Chapter 5

Simple and complex reciprocity in primates

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5.1
Introduction

Ever since Kropotkin (1902), the proposed solution to the evolution of cooperation among non-relatives has been that helping costs should be offset by return-benefits, either immediately or after a time interval. Formalized in modern evolutionary terms by Trivers (1971), this principle became known as reciprocal altruism.

Reciprocal altruism presupposes that: (i) the exchanged acts are costly to the donor and beneficial to the recipient, (ii) the roles of donor and recipient regularly reverse over time, (iii) the average cost to the donor is less than the average benefit to the recipient, and (iv) except for the first act, donation is contingent upon receipt. Although the initial work on cooperation (especially from the prisoner's dilemma perspective) focused primarily on the payoff matrix to distinguish between reciprocity and mutualism, more recent efforts have included a significant time-delay between given and received services as an additional requirement for reciprocal altruism (e.g. Rothstein & Pierotti 1988, Taylor & McGuire 1988). Given that a distinction between immediate and delayed benefits is theoretically richer, we include a time-delay in our definition of reciprocal altruism.

The above considerations outline the steps of an evolutionary argument about how reciprocal cooperation may have come into existence. As such, it applies to organisms from fish to humans. This should not be taken to mean, though, that reciprocal help in human society is essentially the same as in guppies. This would be a fundamental error; the above theoretical framework only deals with the ultimate reasons for the existence of reciprocal exchange. That is, it provides an explanation for why animals engage in such behavior, and which fitness benefits they derive from it. It provides no explanation for how such cooperation is achieved, commonly referred to as the proximate explanation, as discussed by Brosnan & de Waal (2002). While it should be noted that, in the larger scheme of things, it is unlikely that human reciprocity deviates substantially from that of other animals, such as the apes, with which we share a long evolutionary history, humans probably have added unique complexities. The most parsimonious assumption with regards to recently-diverged species is that if they act similarly under similar circumstances, the psychology behind it is most likely similar too (de Waal 1991a).

One can imagine forms of reciprocal altruism in which the time-delay between the exchanged services is short, hence the need for record keeping minimal. Individual recognition is perhaps not necessary in such cases. This mechanism would approach mutualism as the time interval between exchanged favors becomes shorter. But also in the case of significant time-delays, exchanges are not necessarily based on give-and-take contingencies. They may simply reflect underlying characteristics of the relationship between individuals. If so, the role of memory would be minimal. This means that not all forms of reciprocal altruism require the cognition we tend to associate with it, such as scorekeeping, punishment of cheaters, attribution of intentions, and awareness of the respective costs of behavioral currencies.

Skeptics of reciprocal altruism in non-human animals sometimes fail to recognize this distinction between (i) the ultimate explanation, which merely postulates that the cost of help given be offset by the benefits of help received, and (ii) the proximate mechanism, which concerns the precise way in which benefits find their way back to the initial altruist. Satisfied with the most advanced mechanism only, they ignore simpler forms of reciprocity (Hammerstein 2003b, Stevens & Hauser 2004). Instead of wondering why reciprocity in animals is so rare, however, the real question is why we feel animals need to operate at the cognitive level that we are capable of, and even more pertinently, how we can be sure that we ourselves operate at that level most of the time? As soon as we move away from anthropocentric assumptions about the mechanism, reciprocity turns out to be widespread indeed (e.g. Dugatkin 1997).

This is not to say that determination of which behaviors evolved as reciprocal altruism, or not, is an easy task. Numerous examples have been posited, but often it is found that either the animals are related, and an alternative explanation for the observed altruistic exchange is kin selection (Wilkinson 1988), or else previously unnoticed benefits to the presumed altruist are found, indicating that the observed behavior is better described as byproduct mutualism (e.g. both animals benefit simultaneously: Koenig 1988, Clements & Stephens 1995; or pseudo-reciprocity: Connor 1986). Furthermore, it is difficult to assess reciprocity in situations in which the exchanged behaviors are dissimilar since the fitness value of different currencies is hard to compare (Seyfarth & Cheney 1988). Even within the same currency, fitness costs and benefits may vary for the parties involved due to individual differences in rank, size and age (Boyd 1992).

More than two decades ago, chimpanzee society was characterized as a ‘marketplace’ in which a variety of services are traded back and forth among individuals (de Waal 1982a). Here we will go into the quantitative details of this marketplace as expressed in coalitions, grooming and food-sharing among chimpanzees (*Pan troglodytes*). Chimpanzees, for instance, have a wide range of goods and services that can be exchanged, including coalitionary support, mating privileges, grooming and food-sharing.

The exchange of these commodities indicates a fairly high level of cognitive accounting in these marketplaces. Experiments on brown capuchin monkeys (*Cebus apella*) further illuminate the proximate side of cooperation and reciprocal altruism. Animals pursue immediate goals which, in the end, often beyond the cognitive horizon of the actors themselves, translate into benefits that form the material for natural selection. A study of proximate mechanisms helps to determine if evolutionary hypotheses are predicting behavior within the animal's range of abilities, because no matter how elegant or compelling an evolutionary scenario, it is useless if the organism lacks the capacity of behaving as the theory predicts (Stamps 1991).

5.2
Observational studies

5.2.1
Reciprocal coalitions and revenge

De Waal & Luttrell (1988) applied a matrix permutation technique to correlations between given and received agonistic support in over two thousand instances observed over a period of five years in the Arnhem Zoo chimpanzee colony as well as a large sample of interventions in mixed-sex groups of rhesus (*Macaca mulatta*) and stumptail macaques (*M. arctoides*) at the Wisconsin Primate Center. In all three studies, agonistic intervention was defined as a third individual responding with an aggressive act against one, and only one, of two participants in a dyadic confrontation. Interventions were recorded as triplets; individual A helps B against C. Reciprocity could occur in the domains of both *pro* (A helps B) and *contra* interventions (A goes against C), hence may reflect two kinds of *quid pro quo* as in "One good turn deserves another" and "An eye for an eye". The latter kind of punitive reciprocity has received far less theoretical attention than the first (but see Clutton-Brock & Parker 1995).

Table 5.1 presents Pearson correlations as well as partial correlations after statistical removal of the effects of symmetrical relationship characteristics. These effects are removed because any characteristic that is symmetrical between two individuals can be used to create reciprocal distributions of behavior if the characteristic causes both partners to show the behavior in question. The analysis controlled for symmetrical characteristics such as (i) time spent in proximity, (ii) matrilineal kinship and (iii) same-sex combination. The partial correlations resulted after correction for all of these characteristics at once.

