respond negatively to receiving an outcome, which differs from that of their partners. As with humans, the response is sensitive to external contingencies. It is affected by the subjects' social environment and relationships (Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, *in press*;

Brosnan et al., 2005), and the context of the interaction (e.g., the presence or absence of a task; Roma, Silberberg, Ruggiero, & Suomi, 2006; Dindo & de Waal, 2006; Dubreuil, Gentile, & Visalberghi, 2006; Neiworth et al., 2009). Notably, the current task reflects conditions under which responses to inequity have been documented to occur.

Thus, some species, including capuchin monkeys and humans, show responses to both social preferences, raising the issue of how these seemingly incompatible social preferences interact. How can an individual react against inequity in some situations, and yet choose to reward a partner in a situation in which the partner may receive better rewards in others? Among the few studies investigating what occurs in situations with conflicting social motivations, the answer remains controversial (Englemann & Strobel, 2004; Fehr, Naef, & Schmidt, 2006). However, this answer is fundamental to our understanding of cooperation in society. In particular, some degree of inequity tolerance seems critical for the maintenance of cooperation, as it is rare that encounters between parties are always perfectly equitable.

Here we investigate the apparent coexistence of these two factors, the competing demands of prosociality and equity, in capuchin monkeys. Capuchin monkeys are a good model, as they show both robust inequity (Brosnan & de Waal, 2003; Fletcher, 2008; van Wolkenten et al., 2007) and prosocial (de Waal, Dindo, Freeman, & Hall, 2005; Lakshminarayanan & Santos, 2008) responses, and are highly cooperative (de Waal & Berger, 2000). With regard to inequity, subjects refused to participate when receiving a lesser-value reward, both in a token-exchange task (Brosnan & de Waal, 2003, van Wolkenten et al., 2007) and in a barpull task, as was used in the current study (Brosnan, Freeman & de Waal, 2006). With regard to prosocial behavior, in a two-choice task, subjects preferred the option which brought food rewards to both themselves and a partner, to the option which rewarded only themselves (de Waal, Dindo, Freeman, & Hall, 2005).

For the current study, we designed a task in which the monkeys had a single choice between a prosocial option (e.g., pulling in the tray) or no rewards for either monkey (e.g., refusing to pull). From the earlier work, we knew that they have a preference for the prosocial option when rewards are equal; hence, the goal of this investigation was to discover if they would maintain these prosocial preferences when rewards were unequal in favor of the partner.

We used a bar-pull apparatus that has been successfully used before in a variety of studies of cooperation (de Waal & Berger, 2000; de Waal & Davis, 2002; Melis, Hare, & Tomasello, 2006b; Brosnan et al., 2006), but in the present case, there was no opportunity for cooperation. Subjects could choose whether to pull in a tray with two food rewards, one for their partner and one for themselves (except in the conditions in which the subject received no reward). If the tray was pulled in, both monkeys could access any rewards which were available, otherwise neither received any rewards. Rewards for the subject and the partner were either identical or different, favoring the partner. As a control for

social interaction, a second, otherwise identical, set of treatments were run, but without a partner to receive the second reward (i.e., the subject was alone). Comparing pulling behavior with partner present vs. absent yielded data on prosocial preferences, because if subjects pull more often under the first condition they are probably more sensitive to the partner getting rewarded than the presence of rewards (Silk et al., 2005; Jensen et al., 2006; Burkhardt et al., 2007; Vonk et al., 2008; Cronin et al., *in press*). A second series was run to investigate the effects of available food on willingness to behave prosocially, to test the hypothesis that the presence of food may inhibit prosocial behavior (Warneken et al., 2007). In this case, subjects pulled for tokens which were traded for the corresponding foods.

Based on the previous published studies demonstrating that these capuchin monkeys have prosocial tendencies, we predicted that the monkeys would pull more often when the partner was present than absent when the rewards were equal (de Waal et al., 2005) or even unequal favoring the partner (Lakshminarayanan & Santos, 2008). However, based on published studies demonstrating that monkeys quit participating in interactions when their partners receive better rewards than they do (Brosnan & de Waal, 2003; van Wolkenten et al., 2007), we predicted that prosocial behavior would diminish as the discrepancy between the rewards increased. Finally, based on the hypothesis of Warneken et al. (2007) that the presence of food decreases the likelihood of prosocial behavior, we hypothesized that prosocial behavior would be higher in the token than the food condition.

2. Methods

2.1. Subjects

The subjects were 10 brown capuchin monkeys from two social groups at the Yerkes National Primate Research Center, in Atlanta, GA, USA. The groups in which the subjects lived were housed in two large, indoor/outdoor enclosures. Each enclosure contained ample three-dimensional climbing space as well as trapezes, perches, and enrichment items. Purina small primate chow was provided twice a day, at approximately 9:30 and 17:30 h. A tray consisting of fruits, vegetables, and bread with a protein solution was provided to each group every day at approximately 17:30 h. Running water was available *ad libitum*. This feeding schedule was followed regardless of the day's testing, and subjects were never food- or water-deprived. For more details about the testing facility, see de Waal, 1997.

Subjects were tested in a testing chamber which was attached to their home enclosure. Within the chamber, subjects were separated by a clear plexiglass partition that allowed for visual and vocal contact, but did not allow either individual to access the other's rewards. This allowed us to interact with subjects in a controlled manner with minimal

distractions. Subjects were accustomed to the testing chamber and the procedure used to select subjects, as these procedures have been used daily for more than a decade. No subject was ever involved in more than one barpull test on any given day, and test sessions were always performed between 10:00 and 13:00. Testing was performed 5 days a week, and subjects were tested regularly, without gaps, throughout the duration of the study.

