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Review

Prosocial primates: selfish and unselfish motivations

Frans B. M. de Waal* and Malini Suchak

Living Links, Yerkes National Primate Research Center and Psychology Department,
Emory University, Atlanta, GA, USA

Non-human primates are marked by well-developed prosocial and cooperative tendencies as reflected in the way they support each other in fights, hunt together, share food and console victims of aggression. The proximate motivation behind such behaviour is not to be confused with the ultimate reasons for its evolution. Even if a behaviour is ultimately self-serving, the motivation behind it may be genuinely unselfish. A sharp distinction needs to be drawn, therefore, between (i) altruistic and cooperative behaviour with knowable benefits to the actor, which may lead actors aware of these benefits to seek them by acting cooperatively or altruistically and (ii) altruistic behaviour that offers the actor no knowable rewards. The latter is the case if return benefits occur too unpredictably, too distantly in time or are of an indirect nature, such as increased inclusive fitness. The second category of behaviour can be explained only by assuming an altruistic impulse, which—as in humans—may be born from empathy with the recipient's need, pain or distress. Empathy, a proximate mechanism for prosocial behaviour that makes one individual share another's emotional state, is biased the way one would predict from evolutionary theories of cooperation (i.e. by kinship, social closeness and reciprocation). There is increasing evidence in non-human primates (and other mammals) for this proximate mechanism as well as for the unselfish, spontaneous nature of the resulting prosocial tendencies. This paper further reviews observational and experimental evidence for the reciprocity mechanisms that underlie cooperation among non-relatives, for inequity aversion as a constraint on cooperation and on the way defection is dealt with.

Keywords: cooperation; prosocial behaviour; non-human primates; reciprocity

1. INTRODUCTION

The common claim that humans are the only truly altruistic species, since all non-human animals are self-interested and only care about return benefits (e.g. Dawkins 1976; Kagan 2000; Fehr & Fischbacher 2003; Silk *et al.* 2005), conflates individual motivation with the possible reason for a behaviour's evolution, i.e. it confuses proximate and ultimate causes. In order to be literally selfishly motivated, an animal needs to be aware how its behaviour will ultimately benefit itself or its immediate kin. For most altruistic behaviour (e.g. behaviour that increases the fitness of the recipient while decreasing the actor's direct fitness), evidence for such awareness is lacking. Therefore, the more parsimonious assumption about the proximate motivation behind altruistic behaviour is that it is either unconcerned with outcomes or simply altruistic.

It may be useful to divide cooperative and altruistic behaviour into two categories: (i) behaviour that benefits others, but also benefits the actor in such a way that the actor can potentially learn about these benefits and (ii) behaviour that benefits others, whereas its potential return benefits remain obscure either because they are not open to direct experience (e.g. increased inclusive fitness) or so unpredictable and/or distant in time that it is unlikely that the actor will associate them with the original behaviour. Whereas the first category may lead to selfishly motivated altruism and cooperation, this cannot hold for the second category. Even though the second category may very well be evolutionarily self-serving (e.g. ultimately increases the actor's fitness through reciprocal altruism or inclusive fitness), such behaviour is best considered *motivationally autonomous* in the same way that sexual motivation is autonomous, i.e. independent of the ultimate goal of reproduction. Thus, from a proximate perspective, aiding behaviour may be genuinely altruistic in that the actor performs it without selfish ends in mind (de Waal 2008).

In humans, the most widely assumed autonomous motivation for altruism is *empathy* (Batson 1991), which has also been proposed for other mammals (de Waal 1996, 2008). Empathy is the capacity to (i) be affected by and share the emotional state of another (e.g. emotional contagion), (ii) assess the reasons for the other's state and/or (iii) identify with the other, adopting his or her perspective (de Waal 2008). Not all altruistic behaviour requires empathy, though. When animals alert others to an outside threat, sacrifice themselves by stinging an intruder or vocally attract

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* Author for correspondence (dewaal@emory.edu).

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others to discovered food, biologists may speak of altruism or cooperation, yet such behaviour is unlikely to be based on empathy with the beneficiary. Indeed, these behaviours are probably inborn responses to certain stimuli performed with little consideration for the exact situation of the recipients. The role of empathy is limited to so-called *directed altruism*, defined as helping or comforting behaviour directed at an individual in need, pain or distress. A detailed discussion of the neural basis of this mechanism is beyond the scope of this paper, but it has been proposed that empathy relies on automatically activated state-matching that produces shared representations and similar emotions (Preston & de Waal 2002; Decety & Jackson 2006). Probably, this mechanism is a mammalian universal, given that part of its assumed neural underpinnings were first discovered in macaques (e.g. mirror neurons; Rizzolatti *et al.* 1996) and that emotional contagion (often considered the starting point of empathy) is increasingly studied in rodents (Langford *et al.* 2006; Chen *et al.* 2009; Grenier & Lüthi 2010). Mirroring mechanisms permit one individual to resonate with the emotional state of another, thus priming this individual for actions appropriate to the other's state, such as when a mother is distressed at hearing the distress calls of her young resulting in comforting behaviour (Panksepp 1996). Oxytocin acts as a hormonal mechanism to facilitate empathy, which in game theory experiments causes humans to become more generous (Zak *et al.* 2007; Barraza & Zak 2009).

