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RESEARCH ARTICLE

Partner's Behavior, Not Reward Distribution, Determines Success in an Unequal Cooperative Task in Capuchin Monkeys

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It was recently demonstrated that capuchin monkeys notice and respond to distributional inequity, a trait that has been proposed to support the evolution of cooperation in the human species. However, it is unknown how capuchins react to inequitable rewards in an unrestricted cooperative paradigm in which they may freely choose both whether to participate and, within the bounds of their partner's behavior, which reward they will receive for their participation. We tested capuchin monkeys with such a design, using a cooperative barpull, which has been used with great success in the past. Contrary to our expectations, the equity of the reward distribution did not affect success or pulling behavior. However, the behavior of the partner in an unequal situation did affect overall success rates: pairs that had a tendency to alternate which individual received the higher-value food in unequal reward situations were more than twice as successful in obtaining rewards than pairs in which one individual dominated the higher-value food. This ability to equitably distribute rewards in inherently biased cooperative situations has profound implications for activities such as group hunts, in which multiple individuals work together for a single, monopolizable reward. Am. J. Primatol. 68:713–724, 2006.

INTRODUCTION

Reactions to inequity are a strong response in humans. People will not only react negatively if treated unfairly, but will give others benefits in completely anonymous experimental games with no possibility of punishment [Camerer, 2003]. In situations involving punishment, people frequently punish others who behave noncooperatively [Fehr & Rockenbach, 2003; Kahneman et al., 1986; Zizzo & Oswald, 2001]. However, until recently, little was known about the ways

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in which animals responded to inequity [Brosnan, in press]. Previous studies indicated that among primates, individuals respond negatively when they are treated inequitably compared to a group mate—a condition known as distributional inequity [Brosnan & de Waal, 2003; Brosnan et al., 2005]. However, in those studies the responses were elicited in a situation in which the experimenter controlled the distribution and the primates had no control over the result. Given that humans respond very differently in cases in which they do or do not have control (e.g., dictator vs. ultimatum games) [Camerer, 2003], it is important to extend the primate studies to take individual control into account.

With this in mind, we developed a new study to investigate inequity aversion in a situation in which capuchin monkey subjects could control the outcomes. We used a cooperative barpull situation with which they were very familiar [de Waal & Berger, 2000; de Waal & Davis, 2002; Mendres & de Waal, 2000]. The subjects were allowed free access to the apparatus, which let them decide the conditions under which they were willing to participate, and rewards were either equitably or inequitably distributed.

This protocol has several advantages. First, given that the barpull apparatus requires both individuals to work together to pull it in, it can be assumed that they are both exerting similar relative levels of effort. Second, the individuals are tested in their home enclosure rather than in a relatively more restrictive testing chamber, so there is plenty of room for them to avoid their partner and the apparatus if they so desire. This minimizes social pressure or coercion. Finally, the individuals are not assigned or restricted to either side of the apparatus and its two separate cups with rewards, so they can decide for themselves 1) whether to participate, and 2) which food to work for. Thus there is an element of punishment available to individuals since each can refuse to pull if they are not receiving the reward they want in the inequitable situation. This allows us to look at what individuals are willing to sacrifice in order to receive a given reward or to block another individual from receiving that reward.

We chose to use capuchin monkeys for this study for several reasons. First, it has been proposed that inequity aversion evolved to promote successful cooperation [Fehr & Schmidt, 1999], and capuchins are a highly cooperative species in both captivity [Brosnan & de Waal, 2002; de Waal & Brosnan, in press] and the field. In the field, capuchins have shown some evidence of cooperative hunting [Perry & Rose, 1994; Rose, 1997] and reciprocal grooming [Manson et al., 2004]. Moreover, these monkeys show triadic awareness in their choice of coalition partners, and an awareness of other group members' social relationships [Perry et al., 2004], indicating that they are capable of tracking cooperative or reciprocal interactions in the wild, and no doubt in the task we designed as well. Moreover, if inequity aversion is an evolved trait in our own species, we would expect to find some of its precursors in social primates, such as capuchins [Brosnan & de Waal, 2004b]. Finally, given that we know capuchins show an inequity-averse response in situations over which they have little control, except through refusal to participate [Brosnan & de Waal, 2003], it seemed an obvious choice to examine their response in a situation in which they could affect the outcome.