Unrelated individuals from the same group were paired for testing. Pairs consisted of two females of similar age and rank; rank order was determined using data from weekly behavioral observations. These five pairs remained the same for the duration of the study. All subjects had used the barpull apparatus in previous studies, but the most recent was completed approximately 3 years prior to the current study (Brosnan et al., 2006).

2.1.1. Barpull paradigm

Our barpull was designed after Crawford's, developed for use with chimpanzees (Crawford, 1937), and this and similar designs have been used extensively to study cooperation (de Waal & Berger, 2000; de Waal & Davis, 2002), inequity (Brosnan et al., 2006) and prosocial preferences (Lakshminarayanan & Santos, 2008) in capuchin monkeys. The barpull consisted of a tray with a handle which could be used to pull the tray within reach of the monkeys; the barpull apparatus was not counterweighted or otherwise restricted, so pulling the bar to retrieve a reward required very little effort on the part of the individual. Rewards were placed in transparent cups to keep them from sliding off of the tray. Food cups were placed directly in front of each monkey. If the monkeys pulled the tray in all of the way, the tray latched into position adjacent to the subjects, and subjects could pull as many times as they wished. For this test, the barpull was placed directly against the test chamber.

2.1.2. Rewards

Rewards for this test consisted of cucumber slices and grapes. A "lower value" reward was a quarter of a cucumber slice while a "higher value" reward was a single seedless grape. These rewards were chosen because both are favored by the capuchins (hence they are motivated to participate in the test), but there was a strong preference by all subjects for a grape over cucumber slices.

To determine reward preferences, a dichotomous food preference test was done in the presence of the individuals they were paired with for the remainder of the study. Subjects were offered each food for 10 consecutive trials, with the location of foods alternating from side to side, to control for side biases. A food was considered preferred by the individual if they chose it in a minimum of 8 out of 10 trials (Brosnan & de Waal, 2004a, 2004b), although in practice, each subject showed a 100% preference for a grape over the cucumber piece. These results are consistent across time for individuals.

2.1.3. Apparatus habituation

Following the reward preference tests, each monkey was habituated to the barpull apparatus before formal testing began. Habituation was done with the same social partner with which they were paired for the entire experiment. Since individuals were familiar with the barpull from previous studies (e.g., Brosnan et al., 2006), only a single session was used to re-familiarize subjects with the apparatus. During this session, food was placed in both cups and replenished as needed, and in all trials, both cups were baited equally. For the first 5 min of habituation, there was no divider in the test chamber, and both monkeys had unlimited access to the barpull apparatus and the rewards from both cups. In the second half of the session, the monkeys were separated from one another using the plexiglass divider, so only one was able to manipulate the barpull at a time; both monkeys had the opportunity to be alone on the handle side of the apparatus and were allowed either 10 pulls or 5 min, whichever came first. Apples, known to be intermediate in preference between cucumbers and grapes, were used as rewards during the habituation sessions.

2.1.4. Testing conditions

2.1.4.1. Food treatment. In the Food Treatment, the barpull apparatus was baited in four different ways. Each session consisted of 20 trials, with four trials of each type presented in a randomized order within the test session. Each test subject completed two sessions with a partner (Partner sessions) followed by two sessions without a partner (Control sessions). Control sessions were necessary to verify that any responses were due to the presence of the partner and did not occur based on some other aspect of the methodology.

The four conditions were as follows. The “Equal Low” was a control condition which tested subjects’ responses when they received the same low-value reward as a partner, a cucumber piece. The “Equal High” condition was the same, except both subjects received a grape. Part of the reason for including this condition was to maintain subject motivation, and to acquire a baseline pull rate for highly-preferred foods. The “Unequal” condition tested the subject’s response when the partner got a better reward, a grape, than the subject, who received a piece of cucumber. Finally, the “None” condition tested the subject’s willingness to pull when they received no reward, but their partner received either a grape or a cucumber slice. Subjects who pull in this condition: (1) do not understand the contingencies of the methodology (tested with the Control sessions); (2) are accustomed to pulling, based on long experience with the apparatus (also tested with the Control sessions); or (3) are being altruistic. Note there were half as many sessions of none/low and none/high as the others, in order to avoid loss of subject motivation.

Within trials, the subject had 15 s in which to pull the bar and retrieve the reward, upon which both monkeys had an additional 30 s to consume their food before the

commencement of the next trial. If the subject failed to pull the bar within the 15 s window, the food was removed from the cups and there was still a 30-s delay before the next trial began. This delay was maintained to avoid the possibility of subjects choosing not to pull because the time delay was shorter.

2.1.4.2. Token treatment. It has previously been hypothesized that some primates, in particular chimpanzees, respond differently to prosocial situations when food is involved (Warneken, Chen, & Tomasello, 2006). Thus, for the Token Treatment, subjects were given the same series of tests, except instead of pulling for foods, they pulled for tokens which represented foods. Capuchin monkeys are known to form strong associations between tokens and their corresponding food rewards (Addessi, Crescimbeni, & Visalberghi, 2007; Addessi et al., 2008; Brosnan & de Waal, 2004a, 2004b). Thus, in the Token Treatment, the cups were baited with tokens representing the same food reward combinations tested in the Food Treatment, with bolts representing cucumbers and washers representing grapes.

