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Attitudinal reciprocity in food sharing among brown capuchin monkeys

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Capuchin monkeys (*Cebus apella*) share food even if separated by a mesh restraint. Pairs of capuchins were moved into a test chamber in which one of them received apple pieces for 20 min, and the other received carrot pieces for the next 20 min. Previous research had shown a correlation between the rate of food transfer in both directions across female–female dyads. The present study confirmed this result. Reciprocity across dyads can be explained, however, by symmetry in affiliative and tolerant tendencies between two individuals, provided these tendencies determine food sharing. The present study was designed to exclude this symmetry-based explanation by testing each pair (N=16) of adult females on six separate occasions. There existed a significant covariation across tests of sharing in both dyadic directions, a result unexplained by relationship symmetry. Moreover, control procedures (i.e. testing of a food possessor without a partner, or testing of two individuals with the same food or two different foods at the same time) indicated that behaviour during food trials is not fully explained by mutual attraction or aversion. The monkeys take the quality of their own and the partner's food into account, and possessors limit transfers of high-quality foods. Instead of a symmetry-based reciprocity explanation, a mediating role of memory is suggested, and a mirroring of social attitude between partners.

Very few nonhuman primates regularly share food outside the parent–offspring context. The best-known examples are the anthropoid apes: in the field, bonobos, *Pan paniscus*, and chimpanzees, *P. troglodytes*, share large fruits and meat (e.g. Goodall 1963; Teleki 1973; Kuroda 1984; Boesch & Boesch 1989; Hohmann & Fruth 1993), and in captivity, they share attractive plant foods (Silk 1979; de Waal 1989, 1992).

Less widely known is the food sharing by a medium-sized Neotropical primate, the capuchin monkey (*Cebus* spp.). Not only do adult capuchins show remarkable tolerance towards immatures (Janson 1986, 1988; Fragaszy et al. 1997), adults also share amongst themselves. In captivity, both edible and inedible objects change possession peaceably among adults, without the rank asymmetries characteristic of most other primate species (Thierry et al. 1989; de Waal et al. 1993).

Perry & Rose (1994) confirmed earlier reports by Newcomer & de Farcy (1985) and Fedigan (1990) that wild *Cebus capucinus* capture coati pups (*Nasua narica*). They observed monkeys beg for and share the meat of pups. Because coati mothers defend their offspring, coordination among nest-raiding monkeys could conceivably increase capture success. This has also been suggested by Rose (1997) for capuchins hunting squirrels (*Sciurus variegatoides*). Even if these situations are not identical to the cooperative hunting of chimpanzees, and certainly less well documented, there are grounds to assume convergent, hunting-related evolution of food sharing in capuchins and chimpanzees (Rose 1997).

Food sharing offers opportunities for detailed research into reciprocal altruism (cf. Trivers 1971). That is, not only a demonstration of reciprocal exchange and a determination of the conditions that promote its evolution (for overviews see *Ethology and Sociobiology*, 9 (2–4), 1988; Dugatkin 1997), but also research into the underlying mechanisms. Because of the required time delay between given and received benefits (Rothstein & Pierotti 1988), reciprocal altruism is a more complex form of cooperation than mutualism. However, some believe reciprocal altruism is rare or absent in nature (Clements & Stephens 1995; Connor 1995; Pusey & Packer 1997).

The few studies that have addressed the cognitive requirements of reciprocal altruism have generally found it hard to distinguish memory-based mechanisms, such as mental score-keeping, from simpler alternatives. The experimental manipulation of food availability, quality and quantity in a food-sharing species allows the creation

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of situations in which services are predictably exchanged, hence in which contingencies between given and received behaviour can be examined. The first such study presented juvenile chimpanzees with the opportunity to share valuable items through bars (Nissen & Crawford 1932). Since bars prevent the dominant of a pair from using force, interindividual food transfers under this condition are likely to be voluntary. Some of the chimpanzees did indeed share, and the authors suggested that 'this sharing was, essentially, barter on a credit or deferred basis' (Nissen & Crawford 1932, page 415).

De Waal's (1989) data on plant food sharing in a large captive colony of chimpanzees are consistent with the hypothesis that tolerance in relation to food evolved, at least in part, as a form of reciprocal altruism. This study found a positive correlation between the rates of food transfer in both directions within each dyad. The same statistical approach has been applied to other spontaneous social exchanges in primates, such as grooming and agonistic support, claiming the same positive result. Reciprocity correlations for monkeys are generally lower than for chimpanzees (e.g. Packer 1977; Seyfarth 1980; de Waal & Luttrell 1988), and it should be noted that studies on baboons have cast doubt on both the altruistic nature and reciprocal distribution of male–male coalitions (Bercovitch 1988; Noë 1990; but see Smuts 1985).