This paper introduces terminology related to the proximate side of cooperation and prosocial behaviour and starts out with behaviour of which the pay-offs are knowable to the actors, thus permitting them to strive for these pay-offs. Next, it will address cooperation and altruism that serve others without any direct, knowable benefits to the actor, ranging from so-called *other-regarding preferences* to spontaneous consolation of distressed parties. Finally, we will consider circumstances under which these behavioural mechanisms are inhibited or thwarted, and how animals handle cheaters. By the nature of our own research, this review will be biased towards non-human primates, even though the discussed mechanisms probably apply outside the primate order.

2. POTENTIALLY SELFISH COOPERATION AND CONTINGENT RECIPROCITY

(a) *Learning the need for a partner*

Perhaps the easiest way to learn the benefits of cooperation is when all parties receive benefits immediately following the cooperative act. Such cooperation has been observed in a great variety of taxa, including the mutual grooming of impala, mobbing of predators by European blackbirds and cooperative predation on the embryos of large fish by schools of wrasse in order to overcome paternal defences (Dugatkin 1997).

A typical example is cooperative hunting in which the pay-off quickly follows the effort. Among primates, group hunting and meat-sharing are known of capuchin monkeys (Perry & Rose 1994; Rose 1997) and chimpanzees (Boesch 1994). Among chimpanzees at Taï Forest, in Ivory Coast, meat is almost always shared, and active participants in the hunt have easier access to it than individuals that did not help capture the prey (Boesch 1994). It is important to note, however, that meat-sharing following hunting seems to be dependent on whether or not multiple individuals are required to catch the prey. Thus, in Gombe National Park chimpanzees do not reliably hunt cooperatively, since there is high success for single hunters, and as a result there may be less emphasis on sharing (Stanford 1996). Differences in meat-sharing may therefore be explained by differing levels of cooperation required to obtain the food, so that sharing functions more as reciprocal benefits for participating in the hunt than as altruistic provisioning.

Cooperative hunting can be mimicked in the laboratory by letting individuals work together to gain access to food. The first such experiment was conducted by Crawford (1937), who let two juvenile chimpanzees pull ropes simultaneously to bring in a box with food too heavy for a single individual to bring in. After training, the apes worked together and demonstrated their understanding of the task by recruiting reluctant partners whose motivation had been reduced by food intake prior to the test. They activated these partners by gently slapping their backs.

Crawford's classical mutualism experiment inspired many others, including a test by Melis *et al.* (2006*a*) on the chimpanzees' understanding of their partner's role. Chimpanzees were allowed to choose whether or not to recruit a helper. In the solo condition, the apparatus was set up such that the individual could pull in a drawer with food alone. In the mutualism condition, the individual needed a partner to help them obtain food for both. The chimpanzees were able to open a door to give partners access to the testing apparatus and did so significantly more often when they needed help than when they were able to pull by themselves. Furthermore, after learning that certain individuals were more reliable collaborators than others, when given the option of recruiting different collaborators, chimpanzees preferentially gave access to the best ones. A follow-up study gave subjects the option of recruiting a 'nice' partner (who had collaborated with them in the past) and a 'mean' partner (who had chosen to collaborate with another partner than the subject in the past). After a brief learning period to establish the reputation of the partner as 'nice' or 'mean', the chimpanzees more often recruited the 'nice' partner than they had done before (Melis *et al.* 2008).

Whereas these experiments confirm and expand upon Crawford's (1937) initial chimpanzee study, the same level of understanding was thought to be lacking in non-apes. But this may have been due to the fact that the cooperative skills of monkeys were initially tested with a different, less intuitive paradigm. Instead of pulling a box towards themselves, two capuchin monkeys had to press levers or buttons at exactly the same time to receive food. They did succeed at this task, yet without any indication that they actually understood their partner's contribution

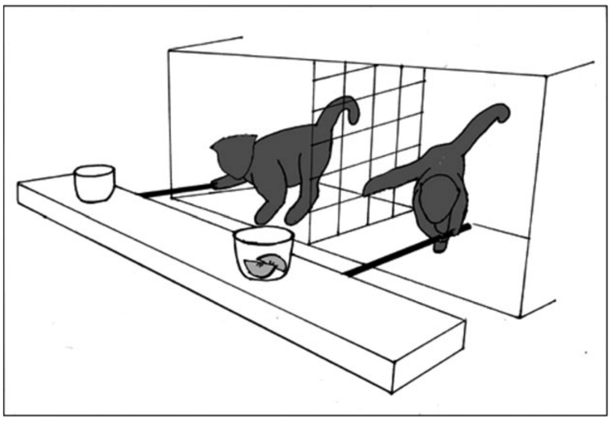

Figure 1. In the cooperative pulling task two capuchin monkeys are situated in adjacent sections of a test chamber, separated by mesh. The apparatus consists of a counterweighted tray with two pull bars, with each monkey having access to one bar. If both cups are filled, success requires mutualistic cooperation, whereas if only one cup is filled (as shown here) cooperation is sustained by sharing through the mesh by the advantaged individual, who pays for the other's labour (de Waal & Berger 2000). Drawing by Sarah Brosnan.

(Chalmeau *et al.* 1997; Visalberghi *et al.* 2000; Brosnan & de Waal 2002). A related experiment with blue jays rewarded two birds for simultaneously pecking at a 'cooperation' key (Clements & Stephens 1995). But since the jays were equally successful regardless of whether or not they could see their partner, and since success seemed to reflect accidental co-occurrence of pecking, it has been argued that their behaviour had little to do with cooperation (Roberts 1997).