Our main focus was interactions between unrelated adults; however, we also had access to three mother–adult daughter pairs. Although the sample was small, we tested these individuals to see whether their responses differed from those of the unrelated pairs. This would be expected because maternally related individuals both share more genes than unrelated individuals and spend more time in proximity, which increases familiarity and possibly reduces the contingency of response. Furthermore, in previous work, capuchins were unlikely to cooperate to pull in a tray of food rewards if they were clumped such that it allowed monopolization by the dominant *unless* the pairs were related, in which case their responses were less affected by the clumped rewards [de Waal & Davis, 2002]. Because our main interest was the behavior of unrelated pairs, we tested all unrelated pairs before we tested the related pairs.

We hypothesized that success would depend on the equity of the reward distribution. Specifically, we predicted that pairs would be less likely to be successful in obtaining food in the unequal situation, in which the rewards differed, than in either the high- or low-value situations, in which the rewards were equal. This would reflect a greater interest in the equity of the distribution of the rewards for a cooperative act than in the value of the food received. We further predicted that individuals would be likely to approach the apparatus in any situation (to investigate the options), but would be less likely to attempt to pull in the tray in the unequal situation. Finally, we predicted that related individuals would be more successful in all situations.

MATERIALS AND METHODS

Subjects

The subjects included 10 brown capuchin monkeys (two adult males and eight adult females) from two social groups housed at the Yerkes National Primate Research Center, Atlanta, Georgia. All but one of the adult females were pregnant and/or carrying a dependent offspring at some point during testing.

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 0930 hr and 1730 hr. A tray consisting of fruits, vegetables, and bread with a protein solution was provided to each group every day at approximately 1730 hr. Running water was available ad libitum. This feeding schedule was followed regardless of the day's testing, and the subjects were never deprived of food or water. For more details about the testing facility, see de Waal [1997].

Their enclosure is divided into an indoor area (approximately two-thirds of the total enclosure) and an outdoor area (the remaining one-third of the enclosure). The subjects had previously been trained to enter transport cages, which allowed us to separate individuals from their group. For testing, each pair was placed in the indoor area, and the rest of the colony was restricted to the outdoor area. This allowed us to interact with the subjects in a more controlled manner with minimal distractions. Dependent offspring were always allowed into the testing area with their mothers. No subject was ever involved in more than one barpull test on any given day.

Unrelated individuals from the same group were paired into same-sex pairs for testing. These eight pairs remained the same for the duration of the unrelated-pairs testing, following which we repaired the mothers and daughters and repeated the experiment on those three pairs. While this may have caused some bias in the related pairs' results (since individuals in these related pairs had previous experience with testing), we were most interested in unrelated pairs and did not want to risk altering the results by collecting data on both simultaneously. The members of each pair were as similar in rank as possible. Rank data were gathered from independent 30-min observations (consisting of scan and ad libitum sampling) completed on each group twice per week.

Barpull Paradigm

The barpull apparatus employed in this study is similar to one developed by Crawford [1937] for use with chimpanzees, and has been used extensively in our laboratory to study cooperation in capuchin monkeys [de Waal & Berger, 2000; de Waal & Davis, 2002; Mendres & de Waal, 2000]. The barpull consists of a counterweighted tray with two handles that can be used to pull the tray within reach of the monkeys. The counterweight can be adjusted so that it is too heavy for either individual to pull in individually, but light enough for the pair to pull in together. Rewards were placed in transparent cups to keep them from sliding off the tray. Food cups were placed directly in front of each bar, and in almost all of the trials the individual received the reward corresponding to the bar they pulled [de Waal & Davis, 2002]. If the monkeys pulled the tray in all the way, the tray latched into position adjacent to the subjects.