A correlation between given and received acts across an entire matrix of relationships can come about in multiple ways. One possibility is that the correlation results from a common underlying variable. The variable most in need of control is time spent in association: if members of a species were to direct aid preferentially to close associates, a reciprocal distribution would automatically result due to the symmetrical nature of association. The same symmetry argument applies to kinship. This reciprocity mechanism, dubbed 'symmetry-based reciprocity', needs to be distinguished from 'calculated reciprocity' which reflects a contingency, based on mental record-keeping, between given and received services (de Waal & Luttrell 1988). In most species for which reciprocal altruism has been reported, including nonprimates such as vampire bats (*Desmodus rotundus*; Wilkinson 1984) and impala (*Aepyceros melampus*; Hart & Hart 1992), symmetry-based reciprocity cannot be ruled out and this is a likely mechanism.

Whereas this issue can be addressed through statistical control of confounding variables (cf. de Waal & Luttrell 1988), a more rigorous solution is to examine exchanges between individuals over time: does a service provided by individual A to B increase the probability of a service by B to A soon thereafter? Such temporal association is not predicted by symmetry-based reciprocity. Following preliminary evidence for a temporal association between grooming and agonistic support in cercopithecine monkeys (de Waal & Yoshihara 1983; Seyfarth & Cheney 1984; Hemelrijk 1994), the first demonstration of partner-specific service exchange concerned chimpanzees. It was found that after individual A had groomed B, B's tendency to share food with A during a subsequent food trial was greater than usual. Significantly, B's sharing increase was not general: sharing with individuals other than the grooming partner remained unaffected. Such a sequence of events is hard or impossible to explain without the involvement of memory. Thus, chimpanzees may possess the cognitive capacities and social tendencies required for calculated reciprocity (de Waal 1997b).

Indications of food-related reciprocity in brown capuchins, *Cebus apella*, also exist. One study documented interactions between two entire captive groups of monkeys in which one group provided tools to a second group, which then shared food obtained with these tools with the first group (Westergaard & Suomi 1997). This study lacked appropriate controls, however: it remained unclear whether tool and food transfers concerned the same individuals, and whether the two services were contingent upon each other.

Inspired by Nissen & Crawford (1932), our own experiments with this species use a mesh restraint between two monkeys isolated from their group. Food transfers are common under this condition, occasionally involving active giving (i.e. the food possessor walks up to the mesh partition and pushes food to the waiting recipient on the other side). Based on records of 9896 food interactions, de Waal (1997a) reports that active giving was rare, however (i.e. 0.3% of food transfers), as was direct taking of food from the possessor's hands or mouth (0.9% of transfers). Negative responses by the possessor to attempts at food collection by the partner occurred in 4% of the interactions, mostly consisting of turning or jumping away, pulling the food away, or slapping the partner. Overtly agonistic responses (i.e. threats and vocalizations) constituted a small minority of these cases. Similarly, attempts by dominant nonpossessors to forcibly take food were rare (0.9% of interactions), and usually unsuccessful.

The overwhelming majority of transfers followed a peaceful, passive mode (e.g. two monkeys sat side-by-side at the partition while the nonpossessor reached through the mesh to collect pieces held or dropped by the possessor). This behaviour is not to be confused with so-called 'tolerated theft', a mechanism that assumes aggressive pressure from nonpossessors (Blurton Jones 1987). Tolerated theft appears a poor explanation of food sharing in nonhuman primates (de Waal 1996, pp. 152–153). The peaceable, relaxed nature of the food interactions in our test paradigm, the requirement of physical proximity, and the occasional rejections by food possessors, indicate that food transfers result from selective tolerance by the possessor combined with the nonpossessor's interest.

Recently we reported reciprocal food transfers through a mesh partition among adult females. These females lived permanently together in a social group but were temporarily removed for testing. Each combination of familiar females was tested only once. One female owned one type of food for 20 min, after which the other female owned another type for the next 20 min. It was found that the transfer rate from female A to B in the first test phase predicted the rate from B to A in the second phase (de Waal 1997a). The mechanism underlying this reciprocity could be rather simple, however. If food sharing is the product of affiliative tendencies (sitting together at the mesh partition) combined with high tolerance (allowing the other to take food), and if affiliative tendencies and tolerance are symmetrical between familiar females, food sharing based on these tendencies will automatically be reciprocal across dyads. Possibly, therefore, we found yet another instance of symmetry-based reciprocity.