In sum, when monkeys (or birds) cannot observe the incremental results of collective action, and need to act in perfect synchrony, they seem to have trouble learning about each other's contributions. They never achieve true cooperation which requires an understanding that their partner is necessary to achieve a goal. But does this mean that such cooperation is beyond their capacity? Cotton-top tamarins were more likely to act in a handle-pulling task when their partner was present than when their partner was absent (Cronin *et al.* 2005). Although partner presence may have served as a conditioned stimulus for action, without the monkeys realizing that their partner was actually helping, there were indications that the monkeys understood they needed their partner's help. For example, individuals would sustain pulling on the apparatus and wait for their partner to pull their handle also before releasing.

When capuchin monkeys were tested with an apparatus similar to Crawford's (1937; figure 1), they showed immediate success. The pulling task has the advantage of both visual and kinesthetic feedback in the course of collective action towards a shared goal, which may be essential to learn about the partner's contribution. When an opaque barrier was placed between both monkeys, their success rate dropped dramatically even though the partner's presence was clear: both monkeys could see each other through a hole at the back of the partition. Knowing that another monkey was there, they nevertheless failed to coordinate. In other tests, the same monkeys would wait for the return of partners who had wandered away before initiating pulling actions. These monkeys gave every indication, therefore, of understanding the need for coordination (Mendres & de Waal 2000).

Outside of the primate order, social carnivores such as hyenas exhibit cooperation and coordination with other individuals in the group. In one experiment, hyenas coordinated their behaviour with a partner to obtain food from a hidden platform (Drea & Carter 2009). They modified their behaviour in response to social stimuli, showing sensitivity to the need for a partner and coordination with other individuals in their group. In fact, experienced hyenas facilitated cooperation with a naive partner by increasing visual monitoring and coordination.

An even higher level of understanding was demonstrated in an experiment in which capuchin monkeys had to perform a closely coordinated sequence to obtain food (Hattori *et al.* 2005). First one partner had to pull a tab, which then allowed the other partner to slide a block. If both actions were done in sequence, both individuals would obtain food. The second individual spent more time looking at its partner when they needed help than when they were able to solve the task by themselves, which suggests visual coordination. As opposed to the lever or button pressing paradigms, where individuals can act independently and succeed by coincidence, in 'communicative cooperation' individuals need to coordinate closely to succeed (reviewed by Noë 2006).

What these mutualism experiments demonstrate is that both monkeys and apes are able to learn the benefits and pay-offs of cooperation and develop a fairly good grasp of the need for and role of a partner, thus achieving true cooperation. The same learning process probably underlies collective action in the field, such as hunting together followed by sharing. Since cooperation produces benefits that are hard or impossible to attain by any individual alone, the resulting behaviour is essentially self-serving even if it benefits others at the same time.

(b) *Contingent reciprocity*

Not all forms of cooperation produce immediate benefits, however. Whenever benefits are exchanged after a time interval, we speak of reciprocal altruism, or reciprocity (Trivers 1971). In the way reciprocity is modelled, it requires certain cognitive abilities (Brosnan *et al.* 2010*b*), which are sometimes assumed too complex for most or all animals (Hammerstein 2003; Stevens & Hauser 2004), whereas in fact reciprocity can be produced by a range of proximate mechanisms, not all of which are cognitively demanding. There is evidence for a variety of these mechanisms in non-human primates (de Waal & Brosnan 2006).

One such mechanism is *attitudinal reciprocity*, according to which individuals mirror the attitudes of their partners over short time intervals (table 1). This type of reciprocity was first experimentally demonstrated in capuchin monkeys using a delayed

Table 1. Various proximate mechanisms that ensure a reciprocal distribution of helping behaviour. These mechanisms are arranged from top to bottom from the least to the most cognitively demanding. Modified from de Waal and Brosnan (2006).

mechanism	catch phrase	definition
generalized reciprocity	‘Thank goodness!’	increased tendency to assist *any* others after having received assistance: no partner-specific contingency
symmetry-based reciprocity	‘We’re buddies’	symmetrical relationship characteristics (e.g. association) prompt similar behaviour in both directions within a dyad without a high degree of contingency
attitudinal reciprocity	‘If you’re nice, I’ll be nice’	Parties mirror each other’s social attitudes with a high degree of short-term contingency
calculated reciprocity	‘What have you done for me lately?’	scorekeeping of given and received favours resulting in partner-specific delayed contingency

exchange task. First, one partner was given pieces of apple for 20 min while her partner sat at the other side of a mesh partition. In the following 20 min, the other was given pieces of carrot. It was found that the amount of food shared through the mesh by the second individual correlated with the amount of food he/she had received from the first. It is important to note that these results do not necessarily indicate that the monkeys were keeping track of food amounts, repaying food with food, even though this was the end result. They may simply have been responding to their partner’s tolerant or intolerant attitude by being, respectively, tolerant or intolerant in return (de Waal 2000). The same monkeys exchanged food preferentially with partners who had just helped them in a cooperative pulling task (figure 1; de Waal & Berger 2000).

