Giving is self-rewarding for monkeys

Frans B. M. de Waal*, Kristin Leimgruber, and Amanda R. Greenberg

Living Links, Yerkes National Primate Research Center, Emory University, Atlanta, GA 30329

Helping and sharing among humans is often motivated by empathy and accompanied by a sense of satisfaction. To determine whether similar self-rewarding mechanisms may underpin assistance among nonhuman primates, eight female brown capuchin monkeys (*Cebus apella*) underwent testing in a simple choice paradigm. Paired with a partner, subjects could select either a ''selfish'' option that rewarded only themselves, or a ''prosocial'' option that rewarded both of them. Subjects systematically favored the prosocial option provided their partner was a) familiar, b) visible, and c) receiving rewards of equal value. Prosocial tendencies increased with social closeness, being lowest toward strangers and highest toward kin. That the monkeys understood the options was suggested by greater orientation to the partner during prosocial than selfish choices. Prosocial preferences were reduced by inequity, when the partner received a superior reward. If the view between both monkeys was blocked, choices became strikingly selfish. Thus, under certain conditions, delivering benefits to others seems gratifying to nonhuman primates.

altruism | capuchin monkey | empathy | inequity | prosocial behavior

The motivation behind animal altruism is little studied, and is to be treated separately from evolutionary causation. Potential benefits accrued after long time intervals, as in delayed reciprocity (1), or via genetic consequences, as in inclusive fitness (2), are unlikely to be cognitively represented in the actors. Motivational analyses need to restrict themselves, therefore, to the immediate circumstances and knowable consequences of behavior (3).

In humans, the dominant theory is that altruism is driven by emotional identification and empathy with the other (4). If empathy is experimentally manipulated through nasally administered oxytocin, generosity is enhanced (5). Because empathy ultimately derives from state matching (6), it automatically produces a stake in the other's welfare (7), which may explain the "warm-glow" effect, i.e., pleasant feelings associated with improvement of another's condition (8). Thus, when human participants do good deeds they report feeling good (9), and show activation of reward-related brain areas (10). Although empathy has been proposed to also underlie the directed altruism of animals (3), little is known about self-rewarding effects. One way to find out is to present animals with choices between other-regarding and selfish outcomes in a discrimination paradigm. A systematic bias toward acts that benefit others would suggest that performance of these acts is intrinsically gratifying.

The first such study yielded ambiguous results for macaques (*Macaca* spp.) (11). Replications with chimpanzees (*Pan troglodytes*) initially failed to bring resolution, leading to claims that our close relatives must be indifferent to each other's welfare (12, 13). This negative outcome was puzzling, however, given the high rates of altruistic behavior and cooperation in the chimpanzee's natural social life (14). Although humans are sometimes considered unique in that they cooperate with unrelated individuals within large groups (15), a comparison of wild chimpanzee behavior with genetic relatedness data confirmed similar tendencies (16). Moreover, the latest experimental results contradict the earlier negative ones in that chimpanzees spontaneously assist both humans and conspecifics regardless of reward prospects (17).

The latter results also contradict the speculation that altruistic tendencies evolved only in the context of cooperative breeding—hence their presence in both humans and the *Callitrichidae* (18)—given that the chimpanzee is not a primate that breeds cooperatively.

The present study concerns another noncooperatively breeding primate, the brown capuchin monkey. The aim was to determine whether these monkeys prefer outcomes that benefit others over outcomes that do not. Everything else being equal, do they take others' welfare into account? Separate but in full view of a partner, one monkey (the subject) was given a choice between two small, differently marked tokens. Selecting one token and returning it to the experimenter resulted in a "selfish" outcome. Selecting and returning the other token resulted in a "prosocial" outcome. The selfish token rewarded the bartering monkey only (outcome: 1,0). The prosocial token, on the other hand, produced a mutual advantage in that it rewarded both monkeys at the same time (outcome: 1,1). Inasmuch as the bartering monkey was rewarded either way, prosocial choices had no added cost.

