

Jessica C. Flack and Frans B.M. de Waal

'Any Animal Whatever'

Darwinian Building Blocks of Morality in Monkeys and Apes

To what degree has biology influenced and shaped the development of moral systems? One way to determine the extent to which human moral systems might be the product of natural selection is to explore behaviour in other species that is analogous and perhaps homologous to our own. Many non-human primates, for example, have similar methods to humans for resolving, managing, and preventing conflicts of interests within their groups. Such methods, which include reciprocity and food sharing, reconciliation, consolation, conflict intervention, and mediation, are the very building blocks of moral systems in that they are based on and facilitate cohesion among individuals and reflect a concerted effort by community members to find shared solutions to social conflict. Furthermore, these methods of resource distribution and conflict resolution often require or make use of capacities for empathy, sympathy, and sometimes even community concern. Non-human primates in societies in which such mechanisms are present may not be exactly moral beings, but they do show signs of a sense of social regularity that — just like the norms and rules underlying human moral conduct — promotes a mutually satisfactory modus vivendi.

Introduction

Any animal whatever, endowed with well-marked social instincts, the parental and filial affections being here included, would inevitably acquire a moral sense or conscience, as soon as its intellectual powers had become as well developed, or nearly as well developed, as in man.

Charles Darwin, *The Descent of Man* (1982 [1871], pp. 71–2)

Thomas Huxley, in his famous lecture, *Evolution and Ethics* (Huxley, 1894), advanced a view of human nature that has since dominated debate about the origins of morality. Huxley believed that human nature is essentially evil — a product of a nasty and unsympathetic natural world. Morality, he argued, is a human invention explicitly devised to control and combat selfish and competitive tendencies generated by the evolutionary process. By depicting morality in this way, Huxley was advocating that the search for morality's origins be de-coupled from evolution and conducted outside of biology.

Proponents of Huxley's dualistic view of nature and morality abound today. Among them is the evolutionary biologist, Richard Dawkins, who in 1976 (p. 3) wrote

Be warned that if you wish, as I do, to build a society in which individuals cooperate generously and unselfishly towards a common good, you can expect little help from biological nature. Let us try to teach generosity and altruism, because we are born selfish.

Another well-known evolutionary biologist, George C. Williams (1988, p. 438), also reaffirmed, with minor variation, Huxley's position when he stated, 'I account for morality as an accidental capability produced, in its boundless stupidity, by a biological process that is normally opposed to the expression of such a capability'. And recently, the philosopher Daniel Dennett (1995, p. 481), although admitting that it is conceivable that perhaps the great apes, whales, and dolphins possess some of the requisite social cognition on which morality depends, wrote

My pessimistic hunch is that the main reason we have not ruled out dolphins and whales as moralists of the deep is that they are so hard to study in the wild. Most of the evidence about chimpanzees — some of it self-censored by researchers for years — is that they are true denizens of Hobbes' state of nature, much more nasty and brutish than any would like to believe.

But if, as Dawkins suggests, the origins of morality — of the human sense of right and wrong used by society to promote pro-social behaviour — are not biological, then what is the source of strength that enabled humanity to escape from its own nature and implement moral systems? And from where did the desire to do so come? If, as Williams suggests, morality is an accidental product of natural selection, then why has such a 'costly' mistake not been corrected or eliminated by the very process that inadvertently created it? Our inability to answer these questions about the origins and consequences of moral systems is an indication that perhaps we need to broaden the scope of our search. After all, the degree to which the tendency to develop and enforce moral systems is universal across cultures (Midgley, 1991; Silberbauer, 1991), suggests that moral systems, contrary to Huxley's beliefs, do have biological origins and are an integral part of human nature.

Morality indeed may be an invention of sorts, but one that in all likelihood arose during the course of evolution and was only refined in its expression and content by various cultures. If, as we believe, morality arose from biological origins, then we should expect at a minimum that elements of it are present in other social species. And indeed, the evidence we will present in this paper suggests that chimpanzees and other social animals are not the 'true denizens of Hobbes' state of nature' they are surmised to be by Dennett. It may well be that chimpanzees are not moral creatures, but this does not mean that they do not have elements of moral systems in their societies. If we are to understand how our moral systems evolved, we must be open to the idea that the sets of rules that govern how non-human animals behave in their social groups provide clues to how morality arose during the course of evolution. These simple rules, which emerge out of these animals' social interactions, create an element of order that makes living together a possibility, and in a liberal sense, reflect elements of rudimentary moral systems. The order that these sets of rules create is vital to maintaining the stability of social systems and probably is the reason why human morality (whether or not an evolutionary accident) has not been eliminated by natural selection (Kummer, 1979). Garret Hardin (1983, p. 412) captured the essence

of this argument in a statement about the importance of justice — ‘The first goal of justice is to create a *modus vivendi* so that life can go on, not only in the next few minutes, but also indefinitely into the future.’

Had Huxley acknowledged that the origins of morality lay in biology but argued against searching within biology for the *specifics* of our moral systems, his case might have been more persuasive today. Such an argument would have at least fit the contemporary framework for addressing questions about why we are the way we are, which in the case of morality has been explored intensely (Nitecki and Nitecki, 1993, and contributions therein). Indeed, the only pertinent question seems to us: *To what degree* has biology influenced and shaped the development of moral systems? One way to determine the extent to which human morality might be the product of natural selection is to explore behaviour in other species that is analogous (similar traits that arose by convergent evolution due to the presence of similar selection pressures or evolutionary conditions), and perhaps homologous (traits that evolved in a common ancestor and that remain present in related species due to common phylogenetic descent) to our own.

Many non-human primates, for example, seem to have similar methods to humans for resolving, managing, and preventing conflicts of interests within their groups. Such methods, which include reciprocity and food sharing, reconciliation, consolation, conflict intervention, and mediation, are the very building blocks of moral systems in that their existence indicates, as Mary Midgley (1991, p. 12) wrote, ‘a willingness and a capacity to look for shared solutions’ to conflicts (see also Boehm, 2000). Furthermore, unlike strict dominance hierarchies, which may be an alternative to moral systems for organizing society, advanced methods of resource distribution and conflict resolution seem to require or make use of traits such as the capacity for empathy, sympathy, and sometimes even community concern. Conflict resolution that reflects concern for and possibly understanding of a predicament in which a fellow group member finds himself or herself provides for society the raw material out of which moral systems can be constructed.

Non-human primates in such societies may not be exactly moral beings, but they do show indications of a sense of social regularity that parallels the rules and regulations of human moral conduct (de Waal, 1996a; 1996b, chapter 3). In addition to conflict resolution, other key components or ‘prerequisites’ of morality recognizable in social animals are reciprocity, empathy, sympathy, and community concern. These components, which also include a sense of justice, and perhaps even the internalization of social norms, are fundamental to moral systems because they help generate connections among individuals within human and animal societies despite the conflicts of interests that inevitably arise. By generating or reinforcing connections among individuals, these mechanisms facilitate co-operative social interaction because they require individuals to make ‘commitments’ to behave in ways that later may prove contrary to independent individual interests (used throughout this paper in reference to those interests that are truly independent as well as in reference to those interests for which pursuit requires engaging in competition) that when pursued can jeopardize collective or shared interests (Frank, 1988; 1992).

Although many philosophers and biologists are sceptical that evolution can produce components of moral systems such as the capacity for sympathy and empathy or even the capacity for non-kin based co-operation that require the suspension of short

term, independent interests, there also exists a tradition going back to Petr Kropotkin (1902) and, more recently, Robert Trivers (1971), in which the view has been that animals assist each other precisely because by doing so they achieve long term, collective benefits of greater value than the short term benefits derived from straightforward competition. Kropotkin specifically adhered to a view in which organisms struggle not necessarily against each other, but collectively against their environments. He strongly objected to Huxley's (1888) depiction of life as a 'continuous free fight'. Although some of Kropotkin's rationale was seriously flawed, the basic tenet of his ideas was on the mark. Almost seventy years later, in an article entitled 'The Evolution of Reciprocal Altruism', Trivers refined the concepts Kropotkin advanced and explained how co-operation and, more importantly, a system of reciprocity (called 'reciprocal altruism' by Trivers) could have evolved. Unlike simultaneous co-operation or mutualism, reciprocal altruism involves exchanged acts that, while beneficial to the recipient, are costly to the performer. This cost, which is generated because there is a time lag between giving and receiving, is eliminated as soon as a favour of equal value is returned to the performer (see Axelrod and Hamilton, 1981; Rothstein and Pierotti, 1988; Taylor and McGuire, 1988).