The table confirms a significant level of reciprocity in *pro* interventions among adults of all three species, even after statistical adjustment for symmetrical relationships. The chimpanzees showed considerably higher reciprocity correlations than the macaques, however. An even more significant difference emerged with regards to harmful *contra* interventions. These interventions were significantly reciprocal in chimpanzees, but significantly anti-reciprocal in macaques. That is, if macaque A often intervenes against B, B will rarely do so against A, whereas in chimpanzees we find that if chimpanzee A often goes against B, B will do the same to A.

De Waal & Luttrell (1988) explain the absence of reciprocal *contra* interventions in macaques by their stricter hierarchy, which prevents subordinates from intervening against dominants. Most data in their study came from females, however. A similar analysis restricted to male bonnet monkeys (*Macaca ra-*

Table 5.1. Pearson reciprocity correlations (r) between given and received agonistic interventions for three primate species. The *pro* rate concerns beneficial interventions, the *contra* rate harmful interventions. Partial correlation coefficients (pr) have been adjusted for the effects of multiple symmetrical relationships characteristics. Probability levels (p) evaluate the partial correlations based on a permutation technique. From de Waal & Luttrell (1988).

Measure	Correlation	Rhesus	Stumptail	Chimpanzee
Pro rate	r	**0.36**	**0.35**	**0.61**
	pr	0.28	0.18	0.55
	p	0.005	0.025	0.005
Contra rate	r	**−0.17**	**−0.23**	**0.33**
	pr	−0.19	−0.29	0.32
	p	0.005	0.005	0.025

diata) did yield evidence for reciprocal *contra* interventions, perhaps reflecting a looser dominance structure among male than female macaques (Silk 1992b). There is also evidence for indirect retaliation among macaques, when defeated subordinates redirect aggression against their opponent's relatives (Aureli et al. 1992). The squaring of accounts in the negative domain, dubbed a revenge system by de Waal & Luttrell (1988), may represent a precursor to human justice, since justice can be viewed as a transformation of the urge for revenge, euphemized as retribution, in order to control and regulate behavior (Jacoby 1983, de Waal 1996b).

Symmetrical relationship characteristics are (or ought to be) an issue in every correlational approach to given and received acts of assistance across dyadic relationships, such as social grooming, food-sharing and agonistic support (e.g. Seyfarth 1980, de Waal & Luttrell 1988, de Waal 1989). Before concluding from a positive correlation that giving depends on receiving, the most obvious variable to control for is time spent in association; if members of a species preferentially direct favors to close associates, the distribution of favors will automatically be reciprocal due to the symmetrical nature of association. A similar argument applies to any symmetrical relationships characteristic (e.g. kinship, age or gender similarity). This mechanism for cooperation, dubbed symmetry-based reciprocity, needs to be distinguished from calculated reciprocity, which is based on mental score-keeping of given and received favors (de Waal & Luttrell 1988). In most species for which reciprocal altruism has been reported through observational methods, symmetry-based reciprocity has not been excluded and hence, remains the most likely mechanism (e.g. blood sharing in vampire bats, *Desmodus rotundus*, Wilkinson 1984; allogrooming in impala, *Aepyceros melampus*, Hart & Hart 1992).

This is not to say that uncorrected positive correlations are meaningless; obviously, symmetries are part of evolved social life. If they assist reciprocal relations that confer benefits, this is all that matters from an evolutionary perspective. Evidence limited to positive correlations, however, does not permit conclusions about contingencies between giving and received behavior. Although we know from experiments (see below) that monkeys are capable of contingent exchange, and although analyses that have gone beyond dyadic relationships, such as in biological markets (cf. Noë & Hammerstein 1994), show behavioral distributions that seem too finely tuned to the supply and demand of benefits as well as partners to be accounted for by symmetry-based reciprocity (e.g. Barrett & Henzi, this volume), we would still argue that correlations cannot reveal underlying processes and that it is best, therefore, to adhere to conservative interpretations.

In view of these problems, observational studies should add sequential analyses, which look at the unfolding of behavior over time. Does a beneficial act by individual A towards B increase the probability of a subsequent beneficial act by B towards A? These analyses get around the problem posed by symmetries. Preliminary sequential evidence for an exchange between affiliative behavior and agonistic support, and *vice versa*, exists for cercopithecine monkeys. De Waal & Yoshihara (1983) found increased post-conflict attraction and grooming between previous alliance partners in rhesus monkeys. Seyfarth & Cheney (1984) employed playbacks of calls that vervet monkeys (*Cercopithecus aethiops*) use to both threaten an aggressor and solicit support to gauge the reaction of individuals that had recently been groomed by the caller. They reported increased attention to previous grooming partners. Finally, Hemelrijk (1994) examined agonistic support after experimentally manipulating grooming among long-tailed macaques (*M. fascicularis*) and found indications that individuals supported those who had groomed them, i.e. individual A supported individual B more if B had groomed A, but not if A had groomed B.

The last study comes closest to demonstrating a temporal relation between one service and another, but what is still missing is evidence for partner-specificity, i.e. that the return service specifically targets the individual who offered the original service. The alternative is generalized reciprocity, or the 'good mood' hypothesis (see below), according to which the receipt of services leads to an indiscriminate increase in beneficial behavior. Our research on food-sharing in chimpanzees attempted to address this important distinction.

5.2.2
Food for grooming in chimpanzees

Although food-sharing outside the mother-offspring or immediate kin-group is rare in the primate order (Feistner & McGrew 1989), it is common in both capuchin monkeys and chimpanzees. Food-sharing lends itself uniquely to experimental research, because the quantity and type of food available, the initial possessor, and even the amount of food shared can be manipulated by the experimenter. Second, food-sharing provides a quantifiable currency. An observer can see exactly how many times the non-possessor obtains food and can estimate quantities shared. Finally, the observer can tell whether the sharing was active or passive.

Active food-sharing, a rare behavior, consists of one individual handing or giving food to another individual, while passive food-sharing, by far the more common type, consists of one individual obtaining food from another without the possessor's active help (Fig. 5.1). The sharing is selective, however, in that possessors are not equally tolerant of all individuals; only approximately half of the interactions between a possessor and an interested non-possessor resulted in an actual transfer of food.