Benefits exchanged in close temporal succession allow actors to learn about behavioural contingencies. These contingencies may be used to develop successful cooperation. In other words, they learn that their partner’s behaviour at trial t is contingent upon their own behaviour at trial $t-1$. If they additionally learn to change their own behaviour so as to manipulate their partner’s future behaviour, we speak of *contingent reciprocity.* Whereas capuchin monkeys seem capable of establishing these contingencies over short time intervals, longer delays may interfere with the learning process. Contingent reciprocity is constrained, therefore, by the time delay between exchanges and the memory capacity of the species under study (see Brosnan *et al.* 2010*b*).

Experiments with apes have yielded conflicting results. Chimpanzees failed to change their behaviour in response to their partner’s previous behaviour: they were equally likely to donate food to a partner regardless of whether or not they had previously received food from this partner (Brosnan *et al.* 2009). This study, however, used a set-up that has thus far never produced altruistic giving in chimpanzees (Silk *et al.* 2005; Jensen *et al.* 2006), thus removing any basis to learn the advantages of reciprocity. Another ape study provides a contrast in that two orangutans learned to reciprocally exchange tokens when each had access to tokens that were of value only to the other (Dufour *et al.* 2009). The orangutans’ behaviour was particularly interesting in that one individual seemed to initiate token transfers, but that over time reciprocity emerged and both partners began to alternate transfers to each other. Similarly, when chimpanzees were given the opportunity to exchange other rewarding tokens, they learned to alternate donating rewards to each other (Yamamoto & Tanaka 2009). However, this type of exchange might be limited to a very specific situation facilitated by human experimenters. For example, a comparative study of many ape species found exchanges to be limited to orangutans (Pelé *et al.* 2009), whereas chimpanzees have thus far failed to show reciprocal exchange without human facilitation (Brosnan & Beran 2009; Yamamoto & Tanaka 2009).

Despite these negative experimental results, we should not forget that observations of reciprocity in chimpanzee’s natural behaviour strongly suggest learning over longer time intervals, i.e. the development not just of attitudinal reciprocity, but also *calculated reciprocity* based on scorekeeping of given and received favours (§3; table 1). For example, male chimpanzees in Bossou, Guinea, sometimes raid papaya plantations (a risky endeavour) and share the highly prized fruits specifically with females, which they hypothesized was a strategy for obtaining future copulations (Hockings *et al.* 2007). This is similar to observations of Stanford *et al.* (1994) of male chimpanzees at Gombe National Park hunting especially at times when there are oestrus females around and sharing meat with these females. It should be added, though, that this ‘meat-for-sex’ hypothesis has come under debate. Other researchers have reported no effect of a female’s reproductive state on the frequency of hunting or food-sharing (Mitani & Watts 2001; Gilby 2006; Gilby *et al.* 2006). Rather, it has been suggested that the primary function of meat-sharing is to foster reciprocal relationships among males. Thus, one population of wild chimpanzees showed a strong association between meat-sharing and agonistic support, thus suggesting that meat plays a ‘political’ role (Mitani & Watts 2001).

Throughout the literature one finds similar suggestions of chimpanzees currying favours with others for strategic reasons in situations which may involve planning. Some of these reports are anecdotal, such as a male at a zoo who secured hard to obtain food and shared it generously with potential supporters at around the time that he began to challenge the established alpha male (de Waal 1982) or the wild male chimpanzee who retained alpha status for an extraordinarily long time while selectively rewarding allies through a 'bribery' system (Nishida *et al.* 1992). There is at least one systematic study confirming these reports for a large zoo colony. Chimpanzees selectively groomed supporters the day before they needed their help in an agonistic confrontation that they themselves initiated. The investigators suggest that chimpanzees groom others in anticipation of future recruitment of their assistance (Koyama *et al.* 2006). If so, reciprocity in chimpanzees may involve more than learning the benefits of exchange, but include planning for these benefits and undertaking actions to secure them. Other studies have confirmed future planning in other contexts in a variety of ape species, for example, in collecting and storing tools or weapons that were needed many hours later (Mulcahy & Call 2006; Osvath 2009).

But even if primates learn the benefits of exchange after considerable time intervals, we should keep in mind that spontaneous prosocial tendencies are a pre-condition for such learning (§3). Reciprocity is never purely a product of learning, but rather of a prosocial tendency fortified by learning. In addition, learned reciprocity is not the only kind in existence. The majority of exchanges may not depend on cognitively monitored contingencies, but rather grow out of long-term social bonds. If members of a species preferentially direct favours to their closest associates, the distribution of favours will automatically be reciprocal owing to the symmetrical nature of association (i.e. if individual A associates with B, B also associates with A). Such *symmetry-based reciprocity* obviates the need for scorekeeping, hence should be the default assumption whenever animals show reciprocity in long-term relations—such as between 'mates', 'friends' or 'buddies'—whether it is among vampire bats (Wilkinson 1984) or primates (e.g. Barrett *et al.* 1999; Gomes & Boesch 2009). Matrix correlations between favours given and received across all dyads in a population can be fully explained by this cognitively less demanding mechanism (de Waal & Luttrell 1988). Affiliative ties act as an overarching emotional and neurohormonal mechanism (such as oxytocin; see Soares *et al.* 2010) to produce mutual benefits, as also suggested for humans (Brown & Brown 2006).