This study offers three advantages over previous experiments. The first is knowledge about the social relationships among the monkeys in their group life. It has been argued that empathy evolved through kin selection and reciprocal altruism as the proximate mechanism that ensures helping consistent with predictions from these theories (3). Thus, empathy is strongest toward familiar and bonded partners, such as kin and group mates, in both human and nonhuman primates (6) as well as rodents (19). The present study tests the prediction that prosocial tendencies in monkeys increase with social closeness.

The second advantage is that the choice paradigm permits left-right randomization of token locations from trial to trial, thus countering potential position (or side) biases. Position biases are a notorious confound in discrimination tasks, and are hard or impossible to control with a fixed apparatus as used in some of the afore-mentioned studies.

The third unique feature of this study is that it documents not only experimental outcomes, but also behavior during tests. Such data may provide an external validation that subjects understand the consequences of their behavior, for example if they pay more attention to their partner during prosocial than selfish choices.

Results

Token Choice. Dividing the 30 trials per test into three 10-trial blocks and comparing these blocks for all four rounds with visible familiar partners and equal rewards (i.e., Nonkin-1 and −2, Kin, Control-1) in a repeated-measures ANOVA shows significant differences between trial blocks ($F_{2,62} = 3.67$, $P = 0.031$) and a linear upward trend in the selection of prosocial tokens ($F_{1,318} = 5.88$, $P = 0.021$). Because prosocial preferences increased considerably in the course of testing (Fig. 1), the analyses below focus on the third 10-trial block.

The proportion of prosocial choices by subjects in the third
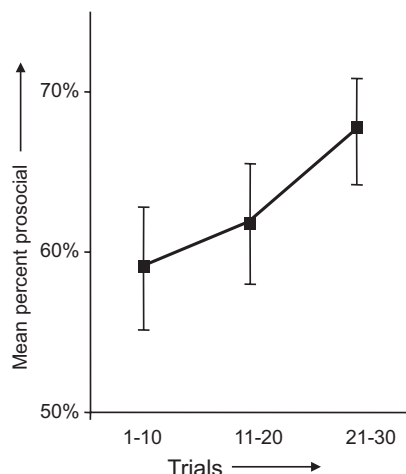
ECONOMIC SCIENCES

PSYCHOLOGY

Fig. 1. The mean (+SEM) percentage of prosocial choices across trials for tests with familiar, visible partners with equal food rewards. The 30 trials per test are divided into three blocks of 10. Chance expectation is 50%. The linear upward trend is significant (see text).

10-trial block was significantly >50% chance in the first round with unrelated partners (i.e., Nonkin-1; one-sample t = 2.43, df = 7, P = 0.045). Replication of this test with fresh tokens yielded the same result (i.e., Nonkin-2; t = 2.40, P = 0.048), and the same result was again obtained with related partners (i.e., Kin; t = 2.58, P = 0.037) but not with partners from another group (i.e., Stranger; t = −0.49, NS). Whereas statistical tests include all eight subjects, Fig. 2 illustrates the outcome while excluding subjects with an extreme side-bias in a given test (see Methods).

The effect of social relationships was investigated by comparing the Group Affiliation measure with the subject's token choices during the third 10-trial block of nonkin rounds (i.e., the average of Nonkin-1 and -2) as well as Kin and Stranger rounds. The Spearman correlation was significantly in the expected direction (rho = 0.48, n = 24, P = 0.009, one-tailed), i.e., prosocial tokens were selected more often the closer the social relationship.