Prior to the commencement of the Token Treatment testing, subjects were conditioned through association that one token (a metal bolt) was worth a piece of cucumber and the other (a large metal washer) was worth a grape. This was done in two 50-trial sessions. Following a previous study which conditioned tokens to different rewards (Brosnan & de Waal, 2004a), in each session, the individuals were paired in the test chamber with their testing partner and separated by the plexiglass divider. Five of each token (washers and bolts) were dropped into the chamber and the individual was able return/ exchange the tokens in any order they chose, and received the corresponding reward. After Individual 1 returned all 10 tokens, their partner completed 10 such trials, and the two continued this process until each monkey had exchanged 50 times (25 times per token). These test sessions were performed on two consecutive days. In previous studies, this number of exchanges or fewer, either personally experienced or observed, resulted in strong preferences for the token worth the higher-value of the two food items (Brosnan & de Waal, 2004a; 2004b).

During testing, tokens were presented in the same manner as the food rewards in the Food Treatment; once the bar was fully pulled in, an experimenter simultaneously replaced the tokens with the appropriate reward(s). As in the Food Treatment, each session consisted of 20 trials, with four of each type presented in a randomized order within the test session. Each test subject completed 2 sessions with a partner (Partner sessions) followed by 2 sessions without a partner (Control sessions).

2.1.5. Testing order

All individuals completed both treatments. Pairs completed all sessions within one treatment before beginning the next. The order in which they completed the treatments was counterbalanced (i.e. half of the pairs were randomly

assigned to begin with the Food Treatment and the other half began with the Token Treatment). There was no break in testing between treatments, with the exception of token training for those pairs completing the Token Treatment after the Food Treatment (all individuals completed token training immediately prior to the Token Treatment to assure that the associations were fresh during the experiment).

Pairs remained consistent throughout testing. Each individual within a pair participated in eight test sessions per treatment. These sessions were comprised of four test sessions in the “partner” role and four test sessions in the “subject” role. The order of sessions for a pair was randomized within a treatment such that either subject could be in either role on any given session. Roles never varied within a session. Complete testing of one pair consisted of 8 sessions per treatment or 16 test sessions total, in addition to token training. Treatments consisted of high/high, low/low, low/high, and none/reward. None/reward was divided in to four sessions of none/low and four sessions of none/high. As noted above, this was done to avoid extinction of pulling behavior if the subjects found the none/reward condition frustrating. The difference in sample size is accounted for in our analysis.

All tests were videotapes using a Canon mini-DV recorder. All video tapes were later coded on multiple passes by a human observer who was blind to the hypotheses. All analyses are based on the coded data.

2.1.6. Statistics

Statistical analyses were accomplished using randomization methods to compute exact sampling distributions for paired-sample Wilcoxon Signed-Ranks test statistics, treating each monkey as a single observation. Based on previously published research, we had specific predictions that subjects would bring food rewards to their partners (e.g., behave prosocially; de Waal et al., 2008; Lakshminarayanan & Santos, 2008) and would dislike conditions in which the partner received a better reward than the subject (e.g., an aversion to inequity; Fletcher, 2008; Brosnan & de Waal, 2003; van Wolkenten et al., 2007; see Introduction for more details). Thus, all statistics related to these predictions are one-tailed tests, a procedure also followed in related previous studies (e.g. Lakshminarayanan & Santos, 2008). As none of our other predictions were directional, all other tests are two-tailed. All of our comparisons were planned comparisons based on the specific hypotheses we were testing. Nonetheless, given that four tests were necessary to compare the partner to control conditions, an adjusted p value is appropriate (Bonferroni correction; $p=.013$).

To analyze pulls, we calculated the mean pull rate for each condition and treatment separately, pooled across all individuals. We had a few instances of pulls which appeared to be outliers, occurring at the end of a trial or as the experimenter re-appeared. Thus, we chose to set a cutoff point to avoid the possibility that these pulls were due to some other feature (e.g., demand characteristics of the

experimenter). The mean latency for partner tests was 2.26 s (S.E.=2.07 s) and the mean latency for the solo tests was 2.31 s (S.E.=2.28 s). We set the cut-off at 15 s.

3. Results

3.1. Food preference tests

Each individual used in this test showed a 100% preference (10 out of 10 choices) for the single grape over the cucumber slice in a dichotomous choice.

3.2. Food treatment

Overall, subjects showed significant variation between conditions, both for the partner conditions (Friedman’s test, $|Z|>3.291$, $df=4$, $p<.001$) as well as the solo control conditions (Friedman’s test, $|Z|>3.291$, $df=4$, $p<.001$).

Purely selfish subjects should decide to pull based only on their own reward and should not vary their decision with the presence or absence of another monkey. Indeed, as expected, subjects pulled nearly all of the time when they received the high-value grapes (high/high) both when the partner was present and absent (means of 100.0% and 98.8%, respectively).

On the other hand, with a less desirable reward (e.g., when there is no ceiling effect based on reward value) prosocial subjects should choose to pull more often when there is a partner present than when there is no other monkey to receive the reward (Fig. 1). We do find a trend towards subjects in this condition pulling more often when their partner was present than absent (low/low: $Z=1.534$, $N=10$, $p=.0625$, one-tailed). This finding accords with previous research (de Waal et al., 2008; Lakshminarayanan & Santos, 2008), both in direction and magnitude (a 15–20% increase).