However, calculated or tit-for-tat reciprocity could not be excluded, and the present series of experiments tries to clarify the underlying mechanism. It follows the same design and uses the same subjects as in the previous study, but now each pair of monkeys is tested repeatedly on separate occasions. The question is whether individual A's sharing with B predicts B's sharing with A on a test-by-test basis. If we assume stability in social relationships, relational symmetries such as mutual affiliation and tolerance cannot account for covariation of mutual sharing tendencies. If such covariation does exist in iterated tests it suggests a contingency between giving and receiving.

Since our previous research indicated that adult males share less reciprocally than females (de Waal 1997a), the present study focuses on females. Apart from 'pair tests' in which females could share mutually with a time delay, we added control procedures intended to measure the degree to which capuchins take environmental variables into account. Control procedures included tests without a partner, and tests in which both partners received different foods at the same time. These procedures may reveal whether the monkeys take partner presence into account and whether they consider the partner a competitor for their food.

METHODS

Subjects and Housing

The Yerkes capuchin colony consisted of two separate social groups of *C. apella*. Each group included two adult males, and four or five adult females, totalling 13 adult subjects in both groups. All 11 offspring in the groups were infants or early juveniles except for one male that was 3.5 years old at the beginning of the study. Seven adult females had one offspring, and two adult females had two offspring at the onset of study.

Because most individuals were of unknown background, we conducted a DNA profile analysis. Of the 36 pairs of adults housed in the same group, only one pair was likely to be related, and two pairs were considered potentially related (de Waal 1997a). The monkeys came to us as juveniles and adults. We did not detect obvious bonds of kinship (e.g. immatures closely associating with particular adult females), and it is unknown whether and how they would know kinship relations. Kinship was subsequently ignored in the data analysis.

The capuchin laboratory offered indoor/outdoor housing for two monkey groups with a total of 25 m^2 of floor space for one group, and 31 m^2 for the other. Normally, the monkeys had free access to the entire space. Visual contact between the groups was controlled by an opaque screen. The facility included a separate office with windows through which researchers could monitor the monkey area. During testing, however, the experimenters followed the monkeys' behaviour on a video screen set up in the office.

Each of the two monkey pens was partitioned into three sections by means of one chain-link partition and one opaque partition (i.e. the outer wall). There were interconnecting doors between adjacent sections, and a tunnel between the two distant sections. The concrete floors were covered with saw dust indoors, but uncovered outdoors. The monkeys received ad libitum water and monkey chow, and a daily tray with bread, fruits and vegetables in the late afternoon after the day's last test.

Experimental Procedures

A mobile test chamber made of vinyl-coated mesh was attached to the front of a group's indoor pen. The test chamber was divided by inserting a partition, providing each subject in a pair test with an area of 72 × 60 × 60 cm. Bowls were attached to the outside of the chamber on either side, well out of reach of the monkey on the other side (Fig. 1). The back of the test chamber was opaque to prevent visual contact between test subjects and groupmates. Monkeys entered the chamber either directly from the pen, or from a transport box. The separation procedure took approximately 10 min, after which the monkeys were allowed to habituate to the test chamber for another 10 min. Following this, the experimenter brought food, turned on a video camera, and left the animal area. Video registration on Super-VHS covered the behaviour of both subjects along with a time counter in tenths of seconds.

Tests were conducted in the morning and early afternoons when the monkeys had not yet received any fruits and vegetables. Because no subject was tested more than once per day, repeated tests on a particular dyad were always conducted on different days. Transcription of the videotaped tests was very detailed (de Waal 1997a provides an ethogram). Every 30 s, we recorded the location of subjects relative to the partition and the partner by dividing each individual section into three equal parts (distance 1: within 24 cm of the mesh partition; distance 2: 25–48 cm from the partition; distance 3: at the far end of the test chamber, away from the partner, and 49–72 cm from the partition.

In the present analysis, the central measure is the frequency of 'tolerant food transfers' defined as the number of times the nonpossessor collects or receives food from the possessor's side either directly from the hands or mouth of the possessor or by picking up dropped food from within easy arm's reach and in full view of the possessor. This measure excludes the collection of food when the possessor had his or her back turned or had temporarily moved away from the partition. The exact amounts of transferred food were not measurable, but it was clear that most of the time the food possessor ate the lion's share, and the partner only received left-overs. Exceptions did occur, however, in which the food possessor moved an entire piece of food to the mesh and let the other take it.