Effect of Inequity. To test whether inequity aversion dampens prosocial preferences, 2 tests concerned unequal rewards (i.e., apple for subject, grape for partner). Preference for the prosocial
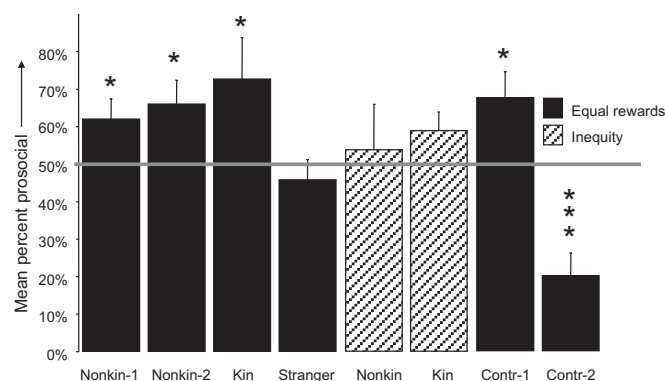

Fig. 2. The mean (±SEM) percent prosocial choices during the third 10-trail block for all eight testing rounds in the order in which they were conducted. This graph excludes individuals with extreme (>85%) side-bias during a given round, even though these individuals were included in statistical evaluations against 50% chance (*, P < 0.05, ***, P = 0.001).

token did not exceed chance in the third 10-trial block of these tests, both for nonkin (t = 0.19, df = 7, NS) and kin, even though the latter came close (t = 2.28, P = 0.056, two-tailed).

Controls. The first control was a replication of earlier nonkin tests but with six jumbled tokens and a face-covered experimenter. Prosocial choices remained significantly >50% chance in the third 10-trial block, however (t = 2.70, df = 7, P = 0.031). The second control was identical to the first, but added an opaque panel between both monkeys. This was the only test in which subjects could not see their partner, and the outcome was a dramatic deviation from 50% chance in the direction of the selfish token (t = −5.29, P = 0.001).

Alternative Explanations. Two alternative hypotheses were considered. The first is amplification of prosocial preference within a pair if the secondly tested subject is affected by the first subject's choices. This could only apply to nonkin pairs, because kin partners never became subjects themselves. For 6 individuals in Nonkin-1 and −2 we were able to compare their choices as first versus second subject. No amplification effect was found: individuals selected prosocial tokens slightly more as first subject (i.e., mean ± standard deviation: 68.5 ± 12.8%) than as second subject (i.e., 63.3 ± 17.5%), without a significant difference (paired t = 1.20, df = 5, NS).

The second alternative explanation is that prosocial choice is motivated by fear of punishment upon return to the group. Since the group itself never witnessed the tests, punishment would need to come from the test partner, hence mostly affect the subordinate partner. This hypothesis, too, could not apply to related pairs, in which all subjects were dominant (see Methods). For the four unrelated pairs from the same group, we compared the average prosocial preference of the dominant and subordinate party during tests with equal rewards and mutual visibility (i.e., Nonkin-1 and -2, and Control-1). Prosocial preferences by the dominant (i.e., mean ± standard deviation: 69.0 ± 11.1%) exceeded those by the subordinate (59.4 ± 3.1%), without a significant difference (paired t = 1.74, df = 3, NS). Given that, in every pair, the more prosocial subject was dominant, fear of punishment was an unlikely explanation.

Behavior During Testing. All trials in which a given subject chose the prosocial token were compared with all trials in which she chose the selfish token. The average location and orientation indices for these two sets of trials were subjected to a repeated-measures ANOVA on individual data with two factors: trial phase (phase 1: token choice; phase 2: reward acceptance and consumption) and token choice (two choices).

With regard to location, small but significant effects were found for both trial phase ($F_{1,7}$ = 6.48, P = 0.038) and token choice ($F_{1,7}$ = 6.11, P = 0.043), without an interaction effect. Subjects were on average closer to their partner when choosing the prosocial token and closer during the second trial phase. Effects were more dramatic for orientation, however, both for test phase ($F_{1,7}$ = 26.63, P = 0.001) and token choice ($F_{1,7}$ = 19.70, P = 0.003), without an interaction effect. Fig. 3 shows that prosocial choices were associated with increased partner orientation. This difference appeared already in phase 1, before any food rewards had been handed out (i.e., orientation index by token choice in phase 1: paired t = 5.06, df = 7, P = 0.001). As a matter of fact, subjects abruptly turned their backs to the other while picking the selfish token on multiple occasions. As Fig. 3 shows, orientation to the partner increased during the second (reward) phase, being especially high after prosocial choices.