For this test, the barpull was placed directly against the indoor section of the monkey's home enclosure. The two subjects could approach or withdraw from the barpull at will, and could retreat to a distance of about 5 m from the barpull. Previous work has indicated that capuchins are more likely to complete a cooperative task if they are restricted (S. Brosnan, L. Antonucci, and F.B.M. de Waal, unpublished data). While this is desirable for many testing situations, in this case we wanted the capuchins to feel free to leave the apparatus and fail to cooperate.

Rewards

The rewards for this test consisted of apple slices and grapes. A ''low-value'' reward was two slices of apple (since each apple was cut into 16 pieces, this represented approximately one-eighth of an apple), while a ''high-value'' reward was a single seedless grape. These rewards were chosen because both are favored by capuchins (hence they would be motivated to participate in the test), but there was a strong preference by all subjects for a grape over two apple slices.

Desirability of rewards was determined in barpulling sessions that consisted of only one type of food reward for all trials, and always in equitable distributions, to ensure that the subjects were willing to pull for the reward in an equitable situation. This was necessary to verify that any unwillingness to perform in the inequitable task was due to a difference in the value of the rewards and not to the fact that one reward was undesirable in any situation.

Preference for one reward over the other was determined using a series of dichotomous choice tests utilizing each food. A food was considered preferred by the individual if they chose it a minimum of eight times out of 10 trials [Brosnan & de Waal, 2004a,c]. These results were consistent across time for individuals. The high-value food was difficult to share (a grape is not easily divisible), and hence the individual that received the high-value reward would likely consume it all.

One difficulty with this choice of rewards is that the two are extremely similar to each other in value (e.g., most capuchins would be happy to receive either a grape or two slices of apple, and in fact two apple slices represent a much larger reward). Thus, the ''inequitable'' situation did not represent a large degree of inequity. However, in the preliminary pulling tests to determine which food would be acceptable, the capuchins declined to pull in the barpull for anything less valuable than two apple slices, so such a large ''lesser value'' reward was required. Bear in mind that all of the subjects preferred the grapes at least 80% of the time to two apple slices.

Testing Conditions

Since the individuals were familiar with the barpull apparatus from previous studies, no training was required for them to use it. For testing the barpull was baited in three different ways: First was the Apple condition (a low-value equal condition), in which both cups were baited with two slices of apple. Second was the Grape condition (a high-value equal condition), in which both cups were baited with a single grape. These two conditions allowed us to determine their success for each food item when inequality was not a concern. Third was the Unequal condition, in which one cup was baited with a grape and the other with two slices of apple. Because capuchin monkeys have strong side preferences, there were two conditions: one in which the high-value food was on the left and one in which the high-value food was on the right. For the purpose of analysis, these two Unequal conditions were combined.

Baiting of the barpull was accomplished by placing one food item in each cup. The experimenter would approach the apparatus and then hold out both food items simultaneously, approximately 10 cm over the cup to be baited by that reward. The rewards were held out for approximately 3 sec and then placed into their respective cups. The capuchins could pull in the tray at any time after this. The experimenter left the room immediately after baiting the cups, and all data were recorded with a digital video camera for data coding purposes. Each trial lasted 60 sec. At the end of that time, the experimenter removed any food that had not been consumed, reset the barpull to prepare for the next pull, and baited the apparatus for the next trial.

Each session consisted of 16 trials (four of each baiting type–Apple, Grape, Unequal grape right, and Unequal grape left–in random order). Each pair received six sessions of 16 trials, for a total of 24 Apple trials, 24 Grape trials, and 48 Unequal trials. No individual participated in more than one session (16 trials) per day. The trials were videotaped with a digital video recorder that time-stamped the tapes to the nearest hundredth of a second.