According to Richard Alexander (1987), reciprocity is essential to the development of moral systems. Systems of indirect reciprocity — a type of reciprocity that is dependent on status and reputation because performers of beneficent acts receive compensation for those acts from third parties rather than necessarily from the original receiver — require memory, consistency across time, and most importantly, a sense of social regularity or consensual sense of right and wrong (Alexander, 1987, p. 95). It is not yet clear whether systems of indirect reciprocity exist in non-human primate social groups, but certainly there is evidence from studies on food-sharing, grooming, and conflict intervention that suggest the existence of reciprocal systems and, at least among chimpanzees, a sense of social regularity (e.g. Cheney and Seyfarth, 1986; de Waal, 1991; 1996a; 1996b, chapter 3; 1997a; 1997b; Silk, 1992).

Food Sharing, Reciprocal Exchange, and Behavioural Expectations in Primates

Food sharing is known in chimpanzees (Nissen and Crawford, 1932; Kortlandt, 1962; Goodall, 1963; Nishida, 1970; Teleki, 1973; Boesch and Boesch, 1989; de Waal, 1989b; 1997a; Kuroda *et al.*, 1996), bonobos (Kano, 1980; Kuroda, 1984; Hohmann and Fruth, 1993; de Waal, 1992b), siamangs (Fox, 1984), orangutans (Edwards and Snowdon, 1980), and capuchin monkeys (Perry and Rose, 1994; Fragaszy, Feuerstein, and Mitra, 1997; de Waal, 1997b; Rose 1997). It is an alternative method to social dominance and direct competition by which adult members of a social group distribute resources among themselves. Most food sharing requires fine-tuned communication about intentions and desires in order to facilitate inter-individual food transfers. The food transfers typically observed are passive, involving selective relinquishment of plant and animal matter more frequently than active giving (de Waal, 1989b). Three non-exclusive hypotheses have been forwarded to explain the proximate reasons why one individual would voluntarily allow another to take food.

Richard Wrangham (1975) suggested that food possessors share with other group members in order to deter harassment and reduce the possibility that, as possessors,

they will become the recipients of aggression. This idea, known as the ‘sharing-under-pressure’ hypothesis, resembles Nicholas Blurton-Jones’ (1987) ‘tolerated-theft’ model, according to which it is more common for possessors to let food be taken from them than for them to actually give it away. Blurton-Jones reasoned that possessors tolerate theft in order to avoid potentially risky fights.

The ‘sharing-to-enhance-status hypothesis’ has been used by Adriaan Kortlandt (1972) and James Moore (1984) to explain male chimpanzee food sharing and the displays that frequently accompany the treatment of objects in the environment such as captured prey. Both the act of sharing and the displays — for example, branch shaking — draw attention to the food possessor in a way that may raise his or her status in the group. Illustrative examples of this strategy can be found in Toshisada Nishida *et al.*’s (1992) description of a chimpanzee alpha male in the wild who kept his position through ‘bribery’ (i.e. selective food distribution to potential allies), and in de Waal’s (1982) account of a male contender for the alpha position in a zoo colony, who appeared to gain in popularity by acquiring and distributing food to the group to which the apes normally had no access.

A similar hypothesis was developed for human food distribution by Kristen Hawkes (1990), an anthropologist, who suggested that men who provide food to many individuals are ‘showing off’. Showing off in this manner, according to Hawkes, signals hunting prowess and generosity, two characteristics that may be attractive to potential mates or potential political allies.

A third hypothesis — the reciprocity hypothesis — proposes that food sharing is part of a system of mutual obligations that can involve material exchange, the exchange of social favours such as grooming and agonistic support, or some combination of the two. For example, de Waal (1982) found that subordinate adult male chimpanzees groom dominant males in return for an undisturbed mating session. Suehisa Kuroda (1984) and de Waal (1987) found indications that adult male bonobos exchange food with adolescent females in return for sex. The reciprocity hypothesis thus differs significantly from the sharing-under-pressure hypothesis because it addresses possessors and ‘beggars’ as potential long-term co-operators rather than merely as present competitors who use sharing to appease one another. It differs from the ‘sharing-to-enhance-status’ hypothesis because it emphasizes the co-operative nature of the relationship between possessors and beggars and, consequently, emphasizes how sharing benefits both the possessor and the beggar rather than just the possessor. One advantage of the ‘sharing-to-enhance-status’ hypothesis is, however, that it provides a testable proximate account of what social factors might motivate possessors to initially share with beggars, in that it suggests that possessors share because by doing so they increase their social status in the group. In fact, the ‘sharing-to-enhance-status’ hypothesis, although a partial explanation of sharing, is useful if considered in conjunction with the reciprocity hypothesis because it provides a proximate motivational explanation for why possessors allow some of their food to be taken by others. Consequently, this hypothesis is not necessarily in conflict with the reciprocity hypothesis, and may be an extension of it. Furthermore, the ‘sharing-to-enhance-status’ hypothesis, like the reciprocity hypothesis, involves the exchange of favours between individuals using apparently equivalent, although unequal, currencies: For example, a form of reciprocal exchange may emerge if A shares food with B,

which makes A more popular with B resulting — as suggested by Hawkes — in agonistic support or matings.

De Waal (1989b; 1997a; 1997b) examined whether food itself is exchanged reciprocally over time or is shared in return for some social favour by investigating the food sharing tendencies of brown capuchin monkeys and chimpanzees. Results of the capuchin study indicated that female brown capuchins share food reciprocally. The methodology used in this study differed substantially from the chimpanzee study described next. The primary difference was that the capuchin's food sharing tendencies were examined in a dyadic context rather than in the presence of the entire group as in the chimpanzee study. As shown in Figure 1, adult capuchins were separated into pairs and placed into a test chamber divided into two sections by a mesh partition. One capuchin was allowed continuous access to a bucket of attractive food. The individual with access to the food was free to monopolize all of it or could move close to the mesh and share actively or passively by allowing his counterpart access to pieces he had dropped. The situation was then reversed so that the second individual had access to the attractive food (which was of a new type) and the first did not. The rate of transfer between pairs of adult female capuchins was found to be reciprocal while the rate of transfer between pairs of adult males was not. Males, however, were less discriminating than females in terms of with whom they shared, and more generous in the amount of food they shared. Although this study examined food-sharing in capuchins in an artificial environment created by the experimenters, the results were not anomalous — food sharing among unrelated adults has been observed both among capuchins in a colony at the Yerkes Regional Primate Centre as well as among wild capuchins (Perry and Rose, 1994; Rose, 1997).