There are three common hypotheses to explain food-sharing in primates: (i) the sharing-under-pressure hypothesis, (ii) the sharing-to-enhance-status hypothesis and (iii) the reciprocity hypothesis (reviewed by de Waal 1989, 1996b). The sharing-under-pressure hypothesis, similar to the tolerated-theft hypothesis of Blurton-Jones (1987), predicts that individuals will share in order to be left alone by potentially aggressive conspecifics (Wrangham 1975, Stevens 2004). This hypothesis is contradicted by the fact that the most generously sharing individuals are often fully dominant, hence have little to fear from anybody around them, and that most of the aggression in feeding clusters, rather than being by non-possessors against possessors, is directed the other way around (de Waal 1989). This confirms the remarkable 'respect of possession' (cf. Kummer 1991) already noted by Goodall (1971) in her first accounts of meat sharing among wild chimpanzees. The sharing-under-pressure hypothesis also fails to explain food transfers in experimental set-ups in which negative consequences of non-sharing are eliminated by physical separation (see below).

What remains, then, are the sharing-to-enhance-status hypothesis and the possibility of reciprocity. The first hypothesis predicts that generosity increases the altruist's standing in the community (Hawkes 1990), but there is as yet no evidence for this effect in non-human animals. The reciprocity hypothesis predicts that food is part of a service economy, hence that it is exchanged reciprocally for other favors. These two hypotheses are, of course, not mutually exclusive.

Our initial studies approached food-sharing by means of matrix correlations. This matrix approach yielded significant results in the predicted direction. However, food-sharing among chimpanzees correlates positively with proximity and grooming, hence the amount of time individuals spend together in non-food situations. As explained before, the effects of association must be removed before any explanation other than symmetry-based reciprocity may be invoked. When the matrix analysis was redone while statistically controlling for the effects of association, the correlation continued to be significant.

Statistical elimination of a variable is not as powerful as experimentally controlling for it, however. A new experiment was designed to measure temporal patterning within each dyad, thereby holding the effect of association constant. Partner specificity was addressed, i.e. whether a beneficial act by individual A towards B specifically affects B's behavior towards A (de Waal 1997a). The difficulty in measuring food-sharing across time is that after a group-wide food-sharing session, as used in these experiments, the motivation to share is changed (the animals are more sated). Hence, food-sharing cannot be the only variable measured. A second service that is unaffected by food consumption needs to

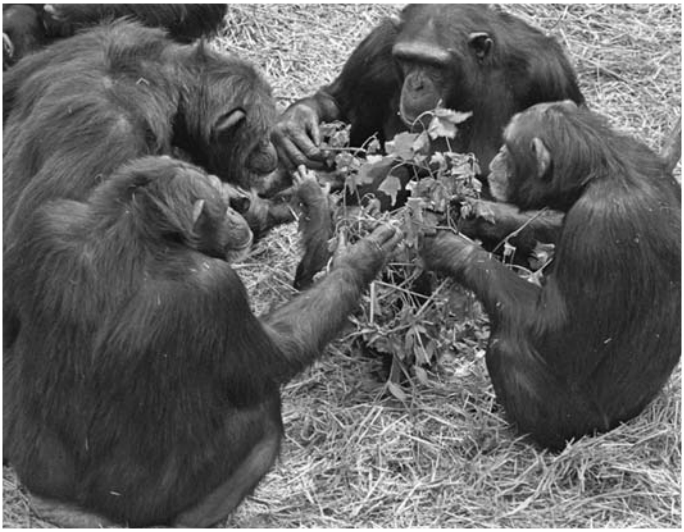

Fig. 5.1. A cluster of food-sharing chimpanzees at the Yerkes Field Station. The female in the top-right corner is the possessor. The female in the lower left corner is tentatively reaching out for the first time, whether or not she can feed will depend on the possessor's reaction. Photograph by Frans de Waal.

be included. For this, grooming between individuals prior to food-sharing was used. The frequency and duration of hundreds of spontaneous grooming bouts among the chimpanzees was measured during 90 minute observation sessions. Within half an hour after the end of these observations, the apes were given two tightly bound bundles of leaves and branches. Nearly 7000 interactions over food were carefully recorded by observers and entered into a computer according to strict empirical definitions described by de Waal (1989). The resulting database on spontaneous services exceeds that for any non-human primate.

It was found that adults were more likely to share food with individuals who had groomed them earlier in the day. In other words, if A groomed B in the morning, B was more likely than usual to share food with A later in the same day (Fig. 5.2). This result, however, could be explained in two ways. The first is the so-called 'good mood' hypothesis according to which individuals who have received grooming are in a benevolent mood leading to generalized reciprocity, i.e. increased sharing with all group members. The second explanation is the exchange hypothesis, in which the individual who has been groomed responds by sharing food specifically and only with the groomer. The data indicated that the sharing was specific to the previous groomer. In other words, each chimpanzee remembered who had just performed a service (i.e. grooming) and responded by sharing more with this particular individual. Also, aggressive protests by food possessors to approaching individuals were aimed more at those who had not groomed them than at previous groomers. All of this is compelling evidence for the reciprocal exchange hypothesis.

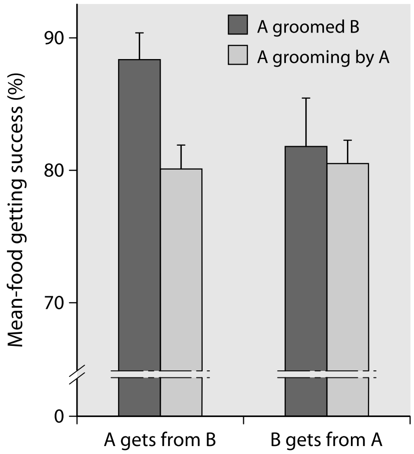

Fig. 5.2. Mean (+SEM) food-getting success per dyadic direction between adult chimpanzees during food trials. Two conditions are distinguished: either individual A had groomed B in the hours prior to the food trial, or no previous grooming by A to B had occurred. The left-hand side of the graph shows the success of A in obtaining food from B (A gets from B); the right-hand side shows the success of B in obtaining food from A (B gets from A). Success is defined as the percentage of approaches to a food possessor resulting in a transfer of food (regardless of whether the transfer is active or passive) from possessor to non-possessor. It was found that A's success in obtaining food from B increased significantly after A had groomed B, whereas B's success in obtaining food from A was unaffected by A's previous grooming. From de Waal (1997a).