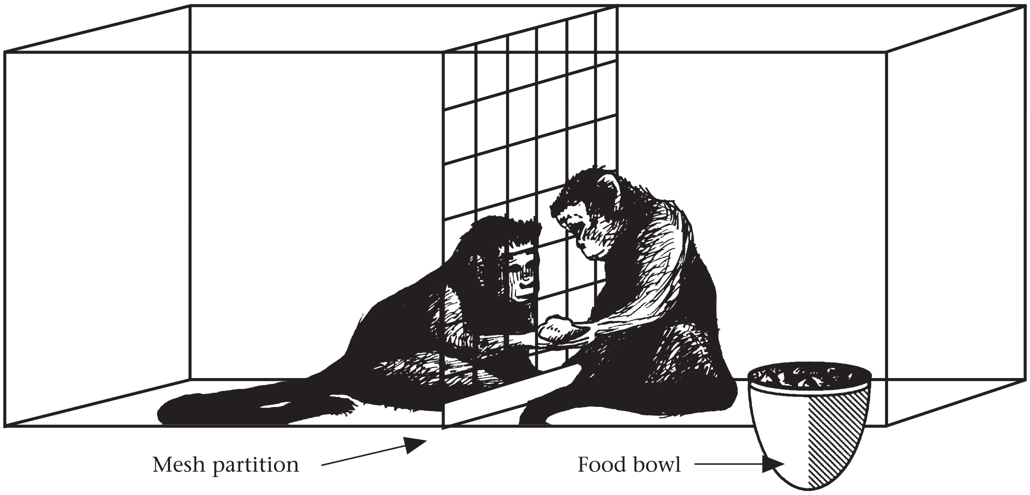

Figure 1. Schematic drawing of the delayed exchange test (DET). One subject at a time receives food from a bowl attached to the chamber's outside. A mesh partition divides the test chamber, preventing direct access to the food by the other individual. In a rare instance of active sharing, a male (right) hands a piece of food to a female who reaches through the mesh to accept it. Both subjects visually monitor the transfer. This drawing, by the author, was made from an actual video still (from de Waal 1997a).

Delayed exchange tests (DET)

We conducted a series of DETs in both directions on all dyads among adult groupmates. This was the only test series including both males and females (72 DETs on 36 dyads). Foods used were different from the DETs of our previous study, which used cucumber first and apple second (de Waal 1997a). In the present series, in the first test phase individual 1 received a handful of apple pieces (half of a medium-sized apple) for 20 min, after which the bowl was removed. The bowl was then filled with carrot pieces (same amount as apple) and given to individual 2 for 20 min in the second test phase. During the next DET on the same pair of individuals, the order between individuals 1 and 2 was reversed. Even though apple is generally preferred over carrot (see Results), both are favoured foods resulting in empty bowls in all tests.

Reiterated DETs

All 16 dyadic combinations between familiar females were subjected to five more apple–carrot DETs with both females always in the same roles of individuals 1 and 2. Because the objective was to determine whether sharing in both dyadic directions covaried across tests, tests with the same individuals in reversed roles would have introduced an additional variable that might have interfered with this objective. Together with the corresponding test from the initial DET series (above), this made for six repeat-trials per female–female dyad.

Same-food trade tests (SFT)

Tests on female dyads in which both individuals received apple pieces at the same time, for 20 min.

Different-food trade tests (DFT)

Tests on female dyads in which individual 1 received apple pieces whereas individual 2 received a different food (either cabbage leaves, grapes, or carrot pieces) at the same time, for 20 min.

Solitary controls (Control)

While in the possession of apple pieces, each adult was tested alone for 20 min, leaving the other section of the test chamber empty.

Food preference tests (FPT)

Each adult was given a choice between two different foods. The experimenter held small pieces of each food in different hands, showing them to the subject (making sure the subject noticed the contents of both hands), before moving the hands to within reach of the subject. Then the subject was permitted to take food from one hand only. These tests were given whenever possible (i.e. when an individual was separated from others) to each adult male or female. The following foods were compared on separate occasions for each individual: apple, cabbage, carrot, cucumber and grape. We conducted a total of 286 food preference tests.

The order of testing followed two phases. In the first phase of 8 months, the first series of DETs, which included both males and females, was followed by the SFTs. Immediately upon completion of this phase, reiterated DETs on female pairs were interspersed with DFTs and Solitary controls in the second phase of 14 months.

Statistics

I made comparisons of individuals or dyads across conditions using the Wilcoxon signed-ranks test. This test is sensitive to both the direction and magnitude of differences. I followed the procedures outlined by Mundry & Fischer (1998), that is, I conducted asymptotic tests only on data meeting the $N>15$ criterion, whereas we used exact tests for smaller sample sizes. All tests were two-tailed, except those for reciprocity. I evaluated reciprocity across tests within dyads using a randomization test, RT 2.1, programmed and explained by Manly (1997).