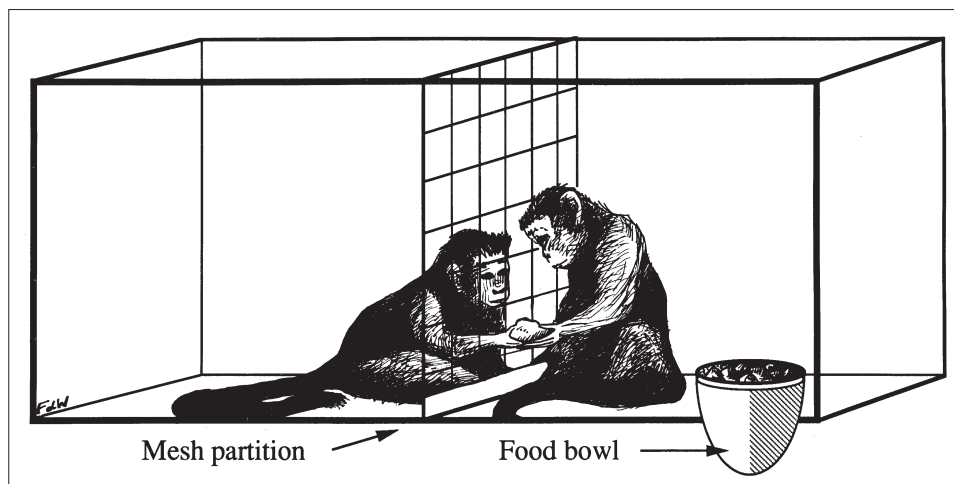


Figure 1

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

In order to study how chimpanzees share food in a social context, a situation was created in which a monopolizable food source was available to individuals in the social group. To accomplish this, a captive group of chimpanzees at the Field Station of the Yerkes Regional Primate Research Centre was provided with branches and leaves that were tightly bundled together so that the possibility existed for some group members to keep all of the food for themselves. Based on an analysis of nearly 7,000 recorded interactions over food, de Waal found that food exchanges between nine adult group members were quite balanced per dyad so that, on average, individuals A and B shared the same amount with each other. If individual A, however, shared a particular day with individual B, this did not necessarily result in B being more likely to share with A the following day. Grooming, on the other hand, did affect the likelihood to share when sharing and grooming occurred on the same day. For example, A was less likely to share with B if A had also groomed B the same day, but A was more likely to share with B if it had been B who had groomed A earlier that day. Other data indicating that food possessors actively resisted approaches by individuals who had not previously groomed them bolstered this result. Lastly, individuals who were reluctant to share their food had a greater chance of encountering aggression when they themselves approached a food possessor.

Although the chimpanzee food-sharing study confirmed one part of the prediction of Wrangham's and Blurton-Jones' hypotheses that there should be a negative correlation between rate of food distribution and frequency of received aggression, de Waal (1989b; 1996b, pp. 152–3) considers his results inconsistent with the tolerated theft model. He found that most aggression is directed not against the possessors of food, as the tolerated theft model predicts, but against beggars for food. In fact, even the lowest-ranking adult possessors are able to hold on to food unchallenged due to the 'respect of possession' first noted, with astonishment, by Goodall (1971, chapter 16), who wondered why the alpha male of her community failed to claim food possessed by others, and actually had to beg for it (Goodall, however, noted that the apparent respect for possession she observed among chimpanzees only applied to animal matter and not to bananas or other kinds of vegetable matter. This led her to suggest another somewhat different, although not mutually exclusive, explanation that focused more on the motivational state of the possessor and the corresponding response to this by the beggars). Respect of possession exists also in other primates, and was experimentally investigated by Sigg and Falett (1985), Kummer and Cords (1991), and discussed by Kummer (1991).

In fact, in de Waal's (1989) study the observed negative correlation between an individual's food distribution rate and the probability of aggression received concerned this individual as an *approacher* rather than as food possessor. This suggests either that food distributors respond to stingy individuals by sharing less with them than with others *or* that individuals, who for whatever reason, are more likely to be aggressively rebuffed when approaching food possessors, in turn become more reluctant themselves when they possess food to share with others.

Thus, the food sharing data are most in line with the reciprocity hypothesis. It is conceivable, though, that receipt of a favour (whether it be a service such as grooming or an object, such as food) positively influences an individual's social attitude so that this individual is willing to share indiscriminately with everyone else in its group (Hemelrijk, 1994). This so-called 'good mood' hypothesis, however, is not supported

by the data (de Waal, 1997a), which show that if A receives grooming from B, A is only more likely to share with B but not with others in the group. The exchange between grooming and food is, therefore, partner-specific.

These studies on capuchins and chimpanzees address whether reciprocity is calculated or a by-product of frequent association and symmetrical relationships (de Waal and Luttrell, 1988; de Waal, 1997a). Calculated reciprocity is based on the capacity to keep mental note of favours given and received. It is a more sophisticated and cognitively complex (and consequently less easily accepted) form of reciprocity than symmetry-based reciprocity, which occurs when individuals preferentially direct favours to close associates. Since association is a symmetrical relationship characteristic (if A associates often with B, B does so often with A), the distribution of favours automatically becomes reciprocal (for a more in-depth discussion of what constitutes symmetry-based reciprocity, see de Waal, 1996b, p. 157). Although important, such symmetry-based reciprocity is not as cognitively demanding as calculated reciprocity, which was shown above to occur in chimpanzees and possibly female capuchins.

Calculated reciprocity — unlike symmetry-based reciprocity — raises interesting questions about the nature of expectations. The possibility that chimpanzees withhold favours from ungenerous individuals during future interactions, and are less resistant to the approaches of individuals who previously groomed them (de Waal, 1997a) suggests they have expectations about how they themselves and others should behave in certain contexts.

Other evidence to suggest that some primates have expectations about how others should behave comes from studies of patterns of conflict intervention. Chimpanzees and some species of macaques exhibit what appears to be calculated reciprocity in beneficial interventions, or the interference by a third party in an ongoing conflict in support of one of the two conflict opponents (de Waal and Luttrell, 1988; Silk, 1992). Thus, if A intervenes in favour of B, B is more likely to intervene in favour of A. In de Waal's and Luttrell's study, chimpanzees, but not macaques, also exhibited reciprocity in harmful interventions, suggesting the existence of a so-called 'revenge system'. In other words, in the chimpanzee group under study there existed a significant correlation between interventions given and received so that if A intervened against B, B was more likely to intervene against A in the future. This retaliatory pattern was not found in stump-tail and rhesus macaque groups. Silk (1992), however, found evidence for a revenge system among males in bonnet macaque society in that the males in her study group appeared to monitor both the amount of aggression that they received from and directed at other males. Although Silk's data and numerous anecdotes suggest that macaques do have the capacity to engage in revenge, it is likely that revenge of this sort is not commonplace due to the greater risks in a macaque society (compared to a chimpanzee society) associated with directing aggression at dominants.

Revenge of another sort — indirect revenge — does, on the other hand, appear to be relatively common in at least one macaque species. Indirect revenge occurs when recipients of aggression redirect their aggression at the uninvolved juvenile or younger kin of their opponents. In this way, these often low ranking macaques are still able to 'punish' their attackers but are able to do so without much cost to themselves (Aureli, Cozzolino, Cordischi and Scucchi, 1992). For example, Aureli and colleagues found that Japanese macaque recipients of aggression were significantly more likely to attack the kin of their former opponents within one hour after the

original conflict had occurred than if no conflict had occurred at all. One could argue, as the authors pointed out, that it is possible that this increase in aggression towards an opponent's kin after a conflict may be due to a general rather than selective aggressive tendency that is triggered by fighting and thus does not reflect a revenge system. Additional analyses revealed, however, that this hypothesis is not supported by the data — the relative probability that the original recipient of aggression would attack, following the conflict, the kin of a former opponent was significantly higher than the probability that the original recipient of aggression would attack following the conflict any group member subordinate to it. The existence of this form of revenge in macaque society suggests that a macaque's capacity to be vindictive is constrained by its rank in society rather than by its cognitive abilities.

These examples of retributive behaviour indicate that some form of calculated reciprocity is present in primate social systems. This kind of reciprocity and the kinds of responses seen by chimpanzees in the food-sharing study exemplify how and why prescriptive rules, rules that are generated when members of a group learn to recognize the contingencies between their own behaviour and the behaviour of others, are formed. The existence of such rules and, more significantly, of a set of expectations, essentially reflects a sense of social regularity, and may be a precursor to the human sense of justice (de Waal, 1991; Gruter, 1992; see also Hall, 1964; Nishida, 1994).

Trivers (1971) daringly labelled negative reactions to perceived violations of the social code, *moralistic aggression*. He emphasized that individuals who respond aggressively to perceived violations of the social code help reinforce systems of reciprocity by increasing the cost of not co-operating and, even more importantly, by increasing the cost of cheating, or failing to return a favour. When one individual cheats another, that individual exploits a relationship that is based on the benefits the partners previously obtained by co-operating. By doing so, the cheater benefits himself or herself at the partner's expense and destabilizes the system of reciprocity. Moralistic aggression, which often manifests itself as protest by subordinate individuals or punishment by dominant individuals, helps deter cheating. Consequently, it contributes to the creation of order, an element essential to the maintenance of the stability or integrity of social systems (de Waal, 1996a; Hardin, 1983). If unchecked, however, moralistic aggression can also lead to a spiral of spiteful retaliation that confers advantage on neither the original defector nor the moralistic aggressor, as is the case when those seeking retributive justice exacerbate conflicts to such a degree that feuds develop (Boehm, 1986; de Waal, 1996b, chapter 4).