Statistics

Statistical analysis was done using the nonparametric Friedman's test. Paired comparisons were done using the exact Mann-Whitney U-test [Mundry & Fischer, 1998]. All statistics are two-tailed.

Unfortunately, only three related pairs were available (one in one group, two in the other), which limited our ability to statistically analyze the data. Nonetheless, such a comparison is useful because related pairs are expected to respond differently from unrelated pairs [de Waal & Davis, 2002], and thus we report these data qualitatively and include the relevant statistics.

RESULTS

Food Preference Tests

Each individual used in this test showed at least an 80% preference for the single grape over the two slices of apple in a dichotomous choice.

Effects of Relatedness

Overall, unrelated capuchins approached in 87% of the trials, but pulled in only 66% of the trials. Similarly, related capuchins approached in 90% of the trials; however, they showed no drop in pulling rates, pulling in 88% of the trials.

More strikingly, related pairs were more than twice as likely to be successful at pulling in the tray as their unrelated counterparts (related: 75.93% success; unrelated: 35.81% success; U = 1, n = 8, m = 3, $P < 0.01$; see Fig 1 for a detailed breakdown of success rates). In fact, only one unrelated pair had a higher rate of success than the least successful related pair. Thus, while both kin and nonkin showed equal interest in the apparatus (e.g., approaches), related capuchins seemed much more likely to translate this interest into successful cooperation. However, the effects of relatedness must be interpreted cautiously here, given that all related pairs were tested following the testing of unrelated pairs. Because of this potential confound, the following analyses were conducted only for unrelated pairs unless otherwise specified.

Approaches, Pulls, and Success Rates

We examined the subjects' willingness to approach the barpull device (defined as being within arm's reach of a pulling pole) or to pull on the device, regardless of the partner's behavior. Since most approaches and pulls consisted of a series of incidents of the behavior in question, which artificially inflated the sample size, we used a one/zero method to code the behaviors for each trial, counting a ''1'' if the individual ever approached or pulled, and a ''0'' if they did not.

Although we predicted, based on previous results [Brosnan & de Waal, 2003], that the capuchins would be least likely to pull in the Unequal condition, in fact they were the least likely to pull in the Apple condition, indicating that the capuchins were less likely to succeed in trials with no grapes present (Friedman's test: χ^2 (2, n = 8) = 6.467, $P = 0.039$; Table I). Unfortunately, there were too few related pairs for us to conduct a meaningful statistical analysis, but it appears that there was no difference in the success rates between conditions in these pairs (Friedman's test: χ^2 (2, n = 3) = 3.000, $P = 0.223$).

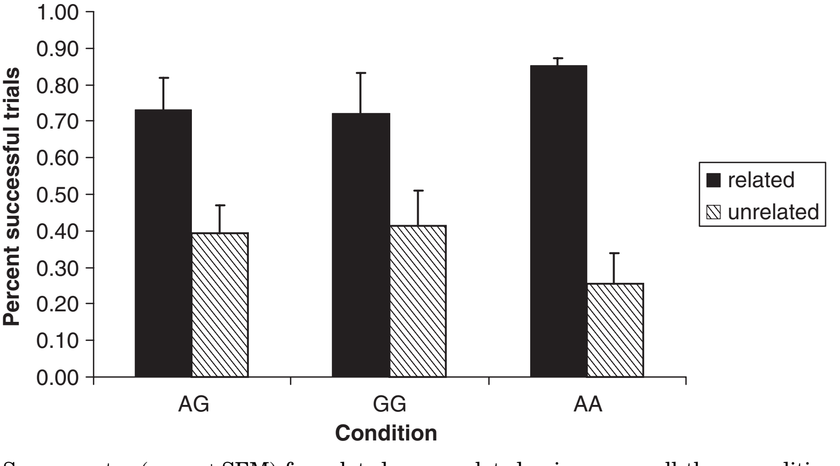

Fig. 1. Success rates (mean ± SEM) for related vs. unrelated pairs across all three conditions in a cooperative barpull with two different rewards. AG = one reward is apple (less favored) and one reward is grape (Unequal condition), GG = both rewards are grape (Grape condition), and AA = both rewards are apple (Apple condition). Solid bars represent related (mother–daughter) pairs, and hatched bars represent unrelated pairs.