RESULTS

Partner Effect

I compared the behaviour of individual 1 across three different conditions (Control: no partner present in the adjacent section of the test chamber; DET (phase 1): partner present, but has no food; SFT: partner present and has the same food as individual 1) in female–female dyads. In all three conditions individual 1 possessed apple pieces for 20 min.

Because we collected the controls by individual, dyadic data on the other tests were converted to individual data for comparison. I did this by averaging results across different partners for each subject in the DET and SFT tests. The first comparison concerned the number of point samples (out of 41 samples per test) at which individual 1 was in the area immediately adjacent to the mesh partition. Figure 2 shows that the tendency to be in this area was lowest in controls and highest in SFTs. The difference between the two was significant (Wilcoxon: $T=1.5$, $N=7$, $P<0.05$, nondirectional), but neither condition differed significantly from the DET condition, which showed an intermediate tendency.

The second comparison concerned the number of times individual 1 took a sizeable food item (e.g. an entire apple piece) from the bowl, carried it to the mesh partition and left it within reach of the partner (or, in controls, within the area where a hypothetical partner could reach it) regardless of what subsequently happened to the food. This form of transportation is not the only way in which a partner can obtain food (sharing mostly concerns food that is being handled and consumed by the possessor), but it does facilitate food acquisition. The food transportation rate was highest in controls, indicating an inhibitory effect of the partner in the other tests (Fig. 2). Controls differed significantly from both DETs (Wilcoxon: $T=0$, $N=8$, $P=0.010$, nondirectional) and SFTs ($T=0$, $N=7$, $P=0.020$, nondirectional), whereas the latter two conditions did not differ significantly.

Effect of Food Quality

The FPTs indicated a clear-cut order among the four food types, which ran from the most to the least preferred: grape, apple, carrot and cabbage. This order applied to seven of the nine females. Of the remaining two, one preferred cabbage over carrot, and the other showed a tied preference for both foods.

The analysis compared DFTs on female dyads in which individual 1 possessed apple while her partner had a different food, and SFTs in which both females had apple. As opposed to the previous analysis, the data were organized by dyad. Figure 3 shows the number of samples in which individuals 1 and 2 were in the area adjacent to the mesh partition. Note that the different food types possessed by individual 2 are arranged from left to right from highest to lowest attractiveness.

Individual 1's rate of sitting close to the mesh depended on the food possessed by individual 2, with the order of 2's attractiveness being grape>carrot>cabbage>apple. That apple was at the low end may be explained by the fact that individual 1 herself had apple. The rate when individual 2 had grapes was higher than when she had apple (Wilcoxon: $Z=2.38$, $P=0.017$, nondirectional) or cabbage ($Z=1.99$, $P=0.047$), but not higher than when she had carrot. Other differences for individual 1 in Fig. 3 were nonsignificant.

Individual 2's tendency to sit close to the mesh decreased linearly with the attractiveness of her own