Conclusion: Monkeys and apes appear capable of holding received services in mind, selectively repaying those individuals who performed the favours. They seem to hold negative acts in mind as well, leading to retribution and revenge. To what degree these reciprocity mechanisms are cognitively mediated is currently under investigation, but at least for chimpanzees there is evidence for a role of memory and expectation.

Conflict Resolution

Conflicts are inevitable in social groups. They may be generated by disagreement over social expectations or simply by competition over access to resources. Regardless of what triggers conflicts, group-living individuals need mechanisms for

negotiating resolutions to them and for repairing the damage to their relationships that results once conflicts of interests have escalated to the point of aggression. One of the simplest ways that conflicts are regulated and resolved is through the establishment of clear-cut dominance relations (see Carpenter, 1942; Mendoza and Barchas, 1983; Bernstein, 1981; Bernstein and Ehardt, 1985; de Waal, 1996b; for a review, see Preuschoft and van Schaik, in press).

Primates in hierarchical social systems typically have many methods by which they communicate who is dominant and who is subordinate. Subordinate rhesus macaques, for example, bare their teeth in a ritualized expression and often present their hindquarters to an approaching dominant group member. Such displays signal to the dominant individual that the subordinate recognizes the type of relationship they share, which consequently eliminates any question of ambiguity or need for aggression and promotes harmony and stability at the group level (de Waal, 1986). Interestingly, it appears that the bared-teeth expression is a *formal* dominance signal in despotic species, such as the rhesus macaque, in that it is almost exclusively displayed by subordinate individuals (de Waal and Luttrell, 1985; Preuschoft, 1999). In more egalitarian and tolerant macaque species, such as Tonkean macaques, power asymmetries between individuals are less evident than in despotic species, like rhesus macaques. Coinciding with this difference in power is a difference in use of the bared-teeth expression, which in Tonkean macaques is neither ritualized nor formal but common to both subordinate and dominant individuals (Thierry, Demaria, Preuschoft and Desportes, 1989).

Strict dominance relationships are often an effective means by which conflicts can be negotiated. When conflicts persist despite dominance relationships, or in primate species where dominance relations are relaxed or almost absent, there must be alternative ways to work out problems and repair relationships (this does not, however, imply that the development of egalitarian social systems led to the development of conflict management devices or vice versa, only that generally the two go together). One of the most important of these post-conflict behaviours is *reconciliation*. Reconciliation, which is defined as a friendly reunion between former opponents not long after a confrontation, is illustrated in the following description of an agonistic interaction between two chimpanzees and the post-conflict behaviour that followed (de Waal, 1989c, p. 41):

... Nikkie, the leader of the group, has slapped Hennie during a passing charge. Hennie, a young adult female of nine years, sits apart for a while feeling with her hand the spot on the back of the neck where Nikkie hit her. Then she seems to forget about the incident; she lies down in the grass, staring into the distance. More than fifteen minutes later, Hennie slowly gets up and walks straight to a group that includes Nikkie and the oldest female, Mama. Hennie approaches Nikkie with a series of soft pant grunts. Then she stretches out her arm to offer Nikkie the back of her hand for a kiss. Nikkie's hand-kiss consists of taking Hennie's whole hand rather unceremoniously into his mouth. This contact is followed by a mouth-to-mouth kiss.

Reconciliation enables the immediate, negative consequences of aggression to be counteracted and reduces the tension-related behaviour of recipients of aggression (de Waal and van Roosmalen, 1979; Aureli and van Schaik, 1991; de Waal and Aureli, 1996; Aureli, 1997). Perhaps more importantly, though, reconciliation enables former opponents to restore their relationship (Kappeler and van Schaik,

1992) and indeed one can increase the rate of reconciliation by experimentally enhancing the value of the relationship, e.g. by making the food-intake of two individuals dependent on their co-operation (Cords and Thurnheer, 1993). This form of post-conflict behaviour has been demonstrated in many primate species, each of which has its own typical 'peacemaking' gestures, calls, facial expressions and rituals, including, for example, kissing and embracing (see de Waal and Yoshihara, 1983; Cords, 1988; de Waal and Ren, 1988; York and Rowell, 1988; Aureli, van Schaik and van Hooff, 1989; Judge, 1991; Ren *et al*, 1991; Kappeler, 1993). We label friendly post-conflict behaviour 'reconciliation' if we can demonstrate empirically that the former opponents are selectively attracted so that they tend to come together in this manner more than usual and more with each other than with individuals who had nothing to do with the fight. In order to determine the percentage of conflicts followed by reconciliation for individuals of a particular species, we compare the post-conflict period (PC) to a matched-control period (MC). We use the matched-control period because it enables us to determine whether the affiliation that takes place during the post-conflict period is triggered by the conflict, or if it is simply due to chance (for a detailed discussion of the PC/MC method, see Veenema, Das and Aureli, 1994). As seen in Figure 2, former stump-tail macaque opponents affiliate considerably more in post-conflict periods than they do in the matched-control periods.

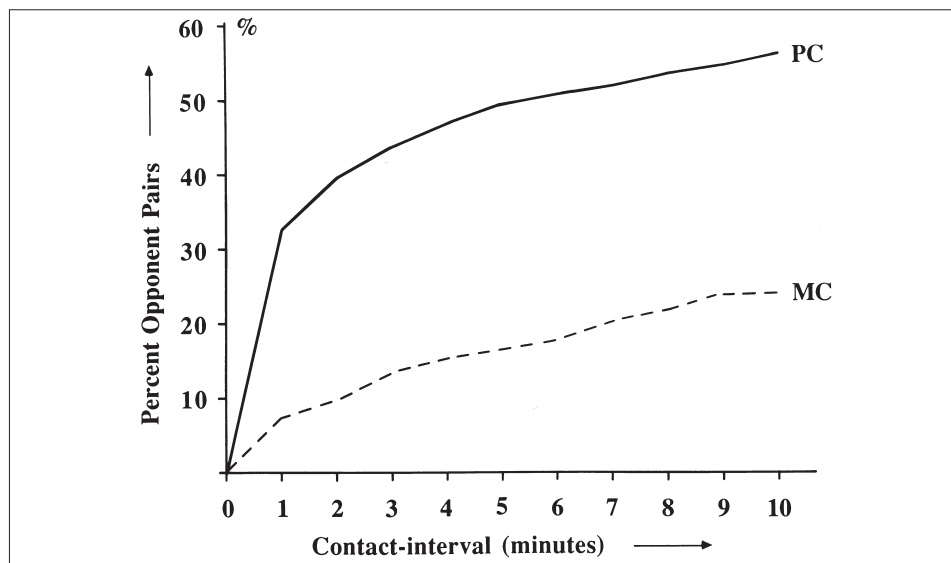


Figure 2

Cumulative percentage of pairs of opponents making their first nonagonistic body contact within a certain time interval. PC = post conflict observation, MC = matched control observation, N = number of pairs. From de Waal and Ren (1988).

Although reconciliation has been observed in most primate species and appears to be a universal method of repairing disturbed relationships, the degree to which it is used differs across primate species in a pattern that may reflect the level of integration and cohesion in a primate society. For example, analysis of post-conflict/matched-control (PC/MC) data from 670 pairs of former stump-tail macaque opponents with PC/MC data from 573 pairs of former rhesus macaque opponents, revealed that

stumptail monkeys reconciled on average significantly more often (i.e. 51.6 per cent) than rhesus monkeys (i.e. 21.1 per cent) (de Waal and Ren, 1988). In general, individuals in despotic species reconcile less frequently after conflicts than individuals in more tolerant and egalitarian species, most likely because the strict dominance hierarchies that are present in despotic species constrain the development of strong symmetrical relationships among group members (de Waal, 1989a).