It was further found that grooming between individuals who rarely did so had a greater effect on subsequent food-sharing than grooming between partners who commonly groomed. Among partners in which little grooming was usually exchanged, there was a more pronounced effect of grooming on sharing. There are several interpretations. It could be that grooming from a partner who rarely grooms is more noticeable, leading to increased sharing by the food possessor. Chimpanzees may recognize unusual effort and reward accordingly. Secondly, individuals who groom frequently tend to be close associates, and favors may be less carefully tracked in these relationships. Close friendships may be characterized by symmetry-based reciprocity, which does not have the high degree of conditionality found in more distant relationships. These explanations are not mutually exclusive; both will lead to a reduced level of conditionality the more common exchanges are in a relationship.

Of all existing examples of reciprocal altruism in non-human animals, the exchange of food for grooming in chimpanzees comes closest to fulfilling the requirements of calculated reciprocity. This study strongly suggests memory-based, partner-specific exchange in chimpanzees. It goes beyond symmetry-based reciprocity inasmuch as symmetry is a constant feature of relationships that cannot explain contingencies across time, as demonstrated here. There existed a significant time delay between favors given and received (from half an hour to two hours); hence, the favor was acted upon well after the previous positive interaction. Apart from memory of past events, for this to work we need to postulate that the memory of a received service, such as grooming, induces a positive attitude towards the same individual, a psychological mechanism described as 'gratitude' by Trivers (1971), and further explored by Bonnie & de Waal (2004).

5.3
Experiments on capuchin monkeys

Even though laboratory work on primate cooperation goes back to Crawford (1937), few experimental studies have been conducted since. What is especially lacking is the experimental manipulation of 'economic' variables, such as the relation between effort, reward allocation, and reciprocity. Recently, this situation has changed thanks to experiments on brown, or tufted, capuchin monkeys.

The *Cebus* genus seems particularly suited for cooperation research. These monkeys show high levels of social tolerance around food and other attractive items, sharing them with a wide range of group members both in captivity and in the field (Izawa 1980, Janson 1988, Thierry et al. 1989, de Waal et al. 1993, de Waal 1997b, Fragaszy et al. 1997). This level of tolerance is unusual in non-human primates, and its evolution may well relate to cooperative hunting. Perry & Rose (1994) confirmed reports by Newcomer & de Farcy (1985) and Fedigan (1990) that wild *Cebus capucinus* capture coati pups (*Nasua narica*) and share the meat. Since coati mothers defend their offspring, coordination among nest-raiders conceivably could increase capture success. This has also been suggested for hunting by capuchins on giant squirrels (*Sciurus variegatoides*; Rose 1997). Rose (1997) proposed convergent evolution of food-sharing in capuchins and chimpanzees based on group hunting. The precise level of cooperation of the hunt is not relevant for such evolution to occur; all that matters is that hunting success increases with the number of hunters. Under such circumstances, every hunter has an interest in the participation of others, something promoted by subsequent sharing.

5.3.1
Reciprocal food-sharing

In the delayed exchange test, or DET, a pair of monkeys is placed in a test chamber, separated from each other by a mesh partition that allows for food-sharing. Monkey A is given a bowl of cucumber pieces, placed well out of reach of monkey B. After 20 minutes, the cucumber is removed, and a bowl of apples is given to monkey B (second test phase). The same pair is given another DET later, on a different day, with the order reversed between the monkeys (Fig. 5.3).

In years of testing with this paradigm, our capuchins displayed an astonishing amount of social tolerance, sharing food on a reciprocal basis. Males tended to share more than females regardless of the sex of the partner. A matrix analysis found that, for the 14 female-female dyads in which the possessor was dominant, more sharing occurred between partners who in the group in which they lived

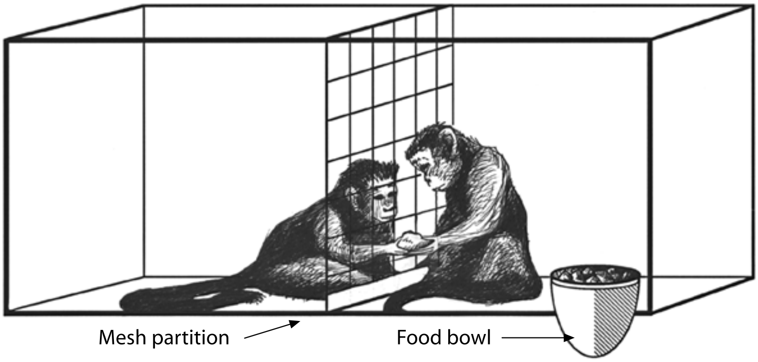

Fig. 5.3. Sketch from an actual video still showing active food-sharing in a pair of capuchin monkeys. The monkeys are separated by a mesh partition, and the monkey on the right has access to a food bowl containing apples. Active food-sharing is rare, but facilitated taking, in which the food possessor drops pieces by the mesh and allows the other monkey to take them, is common. Drawing by Frans de Waal, from de Waal (1997b).

had: (i) fewer agonistic interactions, (ii) shorter rank distances (i.e. were close in the dominance hierarchy) and (iii) higher levels of proximity and grooming. Furthermore, the number of tolerant food transfers in the first test phase was significantly correlated with the number of tolerant food transfers in the second phase (de Waal 1997b). The most parsimonious explanation of this result is symmetry-based reciprocity, i.e. reciprocity based on the symmetrical nature of relationships. The capuchins were already familiar with each other (pair members lived in the same group), and food-sharing might have resulted from a combination of affiliation and tolerance towards conspecifics. Our next concern was whether or not reciprocity could be attributed to anything besides the symmetry inherent in the relationship.

For this, changes within each relationship over time were examined. The test was similar to the previous one, but incorporated six DETs on each pair. For each DET, individual A was given apple pieces for 20 minutes, then these were removed and individual B was given carrot pieces for 20 minutes. The roles between individuals remained the same over the six tests. The results were compared across tests to see how sharing in the second test phase was affected by sharing in the first phase between the same two individuals. This approach allowed us to correlate events over time, rather than across relationships, tightening a possible argument for causality between the behaviors in both dyadic directions. Sharing rates were found to significantly covary over time within each pair of individuals, indicating something more than symmetry-based reciprocity (de Waal 2000c).