In all other conditions, there was an inequity present such that the partner received a higher reward than the subject (puller). Nonetheless, in the one case in which the partner received the lower-value cucumber, the subjects continued to behave prosocially, pulling more often when the partner was present than absent (none/low: $Z=1.761$, $N=10$, $p=.0391$, one-tailed). However, when the partner received a grape, the puller subject did not behave prosocially, regardless whether they received a lower-value cucumber or no reward (low/high: $Z=0.675$, $N=10$, $p=.25$, one-tailed; none/high, $Z=0.626$, $N=10$, $p=.2657$, one-tailed). These results indicate that prosocial behavior may be more dependent on the partner’s outcome (e.g., low- or high-value food) than the subject’s outcome (e.g., low-value or no reward) (Fig. 1).

Another possibility is that subjects’ pulling behavior is based on the relative difference in value between their reward and those of their partners. We have two conditions in which it is possible to investigate this. We can compare the none/low condition to the none/high condition, as the subject’s outcome remains the same (no reward) and there is inequity in both cases (e.g., the partner always receives a better

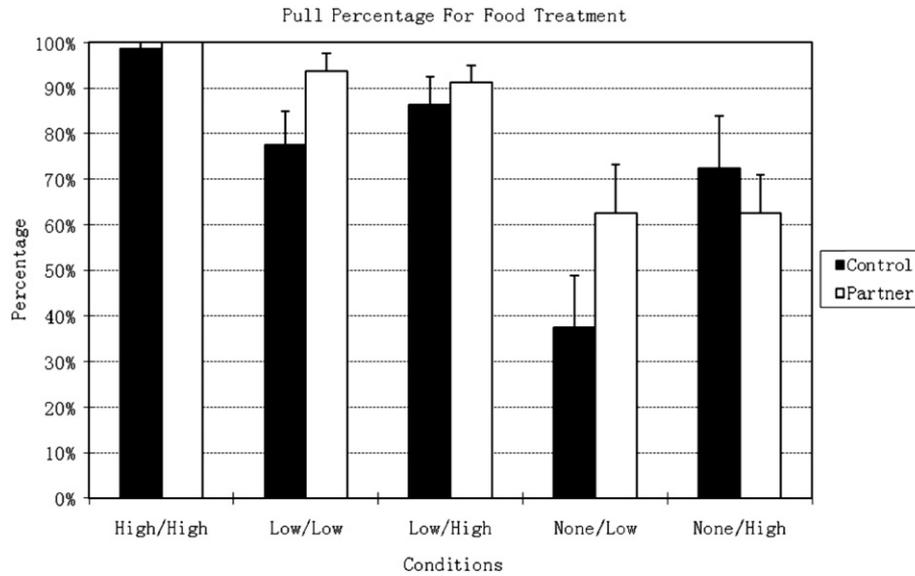


Fig. 1. Pull percentages in food condition by treatment. The x-axis indicates the pulling condition, black bars indicate the control, when no partner was present, and white bars indicate response when a partner was present. Overall, subjects were more likely to pull when a partner was present than absent.

outcome than the subject). We find that when the subject receives nothing, she is nonetheless more likely to pull if the partner received cucumber than grape ($Z=1.717$, $N=10$, $p=.043$, one-tailed). Moreover, when the subject gets a low value reward, there is no difference in pulling rate between the conditions in which the partner receives a cucumber (e.g., equity) versus a more desirable grape (e.g., inequity; comparing the partner condition for low/low and low/high; $Z=0.579$, $N=10$, $p=.2813$, one-tailed). Thus, it is clear that inequity alone is not sufficient to curtail prosocial behavior, nor is the situation in which the puller receives no reward.

We further investigated subjects’ feeding behavior, to provide evidence on whether their acceptance of rewards was affected by the distribution of rewards. We find only an effect of social facilitation (increased eating when group members are eating; James, 1953). Subjects were overall more likely to consume the food reward when a partner was

present than absent (Fig. 2; exact Wilcoxon test, $Z=1.761$, $N=10$, $p=.039$, one-tailed).

Finally, we investigated the latency to pull across conditions. We find no significant difference between the partner absent (solo control) and partner present conditions (exact Wilcoxon test, $Z=0.787$, $N=10$, $p=.216$, one-tailed). However, there is variation between the conditions within both the partner and control treatments (Friedmans’ test: $p=.017$ for control condition, $p=.004$ for partner condition). Examining conditions individually, in the none/high subjects pulled more rapidly in the partner condition than in the solo condition.

3.3. Token treatment

As for the food condition, in the token conditions one’s own reward should be the exclusive modulator of behavior

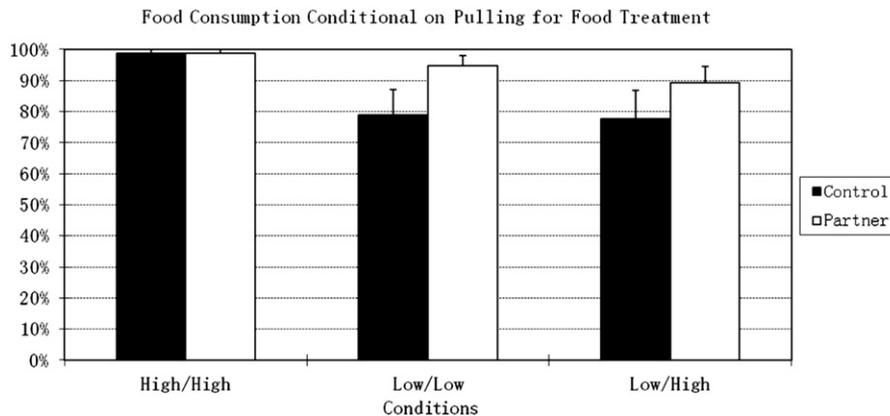


Fig. 2. Food consumption by the subject conditional on pulling for the three conditions (high/high), (low/low), and (low/high) in the food condition. Food consumption data do not exist for (none/low) and (none/high), because no food was available for consumption in these conditions.