Another way primates regulate and resolve conflicts of interests between group members is through conflict intervention. Although many studies have shown that interventions are related to coalition building and alliance formation, some interventions may have other functions as well (e.g. Reinhardt, Dodsworth and Scanlan, 1986; Bernstein and Ehardt, 1986; Boehm, 1994; Petit and Thierry, 1994; for reviews see Harcourt and de Waal, 1992). In some species, interventions by the highest ranking members of the social group end fights or at least reduce the severity of aggression that occurs during fights. The alpha male chimpanzee often plays such a role in fights involving females and/or juveniles in his group (de Waal, 1982). For example, if two juveniles are playing and a fight erupts, the alpha male just has to approach the area of the conflict to stop the fight. By doing so, he directly reduces the levels of aggression within the group, and also prevents the fight from escalating further by ending it before the juveniles' mothers intervene and possibly begin fighting themselves. Another example of this type of intervention in chimpanzees is given by the following excerpt from *Chimpanzee Politics* (1982, p. 124):

On one occasion, a quarrel between Mama and Spin got out of hand and ended in biting and fighting. Numerous apes rushed up to the two warring females and joined in the fray. A huge knot of fighting, screaming apes rolled around in the sand, until Luit leapt in and literally beat them apart. He did not choose sides in the conflict, like the others; instead anyone who continued to fight received a blow from him.

This pattern of behaviour, often referred to as the 'control role' has been described in other species of primates as well, (e.g. Bernstein, 1964; Tokuda and Jensen, 1969; Reinhardt *et al.*, 1986), and is a type of arbitration. The most interesting types of interventions that fall under the control role heading are those that are impartial. Individuals who intervene without choosing sides seem to do so in order to restore peace rather than simply aid friends or family (de Waal and van Hooff, 1981; de Waal, 1982; Goodall, 1986). The ability to put one's own preferences aside in this manner is another indication that a rudimentary form of justice may exist in the social systems of non-human primates (Boehm, 1992; de Waal, 1996a; 1996b). On the other hand, one might argue that although such interventions ultimately may have the effect of restoring the peace and reducing overall levels of aggression in the group, it is possible that the intervener's intentions were simpler, and that he or she was motivated only by the desire to terminate an aversive stimulus — the noisy conflict — and not by any group-oriented motivation. Evidence from chimpanzees and macaques suggests, however, that this explanation for impartial interventions may be inadequate. Such interventions may indeed be motivated in part by a desire to terminate an aversive stimulus but, if that were the only motivation, we might expect the interventions to be severe and partial, and in favour of the individual with whom the intervener shares the best relationship. Furthermore, agonistic interventions, in particular, can trigger agonistic and nonagonistic involvement by other individuals and intense screaming by the target or targets of the intervention (Gouzoules, Gouzoules and

Marler, 1984). Thus, interventions often temporarily exacerbate the aversive stimuli that supposedly the intervener sought to suppress.

Another type of intervention that falls under the control role is the protective intervention. Interventions in this group include those that occur on behalf of recipients of aggression. When expressed in this form, the control role can be viewed as a way that lower ranking or weaker (either physically *or* socially) individuals are protected from higher ranking, stronger (either physically *or* socially) group members.

A particularly salient example of the power of control animals to protect recipients of aggression in some primate societies that demonstrates not only the degree to which a control animal can influence the outcome of a conflict, but also that other individuals in the group recognize this capacity in certain individuals, comes from an experiment in which the composition of a pigtail macaque group was manipulated (Flack and de Waal, unpublished data). During this experiment, the three highest-ranking male pigtail macaques were removed for the day once per week and confined to their indoor housing. We studied the patterns of conflict intervention and aggression that occurred in the group when the males were present and when the males were absent. During removal periods, although confined to their indoor housing, the males had vocal and very restricted visual access to the group in that they were separated from the group by only a two foot long tunnel (to the indoor housing), divided in the middle by a metal door that did not completely seal off the indoor area from the outdoor area.

Three very low-ranking females typically received moderate levels of aggression from other group members when the males were present, but the males often intervened in these conflicts and, when this occurred, the aggression that had been directed at the females usually subsided. During the period when the males were removed, the intensity and frequency of aggression directed at these low ranking females increased substantially, and severe biting (biting for more than five seconds in duration), in particular, was more common. Several times, the aggression directed at these females became so severe that the investigator was forced to intervene.

Over the course of the study period, however, the females discovered a way to deal with the increase in severe aggression that they received when the high-ranking males were absent. This began when one female started running into the tunnel that separated the indoor housing from the outdoor housing. Once in the tunnel, the female solicited support from the males locked inside. The males, who could hear the conflict, were always waiting at the door. The female being attacked would scream, bare her teeth, and stick her arm through a small space in the door as her attackers were rushing forward. Each time this occurred, one of the males confined to the indoor housing would emit a threat bark, and the female would scream, clearly distressed by both her attackers and the threat, but not move from her position. Her attackers, however, would jump back and cease their abusive behaviour. The female would then lie prone in the tunnel for the next fifteen minutes or so, and each time her attackers attempted to bite her, a male inside would emit a threat bark and the attack would cease. The other two females, too, learned that when they were severely attacked they could appeal to the confined high-ranking males in this way, and as the study period progressed, this behaviour increased in frequency. Notably, no individuals ever escaped from aggression by running into the tunnel when the males were present in

the group, presumably because doing so prohibited escape and thus was very dangerous.

Interestingly, among chimpanzees, the individual who plays this control role need not be the alpha male of the group. The control animal may be any group member who the community permits — in the sense that none of the individuals in the social group protests the control animal's involvement in the conflict nor prohibits the particular control animal from 'playing' his or her role (de Waal, 1996b, chapter 3). Pascale Sicotte (1995) described a similar mechanism for resolving conflicts in bi-male groups of mountain gorillas in which females and infants sometimes interposed themselves between two fighting silverbacks. These interpositions, which occurred in 10–25 per cent of conflicts between silverbacks, involved more than just passive or chance interference in the agonistic dyad by a third party. Sicotte only included as interpositions those third party interventions in which a previously uninvolved individual interacted nonagonistically with at least one of the two males engaged in conflict, and in which the course of the initial agonistic interaction between the males was modified because one of the opponents directed its attention towards the third party. Notably, in one of the two groups Sicotte studied, he found that interpositions significantly increased the time between the end of the fight in which it occurred, and the start of the next fight.

One other important method of conflict resolution that has been identified in primate groups is mediation. Mediation occurs when a third party to a conflict becomes the bridge between two former opponents who cannot seem to bring themselves to reconcile without external help. It is characterized in the following example (de Waal and van Roosmalen, 1979, p. 62).

Especially after serious conflicts between two adult males, the two opponents sometimes were brought together by an adult female. The female approached one of the males, kissed or touched him or presented towards him and then slowly walked towards the other male. If the male followed, he did so very close behind her (often inspecting her genitals) and without looking at the other male. On a few occasions the female looked behind at her follower, and sometimes returned to a male that stayed behind to pull at his arm to make him follow. When the female sat down close to the other male, both males started to groom her and they simply continued when she went off.

In the above example of mediation, a female, who apparently is trying to reunite two former opponents in her social group, seems to show community concern in that she apparently cares about resolving a conflict in which she had no part and, more importantly, about restoring a disturbed relationship that is not her own. Although such examples are rare in primates, and perhaps unlikely in any but apes, a very similar pattern of behaviour to that illustrated by the example above was observed in stump-tail macaques (Flack, personal observation), suggesting that individuals in several species may have a sense of community concern that comes from having a stake in the quality of life within the group as a whole.

De Waal (1996b, p. 31) explained the evolution of community concern as follows:

Inasmuch as every member benefits from a unified, cooperative group, one expects them to care about the society they live in, and to make an effort to improve and strengthen it similar to the way the spider repairs her web, and the beaver maintains the integrity of his dam. Continued infighting, particularly at the top of the hierarchy, may damage everyone's interests, hence the settlement of conflict is not just a matter of the parties involved,

it concerns the community as a whole. This is not to say that animals make sacrifices for their community, but rather that each and every individual has a stake in the quality of the social environment on which its survival depends. In trying to improve this quality for their own purposes, they help many of their group mates at the same time. A good example is arbitration and mediation in disputes; standard practice in human society — courts of law serve this function — but recognizable in other primates as well.