TABLE I. Data by Pair

Pair	% Domination	Equitable	Percentage of successful pulls			
			AG	GG	AA	Overall
A	0.67	N	0.18	0.31	0.00	0.17
B	0.73	N	0.41	0.44	0.12	0.33
C	1.00	N	0.45	0.53	0.25	0.42
D	1.00	N	0.04	0.00	0.00	0.01
E	0.78	N	0.26	0.07	0.22	0.21
F	0.67	N	0.51	0.56	0.29	0.47
G	0.53	Y	0.54	0.72	0.59	0.59
H	0.58	Y	0.71	0.71	0.61	0.65
1	0.70	N	0.56	0.50	0.83	0.61
2	0.55	Y	0.81	0.83	0.89	0.83
3	0.57	Y	0.83	0.83	0.83	0.83

Percentage of successful pulls by pair across the three conditions. Lettered pairs are unrelated, numbered pairs are related. ''% Domination'' refers to the percentage of trials in which the grape was obtained by the monkey who claimed it most. ''Equitable'' indicates whether or not one member of the pair dominated the grape more than 66% of the time (inequitable indicates this was the case).

We also investigated approaches and pulls for situations in which the barpull was not pulled in (this could occur due to lack of coordination or lack of interest by one or both parties). Clearly, both subjects approached and pulled in 100% of the trials in which success was achieved. Failure to successfully obtain food could be due to two causes: in some situations only one individual pulled (e.g., the failure was due to lack of interest by one party), and in others both pulled but failed to bring in the tray (e.g., the failure was due to lack of coordination). Unrelated monkeys failed to achieve coordination in all three conditions, indicating that the equity or inequity of the reward distribution played little role in their ability to work together (Friedmans' test: both monkeys approach; success is not achieved: χ^2 (2, n = 8) = 3.250, $P = 0.197$; both monkeys pull; success is not achieved: χ^2 (2, n = 8) = 4.750, $P = 0.093$). Interest in the barpull was occasionally an issue. Approaches limited to a single individual were somewhat more likely in the Apple condition than in either of the other two conditions (Friedman's test: χ^2 (2, n = 8) = 5.600, $P = 0.061$), perhaps indicating a general lack of interest in the barpull when no high-value foods were available.

Effect of Reward-Monopolization on Success Rates

In some pairs, which we here call ''equitable pairs,'' neither partner dominated the grape in the Unequal condition. These pairs were defined by the fact that both individuals received the grape more than 33%, or one-third, of the time. On average, in unrelated pairs the individual with the most claims on the grape received it only slightly more than half of the time (i.e., 56%; see Fig. 2). Other pairs, which we here call ''inequitable pairs,'' were defined by one individual dominating the grape in the Unequal trials and receiving the grape 67% or more of the time (on average, in unrelated pairs the individual with the most claims on the grape received it 81% of the time). We then used this distinction between equitable and inequitable pairs to examine differences in overall success rates.