For partners, the same analyses were run, but results for location were non-significant (phase $F_{1,7}$ = 5.43, NS; token choice $F_{1,7}$ = 1.44, NS), and for orientation the only significant difference concerned trial phase ($F_{1,7}$ = 19.70, P = 0.003), but
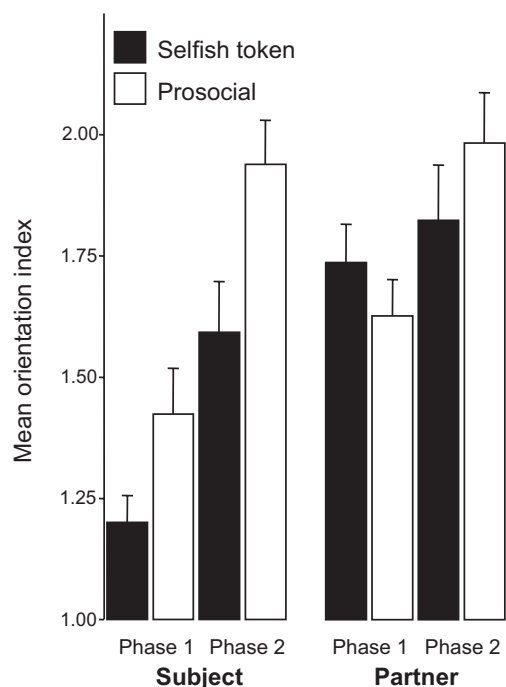
Fig. 3. The mean (+SEM) orientation index for subject and partner during two trial phases (1, token choice; 2, reward acceptance and consumption). Data are divided according to the subject's token selection. The main significant effects (see text) were increased orientation by the subject to the other while making a prosocial choice, and increased mutual orientation during the second trial phase after prosocial choices.

not token choice ($F_{1,7} = 0.09$, NS). Fig. 3 shows that partners oriented more to the subject during the second trial phase.

The observed increase in mutual orientation during the second trial phase was further reflected in mutual (close-up, affiliative) interest between both monkeys. Such interactions did not occur in the first trial phase, but were common in the second. They were six times more frequent if the token choice had been prosocial (i.e., mean ± standard deviation: $3.08 ± 1.96$) than if it had been selfish (i.e., $0.48 ± 0.45$; paired $t = 3.23$, df = 7, $P = 0.014$, two-tailed).

Discussion

Capuchin monkeys predominantly select prosocial outcomes with familiar partners in a token-exchange task, repeating this result in four separate testing rounds. This preference is best explained by assuming that the prosocial option has self-rewarding qualities compared to the selfish option, as alternative hypotheses (e.g., fear of punishment) were unsupported. Aggression was rare, and solicitations were absent. Inasmuch as the subject's own food reward remained the same during prosocial and selfish choices, the prosocial option's added value must be of an intangible nature. It likely derived from seeing the partner receive or consume food, similar to one of the oldest definitions of sympathy, which postulates the "pleasure of seeing" another's fortune (20).

Because, in both humans and animals, empathy is biased toward familiar partners (6), the observed increase of prosocial preferences with social closeness fits the empathy hypothesis. The behavior in kin pairs agrees with this hypothesis, too, even though it should be noted that kinship was not critical: prosocial preferences extended to familiar nonrelatives. Whereas kin selection and reciprocal altruism offer plausible evolutionary accounts of prosocial tendencies, they are flawed as proximate explanations. For example, reciprocity as proximate explanation

would require that animals are able to predict return favors. The empathy hypothesis is cognitively more parsimonious, and by no means rules out an evolutionary role for kin selection and reciprocal altruism (3).

Prosocial tendencies were undiminished if the experimenter's face was obscured and tokens were presented in a jumbled arrangement, thus arguing against unconscious biasing by humans. Moreover, monkeys oriented more to their partner during prosocial than selfish choices even before the reward outcome was effectuated, which suggests that they knew what they were choosing. During prosocial trials, both monkeys were closer to each other, oriented more mutually, and exchanged many more affiliative signals.