Two other patterns of behaviour in monkeys and apes illustrative of community concern are triadic reconciliation — the involvement of third parties in the reconciliation process — and the group-wide celebration that often follows the reconciliation of dramatic conflicts of chimpanzees (de Waal, 1992b; 1996b, chapter 4). These patterns of behaviour suggest that monkeys and apes devote time and energy to making sure their social group remains peaceful, perhaps because group members recognize the value that a harmonious coexistence can have to achieving shared interests. In this sense, community concern can be extremely beneficial to individuals within social groups — even if it requires subordinating independent interests (non-shared), at least on occasion, to community interests — so long as many common goals are shared among group members. This kind of community concern, however, does not require that monkeys and apes worry about how the community, as an abstract entity, is doing. It only requires that the individual works toward creating a community atmosphere that reflects his or her own best interests. Consequently, the evolution of community concern in individuals may not necessarily require group selection. Its evolution can most likely be explained using selection at the level of the individual (although it is possible that individual selection may perhaps provide only a partial explanation for the evolution of such behaviours — for more discussion of this matter, see Wilson and Sober, 1994, and this issue), particularly if we consider the other behaviours that probably co-evolved with community concern in order to mitigate the risks and reduce the short-term costs to individuals generated by investing in the community.

Punishment, for example, or the imposition of a cost or penalty by one individual (usually who has some authority or power over the other individual) on another for its behaviour (Bean, 1981), and perhaps indirect reciprocity and social norms, help offset the cost of placing community (shared) interests above individual (independent) interests. Punishment and indirect reciprocity facilitate the evolution of investment in community interests because they help deter cheating (as discussed earlier) and reinforce community-oriented behaviours by making it possible for reciprocity to become generalized — so that if one individual performs a favour for another, that favour may be returned by a third party (for discussion of punishment, see Boyd and Richerson, 1992; Clutton-Brock and Parker, 1995; for discussion of indirect reciprocity, see Alexander, 1987; Boyd and Richerson, 1989). As Axelrod (1986) discussed, an especially powerful mechanism by which cheating can be deterred emerges when punishment against defectors becomes linked with negative indirect reciprocity, or punishment of nonpunishers. This *metanorm*, as Axelrod calls it, makes the ‘norm’ against defection self-policing. Whether this occurs in non-human primates, however, remains to be empirically demonstrated.

There is, however, evidence from a recent study of play signalling patterns in juvenile chimpanzees that suggests primates may modify their behaviour in anticipation of punishment (Jeannotte, 1996). Lisa Jeannotte found that older play partners were

significantly more likely to emit play signals, such as ‘play face’, during play bouts that occurred in proximity to adults, particularly those adults who were mothers of younger play partners and who were themselves young, than was the case when these adults were absent. These results suggest that an older juvenile play partner may increase its play signalling in the presence of a young mother to make clear that its interaction with the younger play partner is benign and does not warrant intervention or punishment.

Another mechanism that might enable the evolution of community concern is docility, or the receptivity to social influence that is common to social primates and that is useful for acquiring valuable information without the need for direct experience or evaluation (Simon, 1990). Thus, if certain values, like community concern, are fostered in a particular social environment, then an individual, simply due to its docile disposition, may adopt and become committed to those values even though at times those values or sentiments may encourage a course of action that is counter to an individual’s independent (non-shared) interests. In this way, community concern evolves as a by-product of selection for docility (for a related argument about a similar mechanism, the ‘conformist transmission’, by which community concern might evolve, see Boyd and Richerson, 1985; 1992; Henrich and Boyd, 1998; see also Cronk, 1994 for a Marxian argument about how docility may actually make it possible in some moral systems for certain individuals to justify and perpetuate inequalities of power and access to resources).

Although at present, direct evidence for punishment, docility, and especially indirect reciprocity is scant or fragmented in the primate literature, such behavioural mechanisms by which collective action is facilitated do probably exist to varying degrees. The existence of these mechanisms, which are likely complementary rather than alternative methods that act in concert to produce stability in social systems (Henrich and Boyd, 1998), is indirectly supported by the presence of learned adjustment, succourant behaviour, empathy, and sympathy in non-human primates.

Conclusion: Despite inevitable conflicts of interests, a certain degree of stability must be maintained in primate societies so that individuals can realize their collective interests and make worthwhile their investments in sociality. Dominance relationships provide one simple way to regulate and order societies. Social systems with more level dominance relationships require additional mechanisms, however, such as reconciliation; consolation; impartial, protective, and pacifying interventions; and perhaps community concern. All of these mechanisms are present to varying degrees in monkeys and apes.

Empathy, Sympathy and Consolation

Although food-sharing, social reciprocity in general, and the different forms of conflict resolution seen in primates need not require a capacity for sympathy and empathy, it is likely that both are involved to some degree in all of these behaviours, and to a high degree in at least the more sophisticated forms of conflict intervention such as mediation. In order to help others, as the female in the mediation example was doing, individuals need to be concerned about and be able to understand others’ needs and emotions.

Learned adjustment, which is common in primates, is a precursor to such behaviour in that it demonstrates the ability of monkeys and apes to change their behaviour as they become familiar with the limitations of those with whom they interact without requiring that these individuals understand why they should adjust their behaviour. Juvenile chimpanzees, for example, commonly restrict the degree of force they use in wrestling matches while playing with younger juveniles and infants (Hayaki, 1985). Monkeys and apes also adjust their behaviour in the presence of disabled group members (e.g. Fedigan and Fedigan, 1977; de Waal, 1996b, chapter 2; de Waal, Uno, Luttrell, Meisner and Jeannotte, 1996c). The adjustment may include increased social tolerance towards individuals who behave abnormally or intervention on behalf of disabled individuals who seem unaware of when they are involved in a dangerous predicament. Although the examples discussed above are most parsimoniously explained using learned adjustment, the possibility that cognitive empathy — the ability to comprehend the needs and emotions of other individuals — may provide a more accurate explanation for some of these behaviours needs to be explored in future studies.

An especially important area that needs investigation is how learned adjustment and cognitive empathy relate to the internalization of social norms. One study that begins to address this question is Jeannotte's previously mentioned study (1996) of play-signalling in juvenile chimpanzees in relation to social context and environment. Results of this study indicate that an older juvenile is not significantly more likely to play roughly when the age difference between it and its partner is small as opposed to large. Although this result seems to contradict findings from previous research that suggested that juvenile chimpanzees restrict the intensity of play when interacting with younger play partners, it does not necessarily do so. Jeannotte found that there was a strong correlation between the play intensity of one partner with that of the other. One likely explanation for this 'matching' is that it may be a consequence of restraint on the part of the older partner and escalation on the part of the younger partner (Hayaki, 1985).

Succourant behaviour, which includes care-giving and providing relief to distressed individuals who are not kin, is also an example of a category of behaviours that seem to require attachment to and concern for others and, in some cases, an understanding of other's needs and emotions (Scott, 1971). Succourant tendencies develop in primates early in life; even infants respond to tension generated by aggression by mounting one another or by mounting kin or even the individuals involved in the agonism. Although these infants probably are not helping to reduce tensions between the individuals involved in the agonism by responding in this way, they may be comforting themselves. This simple need to comfort oneself after or during a fight in which the infant itself was not involved suggests that the infant perceives distress in others and reacts vicariously to it by becoming distressed itself. This 'emotional contagion' (Hatfield, Cacioppo and Rapson, 1993) may be the mechanism underlying the development of succourance and suggests that primates do have the ability to empathize.

Non-human primates may be able to empathize with one another in that other group member's feelings and actions emotionally affect them, but are non-human primates also concerned about individuals who appear distressed? In other words, do they sympathize with or just react to individuals in their group who are distressed?