3. UNSELFISH COOPERATION AND THE ALTRUISTIC IMPULSE

(a) *Observational data*

Qualitative descriptions of spontaneous assistance among primates are abundant, ranging from bringing a mouthful of water to an incapacitated individual to slowing down travel for injured companions (Boesch 1992; de Waal, 1996, 1997*a*). Similar descriptions exist for both elephants (e.g. Hamilton-Douglas *et al.* 2006; Bates *et al.* 2008) and cetaceans (e.g. Caldwell & Caldwell 1966; Connor & Norris 1982). The help provided can be quite costly. For example, when a female chimpanzee reacts to the screams of her closest associate by defending her against an aggressive male, she takes enormous risks on behalf of the other. Alliances are among the best documented forms of cooperation in primatology, involving many studies and thousands of observations (de Waal 1982, 1992).

Figure 2. Interactions over sharable food are generally tolerant and peaceful, such as here in a cluster of chimpanzees at the Yerkes Field Station. The female in the top-right corner is the possessor of branches with leaves. The female in the lower left corner is tentatively reaching out for the first time. Whether or not she will be able to feed will depend on the possessor's reaction. Photograph by Frans de Waal.

Another well-known form of assistance is food-sharing. Outside the mother–offspring relation or immediate kin-group, sharing is rare in the primate order (Feistner & McGrew 1989), yet common in callitrichid monkeys, capuchin monkeys and chimpanzees. The two main hypotheses to explain this kind of food-sharing are (i) the sharing-under-pressure hypothesis and (ii) the reciprocity hypothesis. According to the sharing-under-pressure hypothesis, individuals share in order to be left alone by potentially aggressive beggars (Blurton-Jones 1987; Stevens & Stephens 2002; Gilby 2006). This hypothesis is contradicted, however, by the fact that the most generously sharing individuals are often fully dominant (de Waal 1989; Nishida *et al.* 1992), aggression is more often shown by food possessors than non-possessors (figure 2; de Waal 1989), food transfers occur even if negative behaviour is prevented by physical separation (Nissen & Crawford 1932; de Waal 1997*a*) and many primates—including wild chimpanzees (Wrangham 1977)—vocally announce the presence of sharable food, thus attracting beggars. In fact, chimpanzee begging behaviour is rarely of a threatening nature as it derives from infant and juvenile expressions of need aimed at the mother (e.g. pouting, whimpering and holding out a hand; van Lawick-Goodall 1968). None of the above observations fits the sharing-under-pressure hypothesis.

The reciprocity hypothesis, on the other hand, predicts that food is part of a service economy, hence exchanged for other favours. It has indeed been shown that adult chimpanzees are more likely to share with individuals who have 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 in the afternoon. Rather than representing

Figure 3. Consolation behaviour is common in humans and apes, but largely absent in monkeys. A juvenile chimpanzee puts an arm around a screaming adult male, who has been defeated in a fight. Photograph by Frans de Waal.

generalized reciprocity (i.e. increased altruism to *any* partner upon receipt of a favour, cf. Rutte & Taborsky 2007, for rats), food-for-grooming exchanges among chimpanzees have been shown to be partner-specific (de Waal 1997*b*). Of all examples of reciprocal altruism in non-human animals, these exchanges come closest to fulfilling the requirements of *calculated reciprocity*, i.e. exchange with the same partner after a significant time delay reflecting memory of previous events and a psychological mechanism described, which Trivers (1971) described as 'gratitude' (Bonnie & de Waal 2004).

The extent to which non-human primates engage in reciprocity is not well recognized in the human literature, however, which often attributes non-human primate altruism and cooperation to kin selection, thus calling human cooperation with non-relatives a 'huge anomaly' in the animal kingdom (Fehr & Fischbacher 2003; Gintis *et al.* 2003; Boyd 2006; see Melis & Semmann 2010, for further discussion of this topic). Even though there is ample evidence that this claim does not hold for captive chimpanzees (de Waal 1982, 1992, 1997*b*; Koyama *et al.* 2006), it has only recently been effectively countered for wild chimpanzees. DNA data from the field demonstrates that most of the cooperative relationships among male chimpanzees are of a reciprocal nature and concern individuals without family ties (Mitani 2006; Langergraber *et al.* 2007). Bonobos may show the same pattern, since females maintain a close cooperative network that allows them to collectively dominate the males (Furuichi 1997; de Waal 1997*c*) despite the fact that females are also the migratory sex, hence largely unrelated within each community (Kano 1992). It seems, then, that both of our closest relatives are marked by frequent cooperation among non-relatives.

A final common form of spontaneous assistance is so-called *consolation*, defined as friendly, reassuring contact directed by an uninvolved bystander at the loser of a previous aggressive incident (figure 3). For example, a third party goes over to the loser and puts an arm around his or her shoulders or provides calming grooming. de Waal & van Roosmalen (1979) based their conclusions on hundreds of post-conflict observations, and a replication by de Waal & Aureli (1996) included an even larger sample in which they sought to test two simple predictions. If third-party contacts indeed serve to alleviate the distress of conflict participants, these contacts should be directed more at recipients of aggression than at aggressors, and more at recipients of intense than mild aggression. Comparing third-party contact rates with baseline levels, the authors found support for both predictions.