Calculated reciprocity, or mental scorekeeping, however, may still be too complex a mechanism. To explain these results, de Waal (2000c) proposed ‘attitudinal reciprocity’, that is, each individual’s behavior mirrors the partner’s attitude in close temporal succession. Instead of the monkeys keeping careful track of how much they gave and received, they may merely have responded positively (i.e. with proximity and tolerance) to a positive attitude in their partner. Such mirroring of social predispositions might explain the reciprocal distribution of food-sharing without the requirement of scorekeeping.

5.3.2
Cooperation

Despite indications of cooperation among wild capuchins, tests of their cooperative abilities in the laboratory initially failed. Early tests used electronically-mediated or other complex devices that were beyond the monkeys' comprehension (Chalmeau et al. 1997, Visalberghi et al. 2000, Brosnan & de Waal 2002). Adoption of the paradigm pioneered by Crawford (1937), on the other hand, quickly led to success. This paradigm, in which two individuals pull food towards themselves, is entirely mechanical. As such, it is intuitive; the monkeys can see how their pulling causes the food to move towards themselves and they also immediately feel the effect of their partner's pulling.

In our case, two capuchin monkeys had to work together to pull in a counterweighted tray, at which point one or both of them would be rewarded (Fig. 5.4). They were placed in the test chamber separated from each other by a mesh partition, giving them the option to share food. Each monkey had its own bar to pull in the tray, although these bars could be removed for control tests. Food was placed in transparent bowls so that each monkey could see which one was about to receive the food.

Initially, monkeys were taught to pull in the tray individually, which they quickly learned. At this point (and throughout the experimental period, which lasted three years) each monkey was given regular strength tests to determine how much weight he or she could pull in individually. For trials in which only one monkey pulled, the tray was weighted just under what this individual could pull. For trials in which both monkeys pulled, the tray was weighted more heavily than the strongest individual could pull alone, but somewhat lighter than their combined strengths. Each test consisted of four 10-minute trials conducted on seven same-sex pairs of adult capuchins. The five test conditions were:

- Solo effort test (SOL), in which only one monkey had a pull-bar and only this individual received food, although both monkeys were present in the test chamber. This required no cooperation.
- Mutualism, or double test (DBL), in which both monkeys were required to pull together and both cups were baited.
- Cooperation test (COP), in which both monkeys were required to pull together but only one food cup was baited. This represented altruism on the part of the helper.
- Obstructed view test (OBS), which was the same as the above COP test except that the mesh partition was replaced by an opaque one. This eliminated visual communication between the monkeys, but they still could both see both cups on the tray, and that only one was baited.

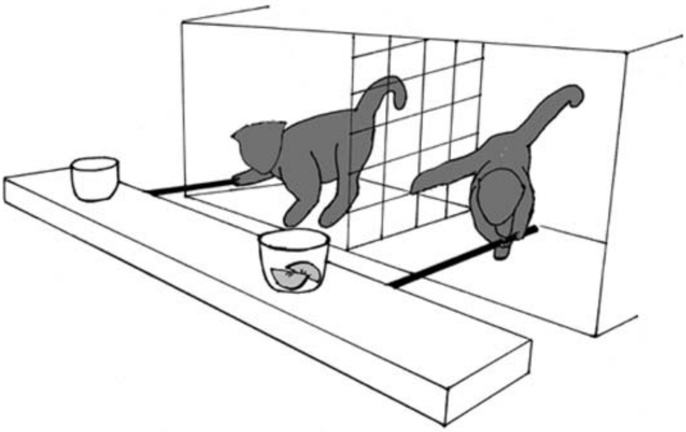

Fig. 5.4. The test chamber used for the cooperative pulling task in capuchin monkeys inspired by Crawford's (1937) classical study. Two monkeys are situated in adjacent sections of the test chamber, separated by a mesh partition. The apparatus consists of a counter-weighted tray with two pull bars, with each monkey having access to one bar. The bars can be removed. In the solo effort test, two monkeys were in the test chamber, but only one monkey had a pull bar and only this individual's food cup was baited. In the mutualism test, both monkeys were required to pull their respective pull bars, and both food cups were baited. In the cooperation test depicted here, both monkeys were required to pull, but only one individual's food cup was baited. Drawing by Sarah Brosnan.

- Unrestricted cooperation test (UCP), which was the same as the COP test, except that the partner was free to move in and out of the test chamber, which had an open connection to part of the group cage. This meant that the helper, needed for successful pulls, was not always at hand.

As expected, the success rate of cooperative trials was significantly lower than that of mutualism tests or solo efforts. In the unrestricted cooperation tests, bar-pulling attempts by the food possessor significantly decreased when the partner left the test chamber, indicating that the monkeys had learned to associate their partner's presence with successful pulling. They might even have made the more complex association that they could succeed only with their partner's help (Mendres & de Waal 2000).

Bar-pulling success also decreased significantly in the obstructed view tests as opposed to the cooperation tests. In the obstructed view test, vocal communication was still possible and the monkeys continued to make pulling efforts at the same rate they did in the cooperation tests. Since both monkeys could see the food cups, their success rates should not have decreased if the impetus to pull simply stemmed from seeing food. What changed was their ability to see each other's behavior, indicating that success was at least partially dependent on visual coordination with the partner. The failure to succeed when visual access was cut off indicates that the monkeys were paying attention to each other's actions and coordinating their efforts. This result countered the claim of Chalmeau et al. (1997) that capuchins do not understand the need for a partner in cooperative tasks (Mendres & de Waal 2000).

5.3.3
Sharing following cooperation

The central question underlying this project was whether food-sharing would increase in the context of a cooperative enterprise. In a service economy, food can be exchanged for assistance in cooperation, or the converse. Our analyses of the amount of food-sharing indicated that capuchins share significantly more in successful cooperative trials than in solo effort trials, in which the partner is present, but does not, and actually cannot, assist (de Waal & Berger 2000).

Furthermore, the partner pulled more frequently after successful trials. Since 90% of successful trials included food transfers to the helper, capuchins are assisting more frequently after having received food in a previous trial. The simplest interpretation of this result is that motivational persistence results in continued pulling after successful trials. But a causal connection is also possible, i.e. that pulling after successful trials is a response to the obtained reward and the expectation of more.