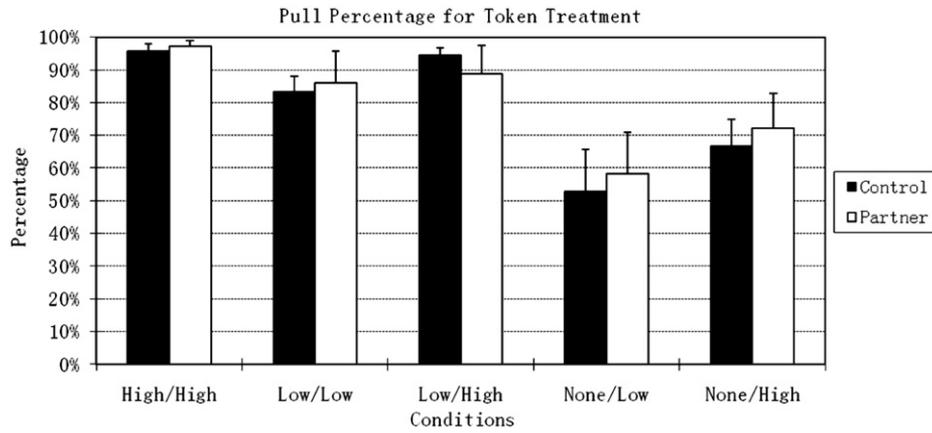


Fig. 3. Pull percentage for token condition by treatment. Subjects did not show any consistent pattern when pulling for tokens associated with food.

for selfish subjects, with the presence or absence of a partner playing no role in decisions. Indeed, as with the food reward, subjects pulled essentially all of the time when they received the high-value grapes (high/high) both when the partner was present and absent (with frequencies 97.2% and 95.8%, respectively). However, unlike the food condition, overall pull rates across all other conditions were insensitive to the presence of a partner (Fig. 3). In no condition did subjects change their pulling rates between partner present and absent conditions (none/low, $Z=0.177$, $N=9$, $p=.4297$, one-tailed; none/high, $Z=0.851$, $N=9$, $p=.1973$, one-tailed; low/low: $Z=0.524$, $N=9$, $p=.30$, one-tailed; low/high: $Z=0$, $N=9$, $p=.50$). Finally, unlike in the Food Treatment, when the subject received no reward she was just as likely to pull when the partner received cucumber (none/low) as when she received grape (none/high; exact Wilcoxon test, $Z=1.150$, $N=9$, $p=.125$, one-tailed).

We find no difference in food consumption behavior dependent upon whether the partner is present or absent (Fig. 4; exact Wilcoxon test, $Z=1.447$, $N=9$, $p=.074$, one-tailed). Latency to exchange also does not differ between the solo (control) and partner conditions (exact Wilcoxon test, $Z=1.270$, $N=9$, $p=.102$, one-tailed), nor is there variation between the conditions (Friedmans' test: $p=.19$ for control condition, $p=.21$ for partner condition).

4. Discussion

We replicate previous findings of prosocial behavior among capuchin monkeys, and moreover demonstrate that prosocial behavior is not always curtailed as a result of the partner receiving a better reward. Subjects behaved prosocially, choosing to access rewards more often when a partner

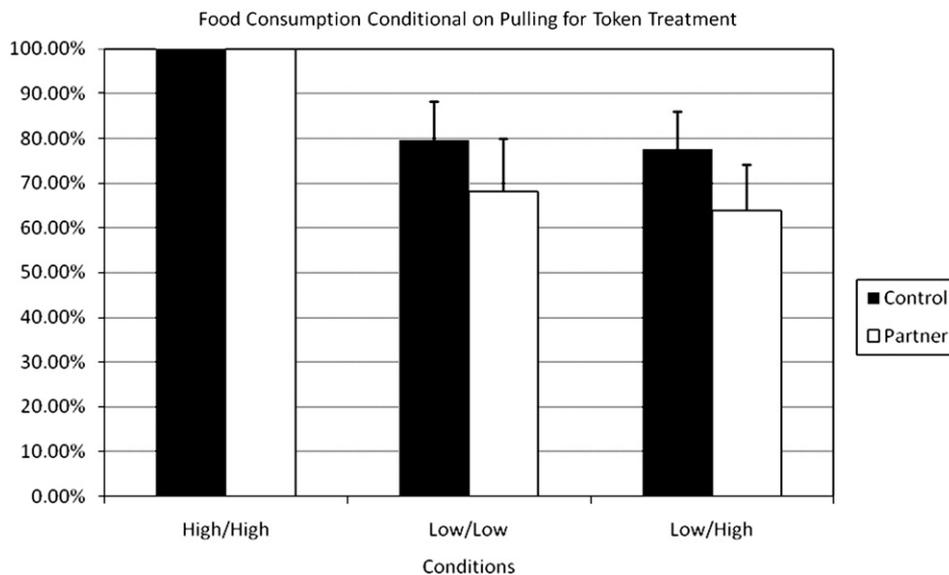


Fig. 4. Food consumption by the subject conditional on pulling for the three conditions (high/high), (low/low), and (low/high) in the token condition. Food consumption data do not exist for (none/low) and (none/high), because no food was available for consumption in these conditions.