Whether consolation produces any direct benefits for the actor remains unclear. In one study, this behaviour was disproportionately directed at conflict participants likely to aggress the actor, hence may have served to forestall aggression (Koski & Sterck 2009). Yet, given the extreme rarity of redirected aggression in chimpanzees (i.e. $<0.5\%$ of agonistic incidents) and that other studies have found consolation to be predominantly provided by friends and relatives, the chief function of this behaviour is probably reassurance of distressed parties (Fraser *et al.* 2008; Romero & de Waal in press). In support of this hypothesis, Fraser *et al.* (2008) found that consolation reduced stress in the victims of aggression.

(b) *Experimental approaches*

The above observational studies show how common helping is, especially among chimpanzees. This behaviour may be partly based on learned contingencies between help given and received (§2), yet since these contingencies are highly probabilistic and occur over intervals lasting days, weeks or longer, it is hard to see how they might explain high-risk helping, such as when Washoe, the world's first language-trained chimpanzee, heard another female scream and hit the water. Fouts & Mills (1997, p. 180) describe how Washoe raced across two electric wires, which normally contained the apes, to reach the victim and waded into the slippery mud to reach the wildly thrashing female and grab one of her flailing arms to pull her to safety. Washoe barely knew this female, having met her only a few hours before.

Even if contingent reciprocity were to play a role, it is good to realize that it is impossible to learn behavioural contingencies without spontaneously engaging in the behaviour in the first place. We must therefore assume an impulse that propels individuals to defend, share with or rescue others. In the case of Washoe, this impulse needed to be strong enough to overcome her species' hydrophobia (chimpanzees cannot swim). Empathy has the potential to provide such an impulse as it produces a stake in the recipient's well-being through shared representations. In the words of Hoffman (1981, p. 133), empathy has the unique property of 'transforming another person's misfortune into one's own feeling of distress'. Inasmuch as both humans and other animals are most empathic towards past cooperators and socially close individuals, empathy biases altruistic behaviour precisely as predicted by theories of kin selection and reciprocal altruism (Preston & de Waal 2002; de Waal 2008).

For both practical and ethical reasons, however, there is a scarcity of experiments on emotionally charged situations that could trigger costly altruism. This is not only true for animal altruism, but equally so for human altruism. Instead, experiments concern low-cost altruism, sometimes called ‘other-regarding preferences’. A typical paradigm is to offer one member of a pair the option to either secure food for itself by manipulating part A of an apparatus or secure food for both itself and the other by manipulating part B of the same apparatus. In the first such experiment, Colman *et al.* (1969) found 1 of 4 tested macaques to be consistently other-regarding. When replications failed to find the same tendency in chimpanzees, however, this led to the suggestion that other-regarding preferences may be uniquely human (Silk *et al.* 2005; Jensen *et al.* 2006). It is impossible to prove the null hypothesis, however, and recent studies with different methodologies have yielded results more in line with expectations based on naturalistic primate behaviour.

In one study, investigators tried to rule out reciprocity by having apes interact with humans they barely knew, and on whom they did not depend for food or other favours (Warneken *et al.* 2007). The investigators also ruled out the role of immediate return benefits by manipulating the availability of rewards. In this experiment, chimpanzees spontaneously assisted persons regardless of whether or not this yielded rewards and were also willing to open a door for conspecifics so that these could reach a room with food. One would think that rewards for the actor, even if not strictly necessary, at least stimulated helping actions, but in fact rewards proved irrelevant. The decision to help did not seem based on a cost/benefit calculation, therefore, consistent with predictions from empathy-induced altruism.

Spontaneous helping has also been experimentally demonstrated in both capuchin monkeys (de Waal *et al.* 2008; Lakshminarayanan & Santos 2008) and marmosets (Burkart *et al.* 2007; although not in closely related cotton-top tamarins, Cronin *et al.* 2009; see also Jaeggi *et al.* 2010). In our study, two capuchin monkeys were placed side by side separated by mesh. One of them needed to barter with us with small plastic tokens, which we would first give to a monkey, after which we would hold out an open hand to let them return the token for a tidbit (figure 4). The critical test came when we offered a choice between two differently coloured tokens with different meaning: one token was ‘selfish’, the other ‘prosocial’. If the bartering monkey picked the selfish token, it received a small piece of apple for returning it, but its partner remained unrewarded. The prosocial token, on the other hand, rewarded both monkeys with apple at the same time. Since the monkey who did the bartering was rewarded either way, the only difference was in what the partner received.

Monkeys preferentially bartered with the prosocial token. This preference could not be explained by fear of future punishment because dominant partners proved to be more prosocial than subordinate ones. Familiarity biased the choices in the predicted direction: the stronger the social tie between two monkeys, as measured by how much time they associated in the group, the more they favoured the prosocial token. Moreover, choices were reflected in accompanying behaviour, with greater orientation towards the partner during prosocial choices (de Waal *et al.* 2008).