There is evidence suggesting that some primates do have concern for fellow group members; it comes from studies of consolation, or the appeasement of distressed individuals through affiliative gestures such as grooming and embracing by third parties following a fight (de Waal and van Roosmalen, 1979). The predominant and immediate effect of consolation — the alleviation of distress (de Waal and Aureli, 1996), is illustrated by the following example observed by Jane Goodall (1986, p. 361):

An adult male challenged by another male often runs screaming to a third and establishes contact with him. Often both will then scream, embrace, mount or groom each other while looking toward the original aggressor. This . . . is how a victim tries to enlist the help of an ally. There are occasions, however, when it seems that the primary goal is to establish reassurance contact — as when fourteen-year-old Figan, after being attacked by a rival, went to hold hands with his mother.

In the above example, however, the recipient of aggression is *seeking* consolation. This type of consolation occurs in several primate species but may not require that the third party sympathizes with the recipient who approaches for reassurance (for other examples see Lindburg, 1973; de Waal and Yoshihara, 1983; Verbeek and de Waal, 1997). *Active* consolation, on the other hand, occurs when a third party approaches and affiliates with a recipient of aggression following a fight. Such action may require that the third party not only recognize the distress of the recipient of aggression but also be concerned enough about that individual to approach and appease it. Sometimes, for example, a juvenile chimpanzee will approach and embrace an adult male who has just lost a confrontation with his rival (de Waal, 1982).

There exist systematic data to support the conclusion that chimpanzees have the capacity to engage in active consolation (de Waal and Aureli, 1996). An analysis of 1,321 agonistic incidents among a captive group of seventeen chimpanzees housed in a large compound at the Field Station of the Yerkes Regional Primate Research Center revealed that significantly more affiliative contacts initiated by bystanders occurred immediately (within several minutes) after a conflict than after longer time intervals or in control periods not preceded by conflict. Furthermore, significantly more affiliative contacts initiated by bystanders occurred following serious incidents than mild incidents (this is particularly important because, if consolation occurs to alleviate distress, and if an individual's level of distress is proportional to the aggression intensity of the conflict in which it participated, then consolation should occur more frequently following serious aggressive incidents). And finally, bystanders initiated significantly more affiliative contact with the recipients of aggression than with the aggressors themselves.

In contrast to these findings for chimpanzees, researchers have been unable to quantitatively demonstrate active consolation in four macaque species (Aureli, 1992; Aureli and van Schaik, 1991; Judge, 1991; Aureli, Veenema, van Panthaleon van Eck and van Hoof, 1993; Aureli, Das, Verleur and van Hooff, 1994; Castles and Whiten, 1998; for a review, see de Waal and Aureli, 1996). This suggests that consolation may be limited to the great apes, possibly because it requires more sophisticated cognition than present in monkeys. Alternatively, it may be limited to apes because within their social systems, such behaviour is more advantageous and perhaps less costly than in monkey social systems in which approaching recipients of aggression, and areas of conflicts generally, can be dangerous due to the frequency with which aggression is redirected to bystanders in many monkey societies (de Waal and Aureli, 1996).

Conclusion: Moral sentiments such as sympathy, empathy, and community concern, engender a bond between individuals, the formation of which facilitates and is facilitated by co-operation. This bond is enabled by an individual's capacity to be sensitive to the emotions of others. Monkeys and apes are capable of learned adjustment, and have succourant tendencies, in that they comfort and console one another when distressed. But are they capable of genuine concern for others based on perspective-taking? There is some evidence to suggest that apes, like humans, are capable of cognitive empathy but its existence in monkeys remains questionable.

Implications of Primate Research for Understanding Human Morality

In the opening pages of a *Theory of Justice* (1971, p. 4), John Rawls elegantly states the central problem that plagues those human (and animal) societies in which implicit or explicit rules of conduct exist to make co-operation possible:

. . . although a society is a co-operative venture for mutual advantage, it is typically marked by a conflict as well as by an identity of interests. There is an identity of interests since social cooperation makes possible a better life for all than any would have if each were to live solely by his own efforts. There is a conflict of interests since persons are not indifferent as to how the greater benefits of their collaboration are distributed, for in order to pursue their ends they each prefer a larger to a lesser share.

This problem, as identified above by Rawls, has in practice no true solutions. Furthermore, the research on the natural history and social behaviour of our non-human primate relatives illustrates how both our capacity and tendency to pursue our independent interests and our capacity and tendency to pursue shared interests are natural and important, at least from a biological point of view (see de Waal, 1992a). This suggests that morality was not *devised* to subjugate the independent interests of individuals. Rather, a moral system *emerged* out of the interaction of the two sets of interests, thus providing a way to express both. This conclusion should not be mistaken as justification for using natural selection as a model for what we ought to do or *not* do. What we ought to do and how we decide this is a separate question from why and how moral systems arose.

It is particularly important that in our pursuit of the origins and purpose of moral systems we resist the temptation to let our moral views frame, and thus obscure, how in the end we describe and explain the moral standards embodied in implicit social contracts. Even more importantly, we need to be careful not to hold up as moral systems only those that in our view wholly subjugate the independent interests of individuals in favour of those interests that are shared, simply because we value that these systems suppress conflict and deliver consensus. Doing so precludes from consideration those systems that from an operational standpoint are moral systems, but that may not fit perfectly our moral views of what is right, of worth, or of value.

Humans, nonetheless, may be the only truly moral creatures. Although one could argue that several elements of human morality are present in non-human primates — particularly in apes — there is no evidence at this time to suggest that non-human primates have moral systems that mirror the complexity of our own. In some species, individuals, by interacting every day, may create a kind of social contract that governs which types of behaviour are acceptable and tolerable and which are punishable —

yet these individuals have no way to conceptualize such decisions or abstract them from their context, let alone debate them amongst themselves. Consensus is only obvious in the absence of protest and prohibition.

Consensus achieved in this tacit manner, however, is not uncommon in our own species. This observation, in conjunction with the above research that suggests that an actual social contract of sorts arises out of interactions between group members in primate societies, makes plausible the idea that human morality is best understood as having arisen out of an implicit agreement among group members that enabled individuals to profit from the benefits of co-operative sociality.

Acknowledging that morality may have a social function and stressing that it may have emerged from such a social contract does not require that we accept this kind of 'actual' social contract as the medium through which we decide what is moral. Nor does it suggest that we revert to some form of Social Darwinism, an approach to deciding what we ought to do that was based not only on a misconceived, red-in-tooth-and-claw representation of natural selection, but worse, also on the idea that this interpretation of 'nature's way' should be used to guide (and justify) our own behaviour. Although we need to recognize that the social contract does in fact often represent the process by which we come to agree (as a group) what is acceptable, we also need to recognize that this is probably the case because the social contract is useful from an evolutionary perspective because it enables individuals in groups to reach consensus with minimal, if any, need for explicit co-ordination. Certainly, from a social perspective, one of the major limitations of any actual social contract is that such contracts do not necessarily produce the most 'moral' solutions to problems. The outcome such contracts produce is no more than a reflection of compromise, and of the behaviour that as a group we practice.

Another important observation about human behaviour made by David Hume (1739), Adam Smith (1759), and Edward Westermarck (1912) is that human morality is powerfully influenced by emotional responses and is not always governed by the abstract, intellectual rules upon which we have supposedly agreed. The primate research implicitly suggests that this emphasis on the role of emotions is both insightful and accurate — in primate groups individuals are motivated to respond to others based on the emotional reactions they have to one another's behaviour. That sympathy, based on empathy, seems to direct the emotional responses of some primates to others may reflect their ability to differentiate between self and other and, more significantly, to care for one another. Yet, the idea that emotion may be fundamental to morality contradicts what many philosophers — most significantly Immanuel Kant (1785) — have argued: That the human sense of right and wrong is more a consequence of rational processes than of emotional reactions. It would be quite erroneous, however, to equate moral emotions with a lack of rationality and judgement. The emotions discussed by Hume, Smith and Westermarck are actually very complex, involving retribution, reciprocity and perspective taking. The latter, as is now increasingly apparent from research into so-called Theory-of-Mind, involves complex mental abilities (for a review of Theory-of-Mind in non-human primates, see Heyes and Commentaries, 1998).