was present than absent, when subjects got the same rewards (low/low), although we found evidence of a ceiling effect when both subjects received grapes (high/high). Moreover, subjects continued to behave prosocially in the other condition in which their partner received a low-value reward (none/low), even though the subject themselves received nothing. This latter result indicates that neither receiving nothing nor inequity between the self and the partner were sufficient to override prosocial behavior. However, prosocial behavior was not seen when the partner received a high value reward and the subject received a less desirable, or no, reward. Thus, subjects may be basing their decision about whether to be prosocial on an interaction between value of the partner's reward and the relative difference between the two rewards. These results indicate that prosocial behavior is substantially mitigated when the partner's reward is too great, or the difference between the rewards given to the partner and subject becomes too extreme.

There are several other possible explanations for these results that can be ruled out. First, the subjects pull quite often, even in the inequitable conditions. This is likely explained by the fact that these subjects have used the barpull apparatus for years, and are likely inclined to pull when given the opportunity. However note that despite high levels, subjects' pulling does vary based on condition, showing that their behavior is affected by the differences in payoffs and partner presence. Second, the prosocial behavior cannot be explained by a tendency to pull more often in the presence of the partner (e.g., increased arousal) since subjects failed to pull more often in some partner conditions (e.g. low/high and non/high), but not others. This variability is not expected if arousal is causing the increases in prosocial pulling. Similarly, prosocial behavior is unlikely to be explained by stimulus enhancement (e.g., learning to pull in the presence of a grape or learning to pull in the presence of a partner) because, again, pulling behavior was not consistent across conditions or partner present vs. absent. Finally, it is possible that the subjects' high level of pulling in the unequal conditions is due to a misunderstanding of the task (e.g., confusion or an expectation that they could receive the higher reward). Two pieces of evidence argue against this possibility. First, subjects had multiple test sessions, and in no session were they able to get the partner's reward, so they should have learned the task contingencies. Second, despite high levels of pulling, their behavior varies between conditions as if they understand that they cannot obtain the higher reward. Considering only the grape conditions, the fact that they pull all the time when they get a grape (high/high) and much less often when the partner only gets the grape (either low/high or none/high) again indicates that, despite being attracted to the grape, they are able to adjust their behavior according to the condition.

Although additional research is needed to quantify the degree of inequity which is "too much," the fact that equity is not a requirement for prosocial behavior makes the evolution

of such behavior more likely, as there are probably few situations in which equity is always possible (e.g., Aghion et al., 1999). This supports the development of cooperation, as the costs of occasional inequity may be outweighed by the benefits gained from prosociality. Thus, individuals who are willing to accept some inequity on some occasions will ultimately reap more benefits than those who do not. On the other hand, if inequity is extreme, individuals may do better to cease interacting and find a new partner elsewhere. In these cases, the cost of inequity outweighs the benefits of sociality, and prosocial behavior disappears.

It initially seems counter-intuitive that monkeys who are averse to inequity can simultaneously favor an outcome which could reward a partner with an even better outcome. These results indicate that this paradox is resolved by the fact that the monkeys are willing to tolerate low levels of inequity in order to behave prosocially. This may also explain seemingly contradictory results in previous studies, in which capuchins varied in their willingness to behave prosocially if their partner received a better reward (de Waal et al., 2008; Lakshminarayanan & Santos, 2008). These studies used different food rewards; thus, the difference in response might be a function differences between values of the items.

This willingness to behave prosocially even when another benefits more than self may also allow individuals to occasionally accept inferior rewards in a mutualistic cooperation situation. In a previous study, capuchin monkeys needed to cooperate to obtain food rewards. If successful, both received rewards; however, sometimes those rewards varied in value. The key was that the monkeys were not separated by the experimenters and, thus, had to choose for themselves the reward for which they were willing to work. In this way, subjects could accept an "offer" to cooperate for a low or high value food item. Capuchins were equally likely to be successful in the cooperative task regardless of whether rewards were equal or unequal; however, they were much more likely to cooperate if the partners split the unequal payoffs such that each monkey received the better reward approximately half of the time (Brosnan et al., 2006). Thus, this behavior was self-serving; monkeys who did not show some willingness to benefit their partner ended up with far fewer rewards overall, due to the fact that their partner ceased cooperating. This supports findings of the current study, indicating that there may be long-term benefits to assisting others, even when these others get more. However, note that the behaviors seen in these two studies are not the same. In the current experiment, there was no opportunity for reciprocity within a test session (e.g., the partner did not need to help the subject to obtain the rewards) yet subjects nonetheless chose to bring better rewards to their partners.

Interestingly, capuchin monkeys showed no differences between conditions in the token session, in which subjects pulled for tokens which were exchanged for food. This condition was included as it has been argued that chimpanzees, at least, behave differently in the presence of

food (Warneken et al., 2007), and capuchins do treat tokens similarly to their corresponding food items (Addessi et al., 2007; Addessi et al., 2008; Brosnan & de Waal, 2004a, 2004b). However, there were no significant differences between conditions when tokens were used rather than foods. There are several potential explanations for this. First, it is possible that this hypothesis holds for chimpanzees, but not capuchin monkeys. Like chimpanzees, capuchins do help (Barnes et al., 2008); however, capuchins seem more food motivated in these studies, and also behave prosocially in other food-related contexts (de Waal et al., 2008; Lakshminarayanan & Santos, 2008). Second, token rewards may lack the emotional salience often if they are connected to prosocial or inequity-based decisions (Xiao & Houser, 2005). A lack of emotional salience could occur, for example, if subjects did not form strong associations between tokens and food rewards. Although the monkeys understood the connection between the tokens and the food rewards, these tokens are still likely to be less salient than the actual grape or cucumber (preferences for tokens are typically weaker than those for the corresponding foods; Brosnan & de Waal, 2004a, 2005). Third, although the number of trials and sessions for conditioning were chosen because they were known to elicit significant token-reward associations in this population of capuchin monkeys (Brosnan & de Waal, 2004a; 2004b), we did not run a separate preference test to verify the strength of the association. Thus, it is possible that, for whatever reason, the monkeys failed to make the association in the current study. However, the increased pulling in the high/high condition (Fig. 3) argues against this.