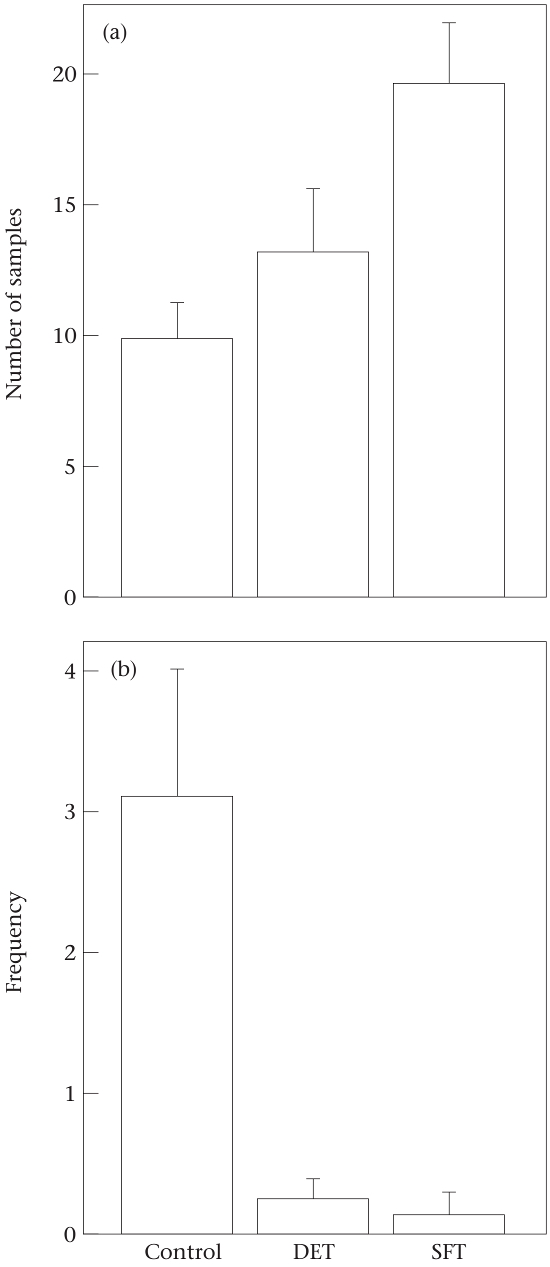

Figure 2. Mean+SE number of (a) samples in which the female food possessor sat close to the mesh partition and (b) entire pieces of food transported and dropped near the mesh partition within reach of the partner under the three conditions: control (in the absence of a partner), the first test phase of a delayed exchange test (DET, a partner without food), and during a same-food test (SFT, a partner with the same food).

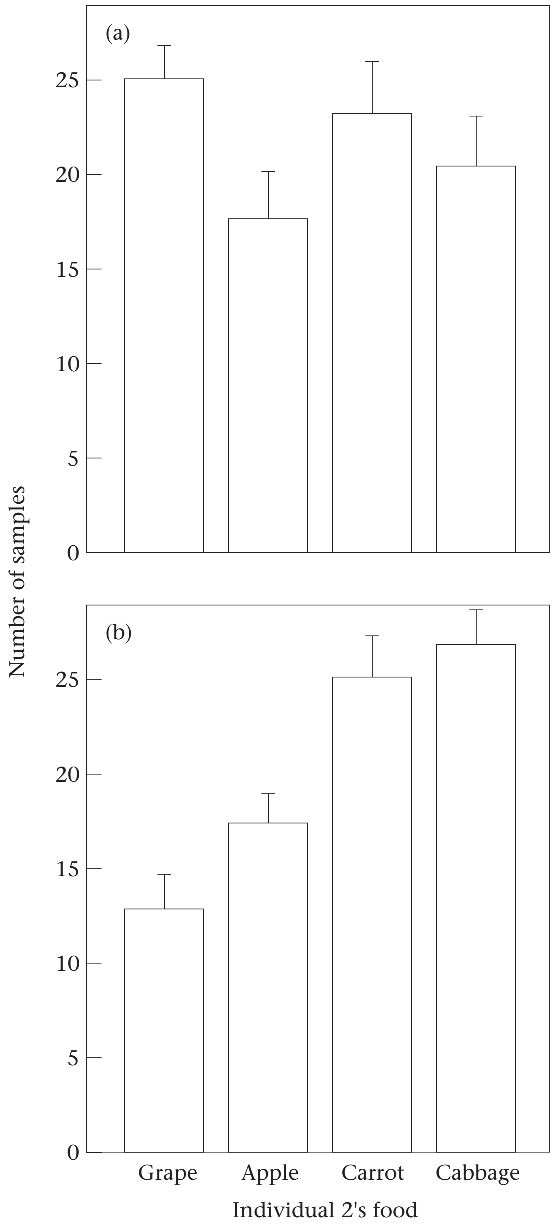

Figure 3. Mean+SE number of samples in which individual 1 (a) and individual 2 (b) sat close to the mesh partition dependent on the type of food possessed by individual 2. Both individuals received food simultaneously, always apple for individual 1.

food: cabbage>carrot>apple>grape. When individual 2 had grapes, the number of samples spent close to the mesh did not differ significantly from when she had apple, but was lower than when she had carrot (Z=2.92, P=0.036) or cabbage (Z=3.41, P<0.001). The number was also lower when she had apple compared with carrot (Z=2.38, P=0.0174) or cabbage (Z=2.52, P=0.012). There was no significant difference between the carrot and cabbage conditions.

Frequencies of food transfer roughly followed the same pattern. Individual 2 obtained increasing amounts of food from individual 1 with decreased attractiveness of her own food (e.g. when she possessed cabbage the average rate with which she collected apple from the other was 13.6 times higher than when she had grapes). Food collection by individual 1 hardly differed across conditions except for a uniformly low rate when the partner possessed cabbage. These differences were not tested for significance as they were not independent from the above data on time spent at the partition (i.e. food sharing requires proximity to the partner).