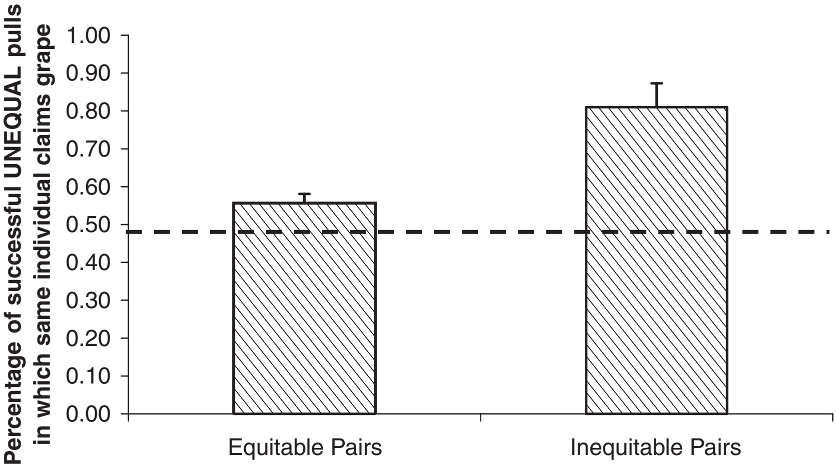

Fig. 2. Distribution of the reward during Unequal trials, in which one reward is an apple and one is a grape. Bars represent the percentage of trials in which the same individual dominated the grape (mean ± SEM). Pairs were considered equitable if no member dominated the grape more than 66% of the time (e.g., both members received the grape at least one-third of the time), and inequitable if one member of the pair dominated the grape more than 66% of the time. Dashed line indicates equal sharing of the grape.

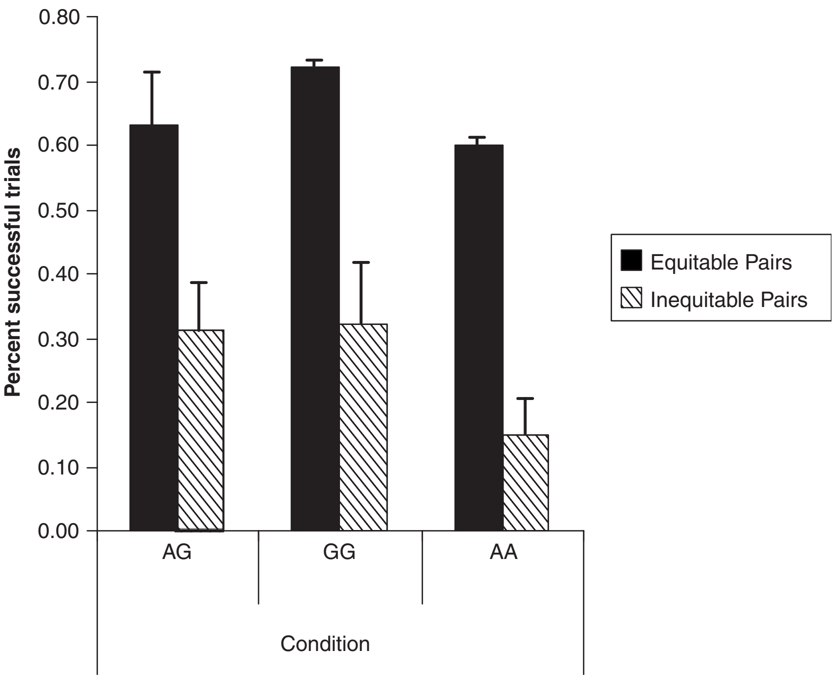

Fig. 3. Success rates (mean ± SEM) for equitable vs. inequitable pairs across the three different conditions. Pairs were categorized as either equitable (both received the better reward in the Unequal condition more than one-third of the time) or inequitable (one individual claimed the better reward two-thirds or more of the time). AG = one reward is apple (less favored) and one reward is grape (Unequal condition), GG = both rewards are grape (Grape condition), and AA = both rewards are apple (Apple condition). Solid bars represent equitable pairs, and hatched bars represent inequitable pairs.

Among unrelated pairs, the mean success rate for inequitable pairs was 26%, while that for the equitable pairs was 65%, which is more than twice as high (U = 0, n = 6, m = 2, $P < 0.025$; Fig. 3). Among the three related pairs, the average success rate for the two inequitable pairs was 61%, while that for the equitable pair was 83% (note the small sample size: U = 0, n = 2, m = 1, $P > 0.05$). Moreover, among equitable pairs there was no difference in the level of success depending on the condition. Thus, sharing of the benefit in inequitable tasks is associated with cooperative success not only in other inequitable endeavors, but also in those in which the potential rewards are equal.