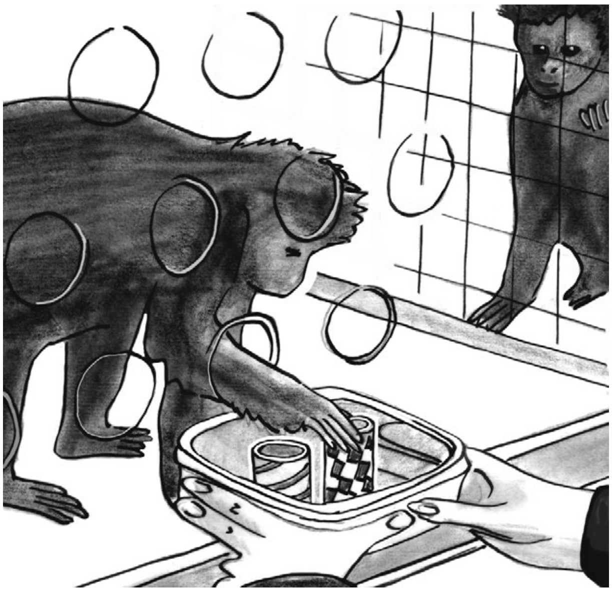

Figure 4. One capuchin monkey reaches through an armhole to choose between differently marked pieces of pipe while her partner looks on. The pipe pieces can be exchanged for food. One token feeds both monkeys; the other feeds only the chooser. Capuchins typically prefer the ‘prosocial’ token (de Waal *et al.* 2008). Drawing from a video still by Frans de Waal.

In short, there is mounting evidence from both naturalistic observations and experiments that primates care about each other’s welfare and follow altruistic impulses in some contexts, probably based on empathy, which in both humans and other animals increases with familiarity. The empathy mechanism automatically produces a stake in the other’s welfare, i.e. the behaviour comes with an intrinsic reward, known in the human literature as the ‘warm-glow’ effect. Actions that improve another’s condition come with pleasant feelings (Andreoni 1989), so that humans report feeling good when they do good and show activation of reward-related brain areas (Harbaugh *et al.* 2007). It will be important to determine if the same self-reward system extends to other primates.

4. CONSTRAINTS ON COOPERATION AND ALTRUISM

(a) *Inequity aversion and tolerance*

How skewed can a pay-off distribution get before it begins to undermine cooperation? Fehr & Schmidt (1999) have argued that the well-known human *aversion to disadvantageous inequity* relates to the need to maintain cooperation. Similarly, cooperative animals may be guided by a set of expectations about pay-off distribution. Thus, de Waal (1996, 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'. Note that the expectations are not specified: they are species-typical. Some primates are so hierarchical that subordinate individuals cannot expect anything, whereas in other species dominant individuals are prepared to share and, correspondingly, the species has evolved a repertoire of begging signals to extract food from them. These animals negotiate their share and may protest if it is too small.

In one experiment, capuchin monkeys were paired to perform a simple task 25 times in a row, alternating between both of them. Food rewards varied from low value (a cucumber piece) to high value (a grape). In equity tests, both the subject and its partner did the same work for the same low-value food. In inequity tests, the subject received low-value rewards, whereas its partner received high-value rewards for the same effort. It turned out that the capuchins were far less willing to complete the task or accept the reward if their partner received a better deal. Subjects receiving the low-value reward in inequity tests showed both passive negative reactions (i.e. refusal to perform or refusing the reward) and active negative reactions (i.e. throwing out the token or the reward; Brosnan & de Waal 2003).

It could be argued that the mere presence of high-value food is what triggers these reactions (e.g. a contrast effect; Roma *et al.* 2006; Silberberg *et al.* 2009). In other words, subjects are holding out for something better. The first argument against this alternative is that if food is merely made available, without any task, there is no sign of inequity aversion even in the same monkeys as those of the original study (e.g. Dubreuil *et al.* 2006; Dindo & de Waal, 2007; Fontenot *et al.* 2007). The second counter-argument is that showing grapes before every equity trial, in which both monkeys receive cucumber, has no effect: the monkeys do not work any less for cucumber after having seen grapes. The grapes need to serve as rewards for the partner to affect a monkey working for cucumber, which implies that the social aspect of the task plays a critical role (van Wolkenten *et al.* 2007). Other task-oriented studies have found signs of inequity aversion in chimpanzees (Brosnan *et al.* 2005, 2010*a*), capuchin monkeys (Fletcher 2008; Takimoto *et al.* 2010) and domestic dogs (Range *et al.* 2008), whereas one study yielded mixed results, with an apparent inequity response in bonobos but not in other apes (Bräuer *et al.* 2009). A study on cotton-top tamarins, finally, found behavioural changes over time that might reflect inequity aversion (Neiworth *et al.* 2009).

Given the above, it is not surprising that unequal outcomes reduce cooperative tendencies. For example, when capuchin monkeys pull cooperatively to obtain unequally distributed food, the most successful pairs are those that alternate positions so that both parties share in the best rewards. In contrast, pairs tend to fail if one individual tries to monopolize the best food (Brosnan *et al.* 2006). Similarly, when inequity was introduced in the aforementioned prosocial versus selfish choice paradigm with capuchin monkeys, their prosociality disappeared. In other words, when prosocial choices produced better food for the partner than the chooser herself, prosocial tendencies fell to chance levels (de Waal *et al.* 2008). However, in a similar study also with capuchin monkeys, unequal rewards led to higher prosocial behaviour (although this could have resulted from the training procedures, rather than an understanding of the task; Lakshminarayanan & Santos 2008).