Capuchin monkeys spontaneously share food in both nature and captivity (21, 22), and commonly sit next to each other while eating. The present study cannot resolve whether the most critical effect of the prosocial outcome was giving (i.e., producing rewards for the other) or sharing (i.e., engaging in joint food consumption). The sharp drop in prosocial outcomes when the partner was out of sight (i.e., Control-2) fails to resolve this issue as this condition prevented both seeing the other receive food and opportunities for joint food consumption. What needs to be tested further is which precise parameters make prosocial behavior rewarding for the performer, but our study strongly suggests a critical role for the visibility of its effect on the other.

Inequity in favor of the partner seemed to interfere with the added value of prosocial outcomes. Even though inequity aversion is strongly indicated for capuchin monkeys (23, 24), in previous studies it was the experimenter who effectuated the inequity, whereas in the present study the monkeys did so themselves.

Finally, in comparison with spontaneous altruism in chimpanzees (17), it is important to note both the differences and similarities. The difference is that the monkeys in the present study did not need to understand the other's goals, only the presence or absence of rewards for the other. In contrast, the chimpanzees showed targeted helping, which requires appreciation of what the other tries to achieve. The underlying motivation may have been quite similar, however, in that both apes and monkeys showed sensitivity to another individual's welfare. The observed choices may in both cases reflect empathy with the other, a mechanism that needs further investigation in animals to illuminate its possible continuity with that in humans.

Methods

Subjects. This experiment required subjects skilled in both token exchange and in paying attention to a partner. Only the most experienced subjects were used. For at least eight years, all of them had been in studies that required the exchange of tokens of different value (25), observing token selection by a partner (26), and comparing food rewards between self and other (23, 24, 27). All subjects were over nine years old at the onset of study. Two had dependent offspring, which were allowed into the test chamber.

Subjects were eight adult female capuchin monkeys from two separate groups. Each group counted 15 individuals of both sexes and all ages. The groups were visually separated, and each enclosure had indoor and outdoor areas. The monkeys received daily Purina monkey chow, fruit, and vegetables, and water ad libitum. Test sessions took place before the evening meal, and the monkeys were never food or water deprived.

One individual served as "subject," which interacted with the experimenter, the other as "partner," which was there to receive food rewards. Partners were usually subjects themselves in other tests, except in kin pairs. Kin partners were untrained close relatives of any sex. All subjects were dominant over their kin partners, which were mostly 3–4 year-old juvenile offspring or siblings. For each of the below combinations, individuals had steady partners:

Nonkin: Two females from the same group, the first one serving as subject and the second as partner, then in reversed roles on another testing day.

Kin: One female subject with a close relative as partner, the latter never serving as subject.

Stranger: Two unrelated females of different groups, matched in approx-

imate age and rank within their group, the first one serving as subject and the second as partner, then in reversed roles on another testing day.

Test Apparatus. Individuals were temporarily removed from their group and placed in a familiar test chamber. The test chamber prevented visual and tactile contact with the rest of the group. For all sessions (except Control-2), a transparent Lexan partition divided the 156-cm long chamber into two equally sized (78 × 58 × 64 cm) compartments. The partition prevented physical contact and food transfers. The monkeys sat side-by-side with full visual and vocal contact.

Small (3 cm in diameter, 5.5 cm in length) PVC pipes were used as nonedible tokens. The two pipes used in each test were painted with a different color as well as pattern, and no color/pattern was ever used twice, i.e., each round of testing used newly painted pipes. The pipes were put flat, equally spaced on a small plastic tray for presentation to the subjects. The left–right positions of the tokens were randomized from trial to trial using a random number generator. In most tests, food rewards were small pieces of apple.

Test Phases. For an entire test session, one individual served as subject (i.e., bartered with the experimenter) and the other as partner. Most pairs went through three phases, of which the first 2 phases occurred in a single session and the third on a separate day soon thereafter.