It is important to remember that related pairs were always more successful than their unrelated counterparts, independently of whether the partnership was equitable, but the same pattern holds true if the related and unrelated data are combined. In this case the mean overall success rate (for all three conditions) for inequitable pairs is 32%, while that for the equitable pairs is 73% (U = 1, n = 7, m = 4, $P < 0.005$; Fig. 2).

Social Dynamics

We were also interested in the social dynamics of the interactions around the apparatus. First, we found that supplants (defined as the second individual to approach the barpull taking the place of the individual already in place by a bar) were rare, occurring in only 4.04% of successful trials and 5.12% of unsuccessful trials among unrelated pairs. Supplants were equally likely in all of the conditions (unrelated pairs: $\chi^2 = 2.97$, df = 7, $P > 0.05$; related pairs: $\chi^2 = 3.00$, df = 2, $P > 0.05$). Virtually all of the supplants (seven of eight) that occurred during successful Unequal trials among unrelated pairs resulted in the monkey that typically dominated the better reward obtaining the grape.

The frequency of supplants was almost the same between related and unrelated pairs (related pairs: 4.63%; unrelated pairs: 4.72%), and in both cases the same individual accounted for the majority of these displacements (percentage of supplants by the same individual: unrelated pairs, 88.9%; related pairs, 80%). Switches, in which both individuals were already in place but subsequently switched bars, occurred only three times among unrelated individuals (two Unequal and one Grape) and seven times among related individuals (four Unequal and three Grape).

DISCUSSION

Contrary to our initial predictions, the capuchins did not alter their behavior depending on the equity of the reward distributions in this cooperative task. Pulling success did vary with the baiting of the reward cups, but the key factor was whether high-value grapes were present in the test, not whether the reward cups were baited with the same food of either high or low quality, or with different-quality foods (one high and one low quality). This differs from previous results that indicated distributional inequity, but may be explained by significant differences in the setup (see below for a more detailed discussion).

However, the monkeys did alter their behavior contingent on the equity of their interactions with their partner. Dyads in which both individuals regularly alternated taking the higher-value reward in the Unequal distribution were more than twice as successful overall than less-equitable dyads. This could be due to two different mechanisms. First, individuals that share rewards equitably may be more likely to help each other since there are incentives for both. Second, individuals that come into a cooperative situation with a preexisting close relationship may both be more likely to share equitably and collaborate. While we cannot determine which of these explanations applies (and perhaps both do), the fact that interaction strategies during cooperation correlate with the equitability of the food division implies that these monkeys are able to work out a successful distribution of rewards over consecutive cooperative situations.

Moreover, individuals that shared rewards equitably in situations with unequal rewards increased their cooperative success not only on those tasks, but also on those in which the rewards were the same. Thus, sharing of inequitable rewards was associated with the likelihood of successful cooperation in all situations. This has profound implications for cooperative interactions such as group hunting, in which individuals work together for a single reward and presumably must distribute that reward equitably to ensure future participation by all parties.

An equitable approach to reward distribution is a robust strategy for maximizing rewards. Based on our data, we can assume that the success rate is more or less the same in each condition, and that equitable behavior increases the rate of cooperation in all situations approximately equally. Therefore, in an inequitable pair the most successful individual received apples and grapes in the 26% of the Apple and Grape trials that were successful, plus 81% of the grapes in the 26% of the Unequal trials that were successful. Assuming six sessions of 16 trials each (four Apple, four Grape, and eight Unequal), the most successful individual received, on average, 8.61 apple rewards and 16.35 grape rewards. However, the most successful individual in an equitable pair received apples and grapes in the 65% of the Apple and Grape trials that were successful, plus 56% of the grapes in the 65% of the Unequal trials that were successful, for an average of 29.33 apple rewards and 33.07 grape rewards. Therefore, even though the most successful individual in an inequitable pair received more of the grapes in the situation that was not equal, overall that individual received about two times less food than successful individuals in equitable pairs. In other words, tolerance pays.