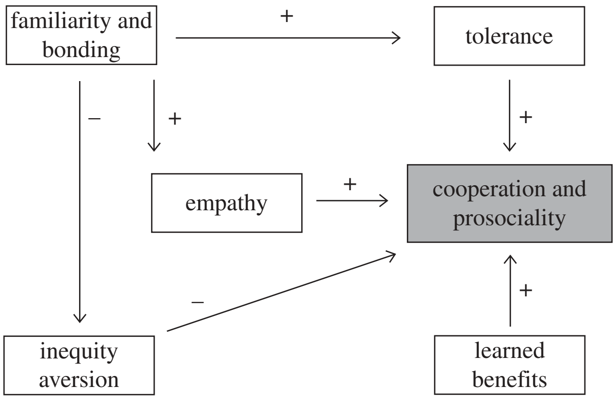

Figure 5. Cooperative and prosocial behaviour is enhanced by familiarity and bonding between parties both via the empathy mechanism, thought to regulate the altruistic impulse and by increased social tolerance, which ensures rewards for the subordinate party. Familiarity and bonding also reduce sensitivity to inequity, while sensitivity undermines cooperative and prosocial behaviour if certain individuals gain conspicuously more than others. Finally, whenever cooperation produces knowable return benefits for the actor, there is the potential of learned reciprocity in which individuals cooperate in order to secure future return favours.

Outcome calculations are very much part of the decision to cooperate: tolerance promotes cooperation and competition undermines it. A real-life example is group hunting (i.e. several individuals cooperate, but only one of them obtains the prize), which is common in both wild chimpanzees and capuchin monkeys (Boesch 1994; Perry & Rose 1994). Since group hunting is sustainable only if the prey is shared at the end, Rose (1997) has proposed a convergent evolution of food-sharing in these two distant primates. The way tolerance affects cooperation has been tested in the laboratory by comparing the effect of clumped versus dispersed food rewards. The more competitive the dominant party in a pair of cooperating capuchin monkeys, the less cooperation will take place when food is monopolizable, whereas cooperation is unaffected under the dispersed condition (de Waal & Davis 2003). When chimpanzees and bonobos face a similar task, both species cooperate equally for a dispersed food source, but with a clumped source the bonobos are more successful because of their more effective conflict resolution techniques (de Waal 1987) resulting in increased tolerance around a clumped reward (Hare *et al.* 2007). Another illustration of the same principle is that both capuchins and chimpanzees cooperate most readily with partners with whom they are socially close, hence enjoy the greatest food tolerance (figure 5; de Waal & Davis 2003; Melis *et al.* 2006*b*).

(b) *Free loaders*

Individuals who give less than they receive need to be discouraged if cooperation is to survive (Trivers 1971). Active punishment may be rare in non-human primates, yet in the food-for-grooming study of de Waal (1997*b*), food possessors showed increased aggressive resistance to approaching beggars who had failed to groom them. They were more than three times as likely to threaten such beggars than those with whom they had previously groomed. This is not punishment *per se*, but an aggressive reaction to those who try to get without giving, which psychologically speaking may not be far removed.

Chimpanzees also reciprocate in the negative sense: retribution is the flip side of reciprocity. Data on several thousand aggressive interventions show a healthy correlation between how often individual A intervenes against B and how often B intervenes against A. As a result, every choice has multiple consequences, both positive and negative. The supported party in a conflict may repay the favour, whereas the slighted party may try to get even in what has been called a *revenge system* (de Waal & Luttrell 1988; see also Jensen 2010).

By far the most common tool to enforce cooperation, however, is partner choice. Unsatisfactory relationships can be abandoned and replaced by ones with greater benefits. With each individual shopping for the best partners and selling its own services, the framework becomes one of supply and demand, as formalized in Noë & Hammerstein's (1994) *Biological market theory*. This theory applies whenever trading partners can choose with whom to deal. Market mechanisms are an effective way of sidelining profiteers.

It takes much energy, though, to keep a watchful eye on cheaters and the flow of favours. This is why both humans and other animals rely on simpler forms of reciprocity much of the time. Instead of keeping track of each and every instant of positive or negative behaviour, events get pooled into the larger framework of a social bond with mutually positive attitudes, resulting in symmetry-based reciprocity (§2). When it comes to distant relations, on the other hand, we tend to keep mental records and react more strongly to inequities. In humans, the reciprocity dynamics of close relationships are radically different from those between distant partners (Clark & Grote 2003). The better two individuals know each other, the longer the time frame over which they seem to evaluate their relationships so that momentary imbalances matter less. This may also apply to chimpanzees, in which familiarity appears to reduce sensitivity to inequity (Brosnan *et al.* 2005) and in which one-on-one exchanges of favours are less pronounced the closer the social relationship between both parties (de Waal 1997*b*).

5. CONCLUSION

Prosocial behaviour can be categorized based on whether or not the actor knows or can potentially learn about its long-term consequences. There is considerable support from both field observations and laboratory experiments that non-human primates exhibit prosocial behaviour both when they know its benefits, such as when they help each other reach a common goal, and when there is little chance for them to have this knowledge. In the latter case, they must be motivated by an altruistic impulse perhaps similar to the main mechanism thought to underlie human altruism: empathy with the distress, pain or need of another. While considerable attention has been given to the ultimate explanations for altruistic behaviour, this paper reviewed proximate mechanisms and concluded that since ultimate reasons rarely figure at the proximate level, primate altruism must occur in many cases without any selfish motivations. On the other hand, inequity aversion, intolerance and negative reactions to cheating constitute constraints on prosocial behaviour. Together, this array of mechanisms provides an understanding of the proximate decision-making regarding prosocial behaviour.

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