The most cognitively-demanding interpretation of these results is that the food possessor understands that its partner has helped and that the partner must be rewarded for cooperation to continue. This would represent calculated reciprocity, in which the exchange of favors on a one-on-one basis drives reciprocal altruism. Each individual understands the other's costs (assistance in pulling or loss of food) and out of gratitude returns the favor.

However, a simpler explanation of the cooperation and food-sharing in these trials is a variation on attitudinal reciprocity (cf. de Waal 2000c), in which the possessor and partner feel closer after a coordinated effort. The attention and coordination that cooperation entails may induce a positive attitude in the partner, which is expressed in social tolerance and mutual attraction, which translate into food-sharing. After a food-sharing episode, similar mechanisms lead to increased pulling by the partner and hence further cooperation.

The conclusion from these experiments is that capuchins are quite good at performing, and probably also understanding, cooperative tasks. The mechanism most likely to underlie cooperation and sharing in these monkeys is attitudinal reciprocity in which cooperation partners mirror the attitude shown by their partner. This is different from symmetry-based reciprocity in that reciprocation is not induced by symmetrical relationship characteristics but by attitudes that vary over time. This rather conservative explanation does not preclude the possibility of more complex processes, though. Indeed, the results of a recent experiment on cotton-top tamarins (*Saguinus oedipus*) indicate that monkeys are sensitive to benefits received from others, and that they may even recognize whether or not these benefits were intended (Hauser et al. 2003). If confirmed, these capacities have the potential of adding considerable complexity to attitudinal reciprocity.

5.3.4
Cooperation based on projected returns

Group hunting is characterized by a phase of coordination followed by a phase in which the parties collect around the captured prey. The latter phase decides who gets what for their efforts. In a variation on the above cooperation paradigm, de Waal & Davis (2003) mimicked this situation by allowing individuals to move around freely during the pulling task instead of being confined to separate areas, as done previously. This way, cooperation partners could compete over the acquired resource. We further manipulated (i) opportunities for competition by presenting the resource in clumped versus dispersed distribution (i.e. the cups with food could be placed far apart at both extremes of the tray or side-by-side, touching each other, in the center), and (ii) the tendency for competition by comparing unrelated pairs and adult mother-daughter pairs. Numerous primate studies indicate greater tolerance and more co-feeding among kin than non-kin (Yamada 1963, Feistner & McGrew 1989, de Waal 1989, 1991b, Schaub 1996).

In investigating how cooperative tendency varied with the potential for competition (clumped versus dispersed rewards), we were particularly interested in the speed of the decision-making process. Monkeys may need to learn incrementally which specific conditions are favorable for cooperation, or they may be able to make instantaneous adaptive decisions. In the first case, the pros and cons of each specific condition need to be learned through direct experience; hence, behavior will gradually change in response to any new condition. In the second case, there is a fast adjustment to new conditions since decisions are based on generalization from pre-existing knowledge.

Questions regarding the role of food distribution and the speed of adjustment are relevant to models of the evolution of cooperation. Imagine a genetic variant that cooperates readily with any member of its group to obtain resources, yet is a slow learner. The variant would have enormous trouble distinguishing profitable from unprofitable partnerships; it would need to go through many reiterated interactions before it understands which partners and situations provide optimal payoffs. Each time a new situation arises it would need to go through this learning process. Unless the cooperative tendencies of this individual selectively favor kin, they would impose serious costs. On the other hand, a variant that could quickly distinguish profitable from unprofitable partnerships would minimize costs in any interaction and hence enjoy higher fitness.

After pre-training, each of eleven pairs of monkeys was subjected to multiple tests consisting of fifteen 2-minute trials each, with rewards available to both parties. Clumped reward distribution had an immediate negative effect on cooperation, which was visible from the first trial (Fig. 5.5). Even in tests in which we alternated clumped and dispersed conditions across trials, there was an adjustment on each trial. The drop in cooperation under the clumped condition was far more dramatic for non-kin than kin, which was explained by the tendency of dominant non-kin to claim most rewards. The immediacy of responses suggests a decision-making process based on predicted outcome of cooperation rather than the totality of rewards available. Decisions about cooperation thus take

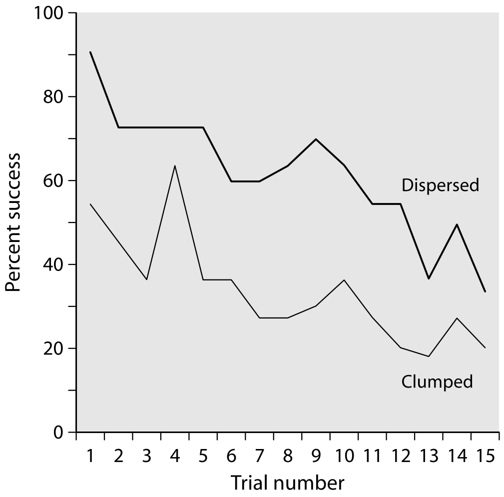

Fig. 5.5. Percentage of trials with successful cooperation for 15 consecutive trials per test in which the two food bowls are far apart (dispersed) or close together (clumped). The latter condition makes monopolization of the food by the dominant partner easy since, in these tests, there is no mesh between the partners. Since the data on all 11 pairs are pooled for each trial number, this graph provides no error data. The graph shows that the rate of success is lower right from the start in the clumped condition.

into account both the opportunity for and the likelihood of subsequent competition over the spoils.

The decisions observed probably reflected a lifetime of exposure to a variety of partners (e.g. dominant versus subordinate, or kin versus non-kin) under competitive conditions. The monkeys thus showed an ability to generalize previous knowledge to the novel test condition. It is particularly important to stress the generalizability of knowledge and the complexity of the variables that enter into decision-making given that social considerations are almost entirely absent from traditional learning research. For example, there is no mention of cooperation or almost any other socioemotional skills (e.g. conflict resolution, alliance formation, empathy) in a recent 700-page book on human and animal cognition (Shettleworth 1998). Many biologists, in contrast, believe that the social milieu has provided the main impetus for the evolution of intelligence in the large-brained order of primates (Humphrey 1976, Byrne & Whiten 1988). ‘Planning’ and ‘foresight’ are terms used in relation to chimpanzee power struggles (de Waal 1982a), and social intelligence is accorded special status in these highly social animals (Gigerenzer 1997, Dunbar 2001).