Darwin (1871; 1872), who was familiar with the thinking of Hume and Smith, advocated a perspective on human morality in line with these ideas in that he saw human nature as neither good nor bad but neutral. He recognized that moral systems

enable individuals to reconcile what Hume saw as two sides to human nature — the dark, competitive side, which is dominated by greed and competition, and the ‘sentimental,’ co-operative side, which is marked by social instincts and compassion. To Darwin, this dualism in human nature arose from the evolution of two strategies (the individual and social) that together provided a method by which individuals can obtain limited resources. Thus, Darwin recognized that moral systems not only govern the expression and use of these strategies but also reflect their interaction.

Opposition to this more integrated view by some contemporary evolutionary biologists, such as Richard Dawkins and George Williams (see Introduction), leads us to propose that their views on morality be classified not as Darwinian but Huxleyan. For example, Dawkins recently reconciled human moral ideals with his interpretation of evolution by saying that we are entitled to throw out Darwinism (‘in our political and social life we are entitled to throw out Darwinism, to say we don’t want to live in a Darwinian world’, *Human Ethology Bulletin*, March 1997). Because Darwin himself perceived absolutely no contradiction or dualism between the evolutionary process and human moral tendencies (e.g. de Waal, 1996b; Uchii, 1996), such views represent a considerable narrowing of what Darwin deemed possible.

The Kantian view of morality as an invention of reason supplemented with a sense of duty remained pervasive despite Darwin’s insights. Perhaps primate research that suggests that morality is a consequence of our emotional needs and responses as well as of our ability to rationally evaluate alternatives is strong enough to warrant making room for a more integrated perspective of morality that acknowledges its biological basis and emotional component as well as the role of cognition. Perhaps Hume and Kant were both correct.

The foundations of morality may be built on our emotional reactions to one another but morality itself is no doubt also tempered and sometimes modified by two additional factors. First, morality may be modified by our ability to evaluate the situation generating these emotional reactions. Second, it may be tempered by our understanding of the consequences that our responses to the behaviour that elicited the emotional reaction have for ourselves and others. A problem, however, remains even after we acknowledge that what generates in each of us an understanding of what is good or virtuous is a combination of two factors: 1) the emotional reaction and intuition of each individual that jump-start the moral process, with 2) the cognitive-rational evaluations that enable the individual to determine what is right. The problem that remains despite this integration is how to translate the resultant conception in the individual of what is good to action at the community level. In human societies, as in animal societies, this is often achieved by some manifestation of the social contract. But as mentioned earlier, ‘actual’ social contracts, as rough compromises between competing agents, often with unequal powers and needs, may be unsatisfactory from a normative standpoint because they do not fully respect worth, value or rights.

Conclusion

Sympathy-related traits such as attachment, succourance, emotional contagion and learned adjustment in combination with a system of reciprocity and punishment, the ability to internalize social rules and the capacity to work out conflicts and repair

relationships damaged by aggression, are found to some degree in many primate species, and are fundamental to the development of moral systems (Table 1).

All of these elements of moral systems are tools social animals — including humans — use to make living together a possibility. These capacities help keep in check the inevitable competition among group members due to conflicting interests. More importantly, however, sympathy-related traits and the capacity to work out con-

Table 1

It is hard to imagine human morality without the following tendencies and capacities also found in other species. These tendencies deserve to be called the four ingredients of morality:

Sympathy Related

Attachment, succourance, and emotional contagion.
 Learned adjustment to and special treatment of the disabled and injured.
 Ability to trade places mentally with others: cognitive empathy.*

Norm Related

Prescriptive social rules.
 Internalization of rules and anticipation of punishment.*
 A sense of social regularity and expectation about how one ought to be treated.*

Reciprocity

A concept of giving, trading, and revenge.
 Moralistic aggression against violators of reciprocity rules.

Getting Along

Peacemaking and avoidance of conflict.
 Community concern and maintenance of good relationships.*
 Accommodation of conflicting interests through negotiation.

*It is particularly in these areas — empathy, internalization of rules, sense of justice, and community concern — that humans seem to have gone considerably further than most other animals.

flicts and repair relationships help promote cohesion, co-operation and social bonding, characteristics of a social group that may, from an evolutionary perspective, make group living a functionally effective strategy and, therefore, an attractive strategy in which individuals should invest resources. As the anthropologist Ruth Benedict wrote in 1934 (p. 251):

One of the most misleading misconceptions due to this nineteenth-century dualism was the idea that what was subtracted from society was added to the individual and what was subtracted from the individual was added to society. . . . In reality, society and the individual are not antagonists. His culture provides the raw material of which the individual makes his life. If it is meagre, the individual suffers; if it is rich, the individual has the chance to rise to his opportunity.

At the end of this paper, in which we have discussed the possible evolutionary building blocks of human moral systems, it is essential to also point out the limitations of biological approaches to human morality. After all, we have in the past seen attempts to derive moral rules directly from nature, resulting in a dubious genre of literature going back to Ernest Seton's (1907) *The Natural History of the Ten Commandments*. Other biblical titles have followed, principally in the German language, spelling out how moral principles contribute to survival (e.g. Wickler, 1971). Much of this literature assumed that the world was waiting for biologists to point out what is Normal and Natural, hence worth being adopted as ideal. Attempts to derive ethical norms from nature, however, are highly questionable.

Our position is quite different. While human morality does need to take human nature into account by either fortifying certain natural tendencies — such as sympathy, reciprocity, loyalty to the group and family, and so on — or by countering other tendencies — such as within-group violence and cheating — it is in the end the society that decides, over a period of many generations, on the contents of its moral system. There is a parallel here with language ability: The capacity to develop and learn a very complex communication system such as language is naturally present in humans, but it is filled in by the environment resulting in numerous different languages. In the same way, we are born with a moral capacity, and a strong tendency to absorb the moral values of our social environment, but we are not born with a moral code in place. The filling in is done by the social environment often dictated by the demands of the physical environment (de Waal, 1996b).

Interestingly, moral development in human children hints at the same emphasis on conflict resolution and reciprocity (principles of 'fairness') as emphasized above for non-human primates. Instead of the traditional, Piagetian view of morality imposed upon the child by the all-knowing adults, increasingly it is thought that children develop moral rules in social interaction with each other, particularly during the resolution of conflict (e.g. Killen and Nucci, 1995; Killen and de Waal, in press).

At the same time that our moral systems rely on basic mental capacities and social tendencies that we share with other co-operative primates, such as chimpanzees, we also bring unique features to the table, such as a greater degree of rule internalization, a greater ability to adopt the perspective of others, and of course the unique capacity to debate issues amongst ourselves, and transmit them verbally, including their rationale. To communicate intentions and feelings is one thing, to clarify what is good, and why, and what is bad, and why, quite something else. Animals are no moral philosophers.

But, while there is no denying that we are creatures of intellect, it is also clear that we are born with powerful inclinations and emotions that bias our thinking and behaviour. It is in this area that many of the continuities with other animals lie. A chimpanzee stroking and patting a victim of attack or sharing her food with a hungry companion shows attitudes that are hard to distinguish from those of a person taking a crying child in the arms, or doing volunteer work in a soup kitchen. To dismiss such evidence as a product of subjective interpretation by 'romantically inspired naturalists' (e.g.: Williams, 1989, p.190) or to classify all animal behaviour as based on instinct and human behaviour as proof of moral decency is misleading (see Kummer, 1979). First of all, it is uneconomic in that it assumes different processes for similar

behaviour in closely related species. Second, it ignores the growing body of evidence for mental complexity in the chimpanzee, including the possibility of empathy.

One wonders if, on the basis of external behaviour alone, an extraterrestrial observer charged with finding the only moral animal on earth would automatically end up pointing at *Homo sapiens*. We think it unlikely that human behaviour in all its variety, including the occasional horror, will necessarily strike the observer as the most moral. This raises of course the question how and whether morality sets us apart from the rest of the animal kingdom. The continuities are, in fact, quite striking, and need to weigh heavily in any debate about the evolution of morality. We do hesitate to call the members of any species other than our own 'moral beings', but we also believe that many of the tendencies and cognitive abilities underlying human morality antedate our species' appearance on this planet.

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