One issue which remains to be addressed is the differences which we see between the different non-human primate species. This study addresses capuchin monkeys, which are a new world primate with many convergences with humans (cooperation, large brain-to-body ratio), but which are not as closely phylogenetically related to humans as the apes. The species most commonly used for such comparisons, chimpanzees (and their sister species, bonobos), show more variation in both prosocial behavior and inequity responses (see Introduction for details). Thus, what this study can tell us about human evolution remains an open question.

Of course, one possibility is that this ability arose independently in humans and capuchin monkeys, but not in other species. However, given that other species, such as chimpanzees, are also sensitive to partners' behaviors (Melis, Hare, & Tomasello, 2006a; Melis et al., 2006b) and inequity (Brosnan et al., 2005), this seems unlikely. Another possibility is that chimpanzees, too, will show some ability to integrate these behaviors, but that other characteristics are standing in the way, for instance, constrained behavior in the presence of food (Warneken et al., 2007). It may also be that chimpanzees are more able to respond with nuance to inequity, responding in some social situations, but not others (Brosnan et al., 2005). Supporting this, chimpan-

zees are much better at cooperative tasks when interacting with tolerant social partners (Melis et al., 2006b) and actively recruit those collaborators which best suit their needs (Melis et al., 2006a). Additional studies on different species, including both chimpanzees and other, less well studied primates may help to elucidate the presence of homologies or homoplasies in these social behaviors.

We find that capuchin monkeys hold multiple social preferences simultaneously. This may have aided in the evolution of cooperation and other social behaviors which require individuals to guard against being cheated while at the same time behaving in such a way that productive social partners desire to continue interactions. These results indicate that social preferences such as an aversion to inequity and a preference for prosociality may have simultaneously co-evolved in the primate lineage. It would be valuable in future research to further clarify how these preferences interact to determine decisions in social environments.

References

- Addessi, E., Crescimbeni, L., & Visalberghi, E. (2007). Do capuchin monkeys (*Cebus apella*) use tokens as symbols? *Proceedings of the Royal Society of London Series B*, 274, 2709–2715.
- Addessi, E., Mancini, A., Crescimbeni, L., Padoa-Schioppa, C., & Visalberghi, E. (2008). Preference transitivity and symbolic representation in capuchin monkeys (*Cebus apella*). *PLoS ONE*, 3(6), e2414.
- Aghion, P., Caroli, E., & Garcia-Penalosaand, C. (1999). Inequality and economic growth: The perspective of the New Growth Theories. *Journal of Economic Literature*, 37, 1615–1660.
- Barnes, J. L., Hill, T., Langer, M., Martinez, M., & Santos, L. R. (2008). Helping behaviour and regard for others in capuchin monkeys (*Cebus apella*). *Biology Letters*.
- 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. (2004a). A concept of value during experimental exchange in brown capuchin monkeys. *Folia primatologica*, 75, 317–330.
- Brosnan, S. F., & de Waal, F. B. M. (2004b). Socially learned preferences for differentially rewarded tokens in the brown capuchin monkey, *Cebus apella*. *Journal of Comparative Psychology*, 118(2), 133–139.
- Brosnan, S. F., & de Waal, F. B. M. (2005). A simple ability to barter in chimpanzees, *Pan troglodytes*. *Primates*, 46, 173–182.
- Brosnan, S. F., Freeman, C., & de Waal, F. B. M. (2006). Partner's behavior, not reward distribution, determines success in an unequal cooperative task in capuchin monkeys. *American Journal of Primatology*, 68, 713–724.
- Brosnan, S. F., Schiff, H. C., & de Waal, F. B. M. (2005). Tolerance for inequity may increase with social closeness in chimpanzees. *Proceedings of the Royal Society of London Series B*, 1560, 253–258.
- Brosnan, S. F., Silk, J. B., Henrich, J., Mareno, M. C., Lambeth, S. P., & Schapiro, S. J. (2009). Chimpanzees (*Pan troglodytes*) do not develop contingent reciprocity in an experimental task. *Animal Cognition*, doi:10.1007/s10071-009-0218-z.
- Brosnan, S. F., Talbot, C., Ahlgren, M., Lambeth, S. P., & Schapiro, S. J. (in press). Mechanisms underlying the response to inequity in chimpanzees, *Pan troglodytes*. *Animal Behaviour*.
- Burkart, J., Fehr, E., Efferson, C., & van Schaik, C. P. (2007). Other-regarding preferences in a non-human primate: Common marmosets provision food altruistically. *Proceedings of the National Academy of Sciences*, 104(50), 19762–19766.