The study by de Waal & Davis (2003) supports the assumption that primates are extraordinarily sensitive to the reactive social field within which they operate. An anecdote (transcribed from a videotaped test) helps show how this sensitivity sometimes expresses itself. In a cooperation task on two female capuchins, Bias was paired with higher-ranking Sammy. Both females pulled in the tray together. Sammy quickly grabbed all of the food on her side, and released the tray without locking it into place, so that the counterweight pulled it away. Bias was left with her food cup out of reach. While Sammy was consuming her rewards, Bias started screaming at her partner until Sammy approached her bar again. While looking at each other, Sammy helped Bias pull in the tray again. Sammy did not do this for herself, because by this time her own cup was empty. This incident suggests protest by Bias for having lost the rewards 'deserved' for the first pull, and Sammy's corrective response.

5.3.5

Expectations about reward division

During the evolution of cooperation, it may have become critical for actors to compare their own efforts and payoffs with those of others (Brosnan, in press). Negative reactions may ensue in case of violated expectations. A recent theory proposes that aversion to inequity can explain human cooperation within the bounds of the rational choice model (Fehr & Schmidt 1999). Similarly, cooperative non-human species seem guided by a set of expectations about the outcome of cooperation and access to resources. De Waal (1996b, p. 95) proposed a "sense of social regularity", defined as: "A set of expectations about the way in which oneself (or others) should be treated and how resources should be divided. Whenever reality deviates from these expectations to one's (or the other's) disadvantage, a negative reaction ensues, most commonly protest by subordinate individuals and punishment by dominant individuals".

The sense of how others should or should not behave is essentially egocentric, although the interests of individuals close to the actor, especially kin, may be taken into account (hence the parenthetical inclusion of others). Note that the expectations have not been specified; they are species-typical (de Waal 1996b). Our experiment on clumped versus dispersed rewards (above) supports the role of expected returns in that it shows that cooperation disappears when subordinates anticipate a disadvantageous outcome. To further explore expectations held by capuchin monkeys, we made use of their ability to judge and respond to value. The ability to notice and respond when either reward value or efforts vary promotes cooperation by allowing individuals to recognize beneficial interactions. We knew from previous studies that capuchins easily learn to assign value to tokens, both through direct interaction with the items and through social learning (Brosnan & de Waal 2004a,b). Furthermore they can use these assigned values to complete a simple barter (Brosnan & de Waal 2004b). This allowed a test to elucidate inequity aversion by measuring the reactions of subjects to a partner receiving a superior reward for the same tokens.

We paired each monkey with a group mate and watched their reactions when their partners got a better reward for doing the same bartering task. This consisted of an exchange in which the experimenter gave the subject a token that could immediately be returned for a reward (Fig. 5.6). Each session consisted of 25 exchanges by each individual, and the subject always saw the partner's exchange immediately before their own. Food rewards varied from lower value rewards (i.e. a cucumber piece), which they are usually happy to work for, to higher value rewards (i.e. a grape), which were preferred by all individuals tested. All

Fig. 5.6. A monkey in the test chamber returns a token to the experimenter with her right hand while steadying the human hand with her left hand. Her partner looks on. The capuchin does not see the reward she is to receive prior to successful exchange. Drawing by Gwen Bragg and Frans de Waal after a video still.

subjects received four tests, including: (i) an Equity Test, in which subject and partner did the same work for the same lower-value food, (ii) an Inequity Test, in which the partner received a superior reward (grape) for the same amount of effort, (iii) an Effort Control Test, designed to elucidate the role of effort, in which the partner received the higher-value grape without any task-performance, and (iv) a Food Control Test, designed to elucidate the effect of the presence of the reward on subject behavior, in which grapes were visible but not given to another capuchin.

Fig. 5.7 shows that individuals who received lower value rewards showed both passive negative reactions (e.g. refusing to exchange the token, ignoring the reward) and active negative reactions (e.g. throwing out the token or the reward). Compared to tests in which both received identical rewards, the capuchins were far less willing to complete the exchange or accept the reward if their partner received a better deal (Brosnan & de Waal 2003). Capuchins refused to participate even more frequently if their partner did not have to work (exchange) to get the better reward, but was handed it for 'free'. Of course, there is always the possibility that subjects were just reacting to the presence of the higher value food, and that what the partner received (free or not) did not affect their reaction. However, in the Food Control Test, in which the higher-value reward was visible but not given to another capuchin, the reaction to the presence of this high-valued food decreased significantly over the course of testing, which is the opposite change from that seen when the high value reward went to an actual partner. In the latter case, the frequency of refusals to participate rose over the

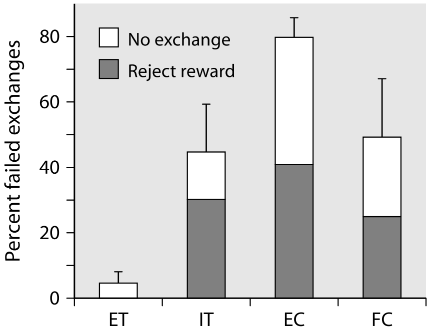

Fig. 5.7. Mean percentage + SEM of failures to exchange for females across the four test types. Black bars (RR) represent the proportion of non-exchanges due to refusals to accept the reward, white bars (NT) represent those due to refusals to return the token. SEM is for combined non-exchanges. ET = Equity Test, IT = Inequity Test, EC = Effort Control, FC = Food Control. The *y*-axis shows the percentage of non-exchanges. From Brosnan & de Waal (2003).

course of testing (Brosnan & de Waal 2004). While it has been suggested that these differences are not significantly variable (Wynne 2004), it is important to note that: (i) some reaction is always expected to the mere presence of a higher value reward, as it is inherently more desirable and (ii) the decrease in the level of response when no partner receives the reward is significantly different than when the partner does, demonstrating that the capuchins make the distinction between the two situations (Brosnan & de Waal 2004c).

Whereas the capuchins' reactions to this situation may not be identical to those of people (Henrich 2004), they fit well with the proposed evolutionary trajectory of inequity aversion (Brosnan & de Waal 2004). In fact, like humans, capuchin monkeys seem to measure reward in relative terms, comparing their own rewards with those available, and their own efforts with those of others. Although our data cannot elucidate the precise motivations underlying these responses, one possibility is that monkeys, like humans, are guided by social emotions. These emotions, known as 'passions' by economists, guide human reactions to the efforts, gains, losses and attitudes of others (Hirschleifer 1987, Frank 1988, Sanfey et al. 2003). As opposed to primates marked by despotic hierarchies, tolerant species with well-developed food-sharing and cooperation, such as capuchins, may hold emotionally-charged expectations about reward distribution and social exchange that lead them to dislike inequity.