Reciprocity Across Dyads

I compared the number of tolerant food transfers during the second test phase of the DETs, from individual 2 to 1, with the number of transfers individual 2 had obtained during the first test phase. This analysis was based on the DET series with one test per dyadic direction, which was the only test series to include males. Measured across dyads with a female in the role of individual 2, regardless of partner sex, the Spearman rank correlation between received and subsequently shared food was r_S=0.28 (Z=1.92, N=50, P=0.028, directional). For dyads in which individual 2 was a male, regardless of partner sex, the result was r_S=0.06 (N=22, NS).

Reciprocity Across Tests within Dyads

We subjected all 16 female–female dyads to six DETs each with both females always in the same roles of individual 1 and 2. I classified the number of food transfers from individual 1 to 2 in the first test phase as 'high' or 'low' dependent on whether this number was above or below the mean for all six tests on the same pair. I then averaged the number of food transfers from individual 2 to 1 in the second phase separately across the 'high' and 'low' tests to investigate whether the transfer tendency in the second phase was, as predicted, positively related to that in the first. Figure 4 shows that the mean number of transfers from individual 2 to 1 was significantly elevated in tests in which individual 1's sharing had been higher than average (randomization test: P=0.0026, directional).

In principle, these results could be due to test-ordering effects (i.e. a general rising or falling of food transfers over consecutive tests). Measured across all dyads at once, however, test order (1–6 per pair) did not correlate significantly with the rate of food transfer in either test phase (phase 1: Spearman r_S=0.116, N=96, NS; phase 2: r_S=0.134, N=96, NS), which contradicts the possibility of a confounding effect of test order. Comparing test order with food transfers in the first test phase separately for the 16 dyads showed significant correlations for two of them only: in both cases the rate dropped over time. These two dyads concerned the same female in the role of individual 1. Elimination of these two dyads from the data set left the connection between sharing in phases 1 and 2 intact, however, with the directional probability based on a randomization test remaining under 0.005. In conclusion, the observed reciprocity appeared to result from a cofluctuation of food transfer rates between both partners rather than being a by-product of linearly rising or falling transfer rates.

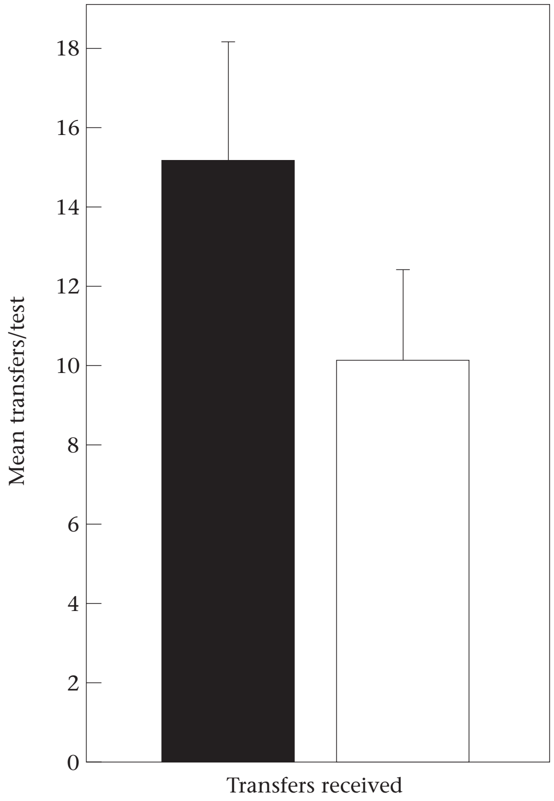

Figure 4. Mean+SE number of food transfers by individual 2 to individual 1 in the second test phase following food transfers by individual 1 to individual 2 in the first phase above (■) or below (□) individual 1's mean. Data for 16 female–female dyads, indicating covariation of sharing in both directions within a dyad.

DISCUSSION

The simplest explanation of food sharing through a mesh partition in capuchins is that these monkeys pay little or no attention to the partner: they just move around with their food, and let the partner opportunistically take whatever comes within reach. Whereas this so-called 'disinterest' hypothesis cannot explain reciprocal sharing, a second relatively simple hypothesis is perfectly capable of doing so. Labelled 'symmetry-based reciprocity' (de Waal & Luttrell 1988), this hypothesis assumes that individuals do take partner identity into account, both by avoiding certain partners and by being attracted to others. If attraction and aversion are symmetrical within each dyad, and if attraction and aversion determine food sharing, a reciprocal distribution of sharing will automatically result.

In our previous studies, the disinterest hypothesis was rejected because of a significant correlation between social relationships and the rate of food transfer (de Waal 1997a). Dominant females tended to share most with adults of both sexes that were familiar groupmates of similar rank and with whom they had had few agonistic encounters. Because the tendency to sit at the mesh partition during food tests and permit the other to collect food is influenced by the relation with the partner, this opens the possibility of symmetry-based reciprocity (i.e. rates of food sharing based on symmetrical attraction or aversion between individuals).