1. *Initial Token Preference:* Token preferences were tested before training to make sure that certain colors/patterns were not preferred over others. Both tokens were presented side by side on a tray, and either choice was rewarded with a single piece of cereal. Each subject was offered 10 choices, and if any token was chosen eight times or more by two or more subjects, both tokens would be replaced. In fact, we never needed to do so, and the strongest initial mean (± standard deviation) preference across subjects for any token was 53.8 ± 4.8%. To further prevent outcomes affected by intrinsic token properties, token meaning was counterbalanced. For half the pairs in each round of testing, one token was assigned to be ''selfish'' and the other ''prosocial,'' whereas the meaning of both tokens was reversed for the other half.

2. *First Test:* a) Training: Each token was presented by itself to the bartering monkey, so no choices were allowed. The token assigned as ''selfish'' rewarded the subject only, whereas the token assigned as ''prosocial'' rewarded both monkeys simultaneously. This was done five times per token for a total of 10 trials. b) Test: The same subject completed 30 trials in which both tokens were presented in a randomized left-right arrangement. Several aspects of the set up facilitated learning: a) the initial training trials, b) the immediate positioning of the selected token in front of both monkeys (see below), c) the demonstrative offering of rewards with the experimenter standing centrally in front of the test chamber and either lifting one hand high with one apple piece for the subject or both hands high with apple pieces for both monkeys, and d) the large number of trials.

3. *Second Test:* On a different day, the same pair was tested again with the same tokens. This time, the monkey who had been partner in the first test, became subject, and the other the partner. The second subject also underwent 10 training trials before she was presented with 30 test trials. Only with kin pairs, no second test was conducted.

Token Exchange. The experimenter displayed two different tokens to subjects by standing in front of them with both tokens on a small plastic tray. The tray was held ≈5 cm above the floor of the test chamber at a specified location, and was within reach of only the subject, although both monkeys had a full view. The front of the chamber consisted of Lexan with many 6 × 6 cm armholes. After the subject had reached for one token, the tray was moved away. Trials in which the subject attempted to pick both tokens were redone. If the subject failed to choose a token in 30 sec the trial was cancelled, and no reward was given. The subject had 30 sec to return the token to the experimenter's open hand. The returned token was subsequently placed upright in a clearly visible spot between both monkeys (but out of reach) to remind them of the choice. Within 5 sec, rewards were distributed according to the token choice to either the subject alone or both monkeys. There was a 15 second inter-trial delay.

Conditions. Eight testing rounds were conducted. In each round, all pairs in a particular category went through all phases outlined above before new tokens were produced and a new testing round was started. The testing rounds are described below in the order in which they were conducted accompanied by their rationale:

1. *Nonkin-1:* Two unrelated females of the same group with equal food rewards.

2. *Nonkin-2:* Same as above with a fresh set of tokens to see if the first outcome could be replicated.

3. *Kin:* Female subjects with a close relative as partner with equal food rewards.

4. *Stranger:* Two unrelated females from different groups with equal food rewards.

5. *Nonkin-Inequity:* The same pairs as in Nonkin-1 and -2, but with differential reward value. The selfish token produced a piece of apple for the subject, and the prosocial token did the same while giving a grape to the partner. Food preference tests confirmed that all subjects still prefer grape over apple (28). This condition was added to determine whether better rewards for the partner would dampen prosocial preferences, as previous studies have shown inequity aversion (23, 24).

6. *Kin-Inequity:* The same unequal rewards as above were used with a close relative as partner.

7. *Control-1:* Two unrelated females from the same group were tested on six tokens by an experimenter with covered face. This control served a) as Nonkin-3 test, to see if the findings of the earlier nonkin conditions could be replicated, and b) to address alternative explanations. The experimenter could unconsciously bias a subject's choices either by moving the tray in a way that facilitates removal of a specific token or through head or eye movements. The latter seems unlikely, because in all videos subjects stare down at the tray rather than up at the experimenter's face, which is above them. Two countermeasures were taken. First, instead of presenting just two tokens, we painted six tokens, three of each kind, and mixed those up in a shallow plastic container. The container was shaken before each trial, hence the token arrangement was jumbled and variable. Second, the experimenter wore a heavily tinted face shield that covered her entire face. Even in daylight, the shield prevented seeing her eyes, let alone under the artificial light in the testing room.