5.4
Summary and conclusions

Although theories about the evolution of cooperation and reciprocal altruism are well established, proximate mechanisms have been little studied. There probably exist several levels of reciprocity, ranging from the more complex end of the spectrum, such as the kind originally proposed by Trivers (1971), which

Table 5.2. Three poximate mechanisms proposed by de Waal & Luttrell (1988) and de Waal (2000) to explain reciprocal distributions of benefits over dyadic relationships. The mechanisms are arranged from the least to the most cognitively demanding.

Mechanism	Catch phrase	Definition
Symmetry-based reciprocity	'We're buddies'	Symmetrical relationship characteristics prompt similar behavior in both dyadic directions: low degree of contingency in close relationships
Attitudinal reciprocity	'If you're nice, I'll be nice.'	Parties mirror each other's social attitudes: high degree of immediate contingency
Calculated reciprocity	'What have you done for me lately?'	Scorekeeping of given and received benefits: high degree of delayed contingency

involves obligations and punishment of cheaters, to reciprocity merely reflecting social symmetries. The evolutionary perspective simply postulates that the cost of help given be offset by the benefits of help received, which can be achieved in multiple ways, all of which fall under the general rubric of reciprocal altruism. Two decades of research on coalitions, grooming and food-sharing in macaques, chimpanzees and capuchin monkeys has allowed us to gauge the cognitive level of cooperation. Table 5.2 proposes three potential mechanisms, but we cannot exclude the possibility of more.

The cognitively least demanding explanation of reciprocal altruism is that individuals interact based on symmetrical features of dyadic relationships, which cause both parties to behave similarly to each other (de Waal & Luttrell 1988, de Waal 1992a). This mechanism requires no scorekeeping since reciprocation is based on pre-existing features of the relationship, such as kinship, mutual association, and similarities in age or sex. It produces reciprocity without a strong contingency between given and received behavior. A certain mutuality in the exchange of benefits is probably required for the stability of any social relationship, but this can be achieved without careful record keeping. All that is required is an aversion to major, lasting imbalances in incoming and outgoing benefits. We believe that such moderately conditional mutual aid is common in primates, including people, not only among kin but also among close friends and associates. The prediction, then, is that the contingency between given and received benefits decreases with closeness of the relationship. Conversely, the impact of a single act on future exchanges will be greatest in more distant relationships, as found by de Waal (1997a) in chimpanzees. Similar issues have been addressed in close versus distant human relationships by Clark & Mills (1979) and Clark & Grote (2003).

The second proposed mechanism is attitudinal reciprocity in which an individual's willingness to cooperate cofluctuates with the attitude the partner shows or has recently shown (de Waal 2000c). This 'If you're nice, I'll be nice' principle divorces cooperative interactions from the symmetrical state of the relationship, making them contingent upon the partner's immediately preceding behavior. The principle appears to approximate mutualism, but with the difference that both parties do not benefit at the same time. The involvement of memory and scorekeeping seems rather minimal, as the critical variable is general social disposition rather than specific costs and benefits of exchanged behavior.

The third and final mechanism is calculated reciprocity, in which individuals reciprocate on a behavioral one-on-one basis with a significant time interval. This requires memory of previous events, some degree of scorekeeping, partner-specific contingency between favors given and received, and perhaps also punishment of cheaters. The best evidence for this 'What have you done for me lately?' principle of reciprocity in non-human animals concerns, perhaps not coincidentally, our closest relative, the chimpanzee (de Waal 1997a). Whereas active punishment was not demonstrated in chimpanzees, we did find aggressive protest against partners trying to obtain services without previous payment. In addition, the demonstrated principle of exchange entails passive punishment in that it predicts forfeited services for those who fail to provide services themselves.

It is logical to expect that calculated reciprocity, with its higher cognitive requirements, will be found only in a few species whereas cognitively less demanding forms will be more widespread. For any species for which reciprocal exchange is reported, we suggest that the default mechanism is symmetry-based. The burden of proof rests on those who assume more complex mechanisms. With respect to primates, it could be argued that we know enough, based on studies such as those reported here, to consider complex exchange within their capacity. This sounds reasonable, but should never be taken to mean that these animals necessarily rely on these capacities all the time. So as to reduce memory overload, non-human primates, and probably humans as well, can most of the time be expected to follow processes simpler than calculated reciprocity. We therefore recommend that correlational studies on primate behavior always be complemented with sequential ones, in which behavior is tracked over time. Such studies allow a more careful monitoring of exchange, including the establishment of contingency between given and received behavior. Such monitoring is necessary given that seemingly complex levels of reciprocity can easily be explained by a combination of symmetry-based and attitudinal reciprocity.

One factor that has made scholars skeptical about reciprocity among unrelated individuals has been a concern about how such behavior could possibly have evolved in the face of its high initial costs. It has recently been suggested, however, that cooperation could evolve if the initial investment were minimal after which cooperators increased their investment contingent upon increasing confidence in the relationship (Roberts & Sherratt 1998). All of the above forms of reciprocity have been found in relatively low-cost exchanges and may well have provided the evolutionary starting point for more risky and costly forms of reciprocity. Our findings suggest that primates keep a close eye on exchanges, respond immediately if the outcome of cooperation risks being asymmetrical, and react negatively if they receive less than others. These findings are consistent with the view that cooperation is not pursued purely for the probability that it will be rewarded but rather as a social enterprise in which payoffs are compared between individuals and decisions are based on the likelihood of equitable outcomes. The study of proximate mechanisms thus enriches our view, adding a cognitive component that seems more variable than commonly assumed.

Acknowledgments

We are grateful for constructive comments from John Mitani, Peter Kappeler and one anonymous referee. The authors thank the technicians, animal care staff and undergraduate students who helped during their projects. The capuchin work was supported by the National Science Foundation (IBN-0077706) to the first author, and a grant from the National Institutes of Health (RR-00165) to the Yerkes Regional Primate Research Center. The Center is fully accredited by the American Association for Accreditation of Laboratory Animal Care.