- Crawford, M. (1937). The cooperative solving of problems by young chimpanzees. *Comparative Psychology Monographs*, 14(2), 1–88.
- Cronin, K. A., Schroeder, K. K. E., Rothwell, E. S., Silk, J. B., & Snowdon, C. (in press). Cooperatively breeding cottontop tamarins (*Saguinus oedipus*) do not donate rewards to their long-term mates. *Journal of Comparative Psychology*.
- Dawes, C. T., Fowler, J. H., Johnson, T., McElreath, R., & Smirnov, O. (2007). Egalitarian motives in humans. *Nature*, 446, 794–796.
- de Waal, F. B. M. (1997). Food transfers through mesh in brown capuchins. *Journal of Comparative Psychology*, 111(4), 370–378.
- de Waal, F. B. M., & Berger, M. L. (2000). Payment for labour in monkeys. *Nature*, 404, 563.
- de Waal, F. B. M., & Davis, J. M. (2002). Capuchin cognitive ecology: Cooperation based on projected returns. *Neuropsychologia*, 1492, 1–8.
- de Waal, F. B. M., Dindo, M., Freeman, C. A., & Hall, M. J. (2005). The money in the mirror: hardly a stranger. *Proceedings of the National Academy of Sciences*, 102(32), 11140–11147.
- de Waal, F. B. M., Leimgruber, K., & Greenberg, A. (2008). Giving is self-rewarding for monkeys. *Proceedings of the National Academy of Sciences*, 105, 13685–13689.
- Dindo, M., & de Waal, F. B. M. (2006). Partner effects on food consumption in brown capuchin monkeys. *American Journal of Primatology*, 69, 1–6.
- Dubreuil, D., Gentile, M. S., & Visalberghi, E. (2006). Are capuchin monkeys (*Cebus apella*) inequity averse? *Proceedings of the Royal Society of London Series B*, 273, 1223–1228.
- Englemann, D., & Strobel, M. (2004). Inequality aversion, efficiency, and maximin preferences in simple distribution experiments. *American Economic Review*, 94, 857–869.
- Fehr, E., & Fischbacher, U. (2003). The nature of human altruism. *Nature*, 425, 785–791.
- Fehr, E., Naef, M., & Schmidt, K. M. (2006). Inequality aversion, efficiency, and maximin preferences in simple distribution experiments. *American Economic Review*, 96, 1912–1917.
- Fehr, E., & Schmidt, K. M. (1999). A theory of fairness, competition, and cooperation. *The Quarterly Journal of Economics*, 114, 817–868.
- Fletcher, G. E. (2008). Attending to the outcome of others: Disadvantageous inequity aversion in male capuchin monkeys (*Cebus apella*). *American Journal of Primatology*, 70, 901–905.
- James, W. T. (1953). Social facilitation of eating behavior in puppies after satiation. *J Comp Physiol Psychol*, 46, 427–428.
- Jensen, K., Hare, B., Call, J., & Tomasello, M. (2006). What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proceedings of the Royal Society of London Series B*, 273, 1013–1021.
- Lakshminarayanan, V., & Santos, L. R. (2008). Capuchin monkeys are sensitive to others' welfare. *Current Biology* (in press).
- Melis, A. P., Hare, B., & Tomasello, M. (2006a). Chimpanzees recruit the best collaborators. *Science*, 311, 1297–1300.
- Melis, A. P., Hare, B., & Tomasello, M. (2006b). Engineering cooperation in chimpanzees: Tolerance constraints on cooperation. *Animal Behavior*, 72, 275–286.
- Neiworth, J. J., Johnson, E. T., Whillock, K., Greenberg, J., & Brown, V. (2009). Is a sense of inequity an ancestral primate trait? Testing social inequity in cotton top tamarins (*Saguinus oedipus*). *Journal of Comparative Psychology*, 123(1), 10–17.
- Range, F., Horn, L., Viranyi, Z., & Huber, L. (2008). The absence of reward induces inequity aversion in dogs. *Proceedings of the National Academy of Sciences*.
- 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(1), 67–73.
- Silk, J. B. (2005). The evolution of cooperation in primate groups. In H. Gintis, S. Bowles, R. Boyd, & E. Fehr (Eds.), *Moral sentiments and material interests: On the foundations of cooperation in economic life* (pp. 43–73). Cambridge: MIT Press.
- Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., et al. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. *Nature*, 437, 1357–1359.
- van Wolkenten, M., Brosnan, S. F., & de Waal, F. B. M. (2007). Inequity responses in monkeys modified by effort. *Proceedings of the National Academy of Sciences*, 104(47), 18854–18859.
- Vonk, J., Brosnan, S. F., Silk, J. B., Henrich, J., Richardson, A. S., Lambeth, S., et al. (2008). Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Animal Behaviour*, 75(5), 1757–1770.
- Warneken, F., Chen, F., & Tomasello, M. (2006). Cooperative activities in young children and chimpanzees. *Child Development*, 77(3), 640–663.
- Warneken, F., Hare, B., Melis, A. P., Hanus, D., & Tomasello, M. (2007). Spontaneous altruism by chimpanzees and young children. *PLoS Biology*, 5(7), e184.
- Warneken, F., & Tomasello, M. (2006). Altruistic helping in human infants and young chimpanzees. *Science*, 311, 1301–1303.
- Xiao, E., & Bicchieri, C. (forthcoming). When equality trumps reciprocity. *Journal of Economic Psychology*.
- Xiao, E., & Houser, D. (2005). Emotional expression in human punishment behavior. *Proceedings of the National Academy of Sciences*, 102(20), 7398–7401.