8. *Control-2:* Unrelated females from the same group were tested with the same protocol as in Control-1 (i.e., 6 tokens in container, dark face-shield) but the transparent Lexan partition between both monkeys was replaced by an opaque one. This partition had a small (8 × 8 cm) ''peephole'' in the back, away from where the monkeys usually sit, to ensure that they knew the presence and identity of their partner. This control was added to determine how partner visibility affects selfish versus prosocial choices. All other procedures remained the same, and the visibility of the experimenter was unaffected. The only difference was that the subject could not see her partner actually accept and consume rewards.

Behavioral Data. All tests were taped on digital video with a view of both partners. Behavior was coded for the first 4 rounds (i.e., Nonkin-1 and -2, Kin, and Stranger). To examine the behavior during every trial, trials were divided into two phases after token presentation. Phase 1: token selection and return of token to the experimenter. Phase 2: acceptance and consumption of reward(s).

Aggressive behavior toward the partner or experimenter was recorded during both phases, defined as facial threats, lunging movements, and agitated body movements. This behavior was too uncommon and occurred in too few pairs for analysis: the majority of pairs had zero rates. Solicitation behavior (e.g., begging for food) was never observed. Behavior that we did analyze for both trial phases are location, mutual interest, and orientation:

Location index: Each chamber compartment was divided into three equal zones: zone 3 being closest to the partition between both monkeys, zone 2 in the middle, and zone 1 furthest away. For each trial phase, the closest position for each monkey was recorded.

Mutual interest: Both individuals sit near each other at the partition (i.e., location 3 for both), either staring mutually at each other, intermittently glancing at each other, or otherwise directly interacting in an affiliative manner (e.g., lip-smacking).

Orientation index: The body orientation of each monkey toward the other was assessed, recording the greatest orientation observed during a given trial phase, ranging from orientation 4 (i.e., staring or looking at partner), 3 (i.e., no clear gaze direction but frontal orientation to partner), 2 (i.e., laterally oriented without clearly looking at partner), and 1 (i.e., partially or completely turned away from partner).

Group affiliation: To evaluate the social relationships between individuals in their group, data were extracted from a two-year database of regular 30-min observations (two per group per week) during spontaneous interaction. Affiliative behavior was recorded with a 5-min scan sampling method, while the monkeys were confined to their indoor living quarters. Based on 2,988 and 2,634 recorded affiliations (i.e., contact-sitting, grooming, and play) in the respective groups, we calculated for each subject what percentage of affiliations was spent with the test partner. This percentage served as Group Affiliation measure, which was put at 0% for partners from different groups.

Analysis and Interobserver Reliability. Subjects showing an extreme side-bias during a given test (i.e., choosing either right or left >85% of the trials regardless of token), were tested a second time on a different day. The latter data were included in statistical analyses regardless of whether or not the individual persisted in her side-bias. Extremely side-biased performances were excluded from the graphs in this paper, however. According to goodness of fit tests (Kolgomorov-Smirnov) no data set violated a normal distribution, hence one-sample and paired t-tests were applied to data per individual subject.

Four test sessions were randomly selected and the videotapes coded by an independent rater familiar with the monkeys but not the study's purpose (i.e., a total of 240 trial phases). Cohen's kappa (κ) was calculated for agreement on three behavioral measures, and found to be as follows: orientation, $\kappa = 0.68$, location, $\kappa = 0.77$; mutual-interest, $\kappa = 0.92$.