The present study throws new light on the tendencies involved in food transfers, including the question of whether 'sharing' is an appropriate label for this phenomenon. First, the amount of time females spent close to the mesh partition depended on the quality of food in their own possession and that in their partner's possession. Specifically, females spent more time close to the mesh when there was a partner versus no partner, but dropped fewer pieces of food near the mesh when a partner was present. This suggests attraction to the other while at the same time a reluctance to leave food around when another monkey is nearby. The same reluctance to let another monkey remove food was indicated by experiments in which both partners received food at the same time: the more attractive the monkey's own food was relative to the other's food, the less she would stay close to the mesh. Conversely, the less attractive the individual's own food compared with the other's, the more time she would spend close to the other. Thus, in addition to the social relationship, several other variables seem to affect the tendency to sit close to the mesh, such as the likelihood that food will be taken, the partner's interest in the food, and the individual's own interest in the partner's food. Time spent at the mesh partition was, therefore, not simply a product of mutual attraction or aversion. Most importantly, these experiments on the role of food quality indicated that the monkeys take into account the cost of losing food to the other. Thus, whereas our capuchins show extremely little aggression in pair tests (see Introduction, and de Waal 1997a) compared with the whole group condition (Verbeek & de Waal 1997), an element of competition is clearly recognizable in pair tests.

This competitive element suggests that the monkeys' behaviour rests on more than tolerance. They seem aware that the other may take their food, and they know how to prevent this, but nevertheless commonly adopt a position in which the other can freely collect part of their food. Instead of sitting in the far corner, which would permit them to clean out the food bowl undisturbed, they voluntarily create a context in which food is 'lost' to the other. The cost of doing so is low (the food possessor eats the most, and probably, the best parts), but it is more than most primates would ever do (for an illustrative example concerning macaques, see Schaub 1995). Because of the active seeking of proximity in which food transfers can take place and the possessor's otherwise general passivity in the sharing process, the best term to employ is 'facilitated taking': the possessor facilitates the process by approaching the other with food, while the other is permitted to take. This term recognizes the active involvement of both parties, and avoids the human connotations of the term 'sharing'.

The main argument against symmetry-based reciprocity in facilitated taking is the positive relation between food permissiveness in both dyadic directions in reiterated tests on female–female dyads. Stable symmetrical aspects of relationships, such as preferential association between individuals, may explain reciprocity across dyads, but they do not predict a cofluctuation of facilitated taking in both directions within each dyad. On the other hand, we cannot exclude the possibility that a short-term covariate, such as a pre-existing temporary but symmetrical condition of the relationship between any two test subjects, underlies the behaviour in both dyadic directions. The only way to exclude this possibility would be to manipulate or control the rate of food transfer in the first test phase, something we did not do.

However, a more likely explanation is that what happens in the first test phase sets the tone for the remainder of the test, including the second test phase. Note that such an explanation assumes no strict contingency between given and received services, as required for calculated reciprocity (cf. de Waal & Luttrell 1988). The mechanism I propose is that rather than the amount of transferred food, other aspects of the social interaction in the first test phase matter at least as much in determining proximity, tolerance and ultimately food transfer in the second test phase. If the first food possessor spends much time close to the other and tolerates the other's food collection this may predispose the other to show a similar attitude towards the first individual later on in the test. If facilitated taking is mediated by such general social predispositions, this would mean that, rather than keeping track of exact amounts of given and received food, the monkeys follow a simple tolerance-breeds-tolerance scheme.

This hypothetical mechanism, which I will dub 'attitudinal reciprocity', resides somewhere between symmetry-based and calculated reciprocity in terms of complexity. It is less cognitively demanding than calculated reciprocity, because it does not assume mental score-keeping of given and received services nor expectations about appropriate return-favours, or the punishment of cheating. It is more complex than symmetry-based reciprocity, however, in that memory of previous events is implicated, which in turn affects current behaviour. Our work on food transfers after cooperation suggests a similar mechanism, in which joint action induces a positive, tolerant attitude towards the partner (de Waal & Berger 2000). Attitudinal reciprocity follows from variability in social predispositions, ranging from friendly to hostile, and a tendency to adjust to the predisposition perceived in the other: if individual A acts friendly towards B, this stimulates B to act friendly towards A. Such mirroring of attitudes may operate especially when time intervals between events are short, and hence may explain our test results. It is one more hypothesis to consider in studies of proximate aspects of animal cooperation.

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