As expected, mother–daughter pairs were more than twice as likely to achieve success as their unrelated counterparts. While these data are confounded with testing order, this does match with a previous study indicating that related pairs are more likely to complete a barpull in a competitive situation [de Waal & Davis, 2002]. In that study, rewards were clumped such that one individual could monopolize them. Nevertheless, related pairs showed continued high rates of success, possibly because the mothers frequently left some rewards for their (subordinate) daughters. However, mother–daughter pairs did not seem to differ from related individuals in any other aspect of testing. Further research focusing on the effects of relatedness will help determine the conditions under which a related pair's reactions differ from those of unrelated pairs.

Contrary to our predictions, the capuchin monkeys did not adjust their cooperative pulling behavior depending on the equality of the food distribution to be achieved by the pull. Based on previous work, we expected the Unequal test to be the least successful if reward distribution were the major motivating force, and the Apple condition to be the least successful if reward quality were the most important determinant. Our data show no indication that equity of reward distribution was a factor in whether a pair was successful in any given trial; rather, the presence or absence of high-value grapes appeared to matter the most. This result is somewhat different from our previous findings, which suggested negative reactions to inequity [Brosnan & de Waal, 2003]. We believe there are several reasons for this difference, and several implications for the fact that the monkeys seem to be focused on their partner's behavior rather than on the distribution of rewards when they made their decisions.

We believe that if the rewards had been more disparate in value, there might have been more of an effect on their willingness to pull in the different situations. While these two rewards differed in value, the difference was not as extreme as in our previous test with cucumber and grape [Brosnan & de Waal, 2003]. As discussed in the Introduction, the current rewards were carefully chosen to meet two criteria. First, the capuchins had to be sufficiently motivated to pull in the barpull for either reward in preliminary trials. Second, every capuchin in the test had to prefer one reward over the other at least 80% of the time. The first turned out to be the limiting criterion, since the subjects were unwilling to cooperate on a regular basis for anything less desirable than the two slices of apple (including cucumbers). Given that both grapes and apples are quite attractive rewards, it may be that the difference between them, while present, is not sufficiently great to merit refusal to attempt the cooperative endeavor on the grounds of inequity. In chimpanzees at least, fairly small differences in preference for different food rewards can lead to dramatically different outcomes (S. Brosnan, unpublished data). This should be taken into account in further explorations of equity involving reward value in animals.

Interactions with the experimenter may have played a role as well. In our previous study [Brosnan & de Waal, 2003], the interaction was mainly between the monkey and the experimenter, rather than between conspecifics. Since the partner was unable to alter the reward distribution (except by sharing food through the mesh with its partner), there was no chance of creating equity in the relationship over time, as some pairs did in the present study. Instead, they may have reacted to the reward distributions or even the experimenter's inequitable behavior. In the present study the experimenter left the room after baiting the barpull and had no influence over the distribution of the food between the monkeys.

In the absence of the human experimenter, the behavior of the partner may become the more salient feature, and thus the equity of the partner's *behavior* rather than the equity of the *distribution* becomes the decisive factor. This finding may have profound implications for cooperation in situations in which rewards are inherently indivisible (e.g., a group hunt with a single prey) or for reciprocal situations in which individuals may eventually decide to end the partnership if their partner does not reciprocate in kind (e.g., grooming or support alliances). Apparently our monkeys are willing to participate in inequitable cooperative endeavors as long as they regularly receive the bulk of the benefit. This suggests that recognition of and aversion to inequity may be an evolutionary response to the problem of cooperation with unequal rewards.

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