1. Trivers RL (1971) The evolution of reciprocal altruism. *Q Rev Biol* 46:35–57.
2. Hamilton WD (1964) The genetical evolution of social behaviour. I & II. *J Theor Biol* 7:17–52.
3. de Waal FBM (2008) Putting the altruism back into altruism: The evolution of empathy. *Ann Rev Psychol* 59:279–300.
4. Batson CD (1991) *The Altruism Question: Toward a Social Psychological Answer* (Erlbaum, Hillsdale, NJ).
5. Zak PJ, Stanton AA, Ahmadi S (2007) Oxytocin increases generosity in humans. *PLoS ONE* 2:e1128.
6. Preston SD, de Waal FBM (2002) Empathy: Its ultimate and proximate bases. *Behav Brain Sci* 25:1–72.
7. Cialdini RB, Brown SL, Lewis BP, Luce C, Neuberg SL (1997) Reinterpreting the empathy-altruism relationship: When one into one equals oneness. *J Pers Soc Psychol* 73:481–494.
8. Andreoni J (1989) Giving with impure altruism: Applications to charity and ricardian equivalence. *J Polit Econ* 97:1447–1458.
9. Steger MF, Kashdan TB, Oishi S (2008) Being good by doing good: Daily eudaimonic activity and well-being. *J Res Person* 42:22–42.
10. Harbaugh WT, Mayr U, Burghart DR (2007) Neural responses to taxation and voluntary giving reveal motives for charitable donations. *Science* 326:1622–1625.
11. Colman AD, Liebold KE, Boren JJ (1969) A method for studying altruism in monkeys. *Psychol Record* 19:401–405.
12. Silk JB, *et al.* (2005) Chimpanzees are indifferent to the welfare of unrelated group members. *Nature* 437:1357–1359.
13. Jensen K, Hare B, Call J, Tomasello M (2006) What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proc Royal Soc B* 273:1013–1021.
14. de Waal FBM (2007) With a little help from a friend. *PLoS Biol* 5:e190.
15. Fehr E, Fischbacher U (2003) The nature of human altruism. *Nature* 425:785–791.
16. Langergraber KE, Mitani JC, Vigilant L (2007) The limited impact of kinship on cooperation in wild chimpanzees. *Proc Natl Acad Sci USA* 104:7786–7790.
17. Warneken F, Hare B, Melis AP, Hanus D, Tomasello M (2007) Spontaneous altruism by chimpanzees and young children. *PLoS Biol* 5:e184.
18. Burkart JM, Fehr E, Efferson C, van Schaik CP (2007) Other-regarding preferences in a non-human primate: Common marmosets provision food altruistically. *Proc Natl Acad Sci USA* 104:19762–19766.
19. Langford DJ, *et al.* (2006) Social modulation of pain as evidence for empathy in mice. *Science* 312:1967–1970.
20. Smith A (1937) *The Theory of Moral Sentiments* (Modern Library, New York, NY).
21. de Waal FBM, Luttrell LM, Canfield ME (1993) Preliminary data on voluntary food sharing in brown capuchin monkeys. *Am J Primatol* 29:73–78.
22. Perry S, Rose L (1994) Begging and transfer of coati meat by white-faced capuchin monkeys, Cebus capucinus. *Primates* 35:409–415.
23. Brosnan SF, de Waal FBM (2003) Monkeys reject unequal pay. *Nature* 425:297–299.
24. van Wolkenten M, Brosnan SF, de Waal FBM (2007) Inequity responses of monkeys modified by effort. *Proc Natl Acad Sci USA* 104:18854–18859.
25. Brosnan SF, de Waal FBM (2004) A concept of value during experimental exchange in brown capuchin monkeys, *Cebus apella. Folia Primatol* 75:317–330.
26. Brosnan SF, de Waal FBM (2004) Socially learned preferences for differentially rewarded tokens in the brown capuchin monkey (*Cebus apella*). *J Comp Psychol* 118:133–139.
27. Dindo M, de Waal FBM (2007) Partner effects on food consumption in brown capuchin monkeys. *Am J Primatol* 69:448–456.
28. de Waal FBM (1997) Food-transfers through mesh in brown capuchins. *J Comp Psychol* 111:370–378.

ECONOMIC SCIENCES

PSYCHOLOGY