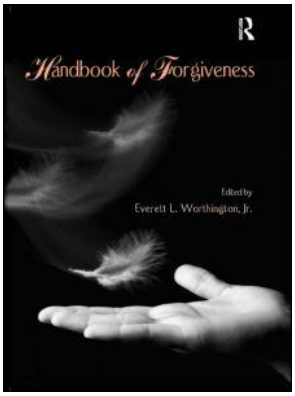

Handbook of Forgiveness

Everett L. Worthington, Jr.

Primate Conflict and Its Relation to Human Forgiveness

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Frans B. M. de Waal, Jennifer J. Pokorny
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Part One

NATURE, PHILOSOPHY, RELIGION, AND FORGIVENESS

Chapter Two

Primate Conflict and Its Relation to Human Forgiveness

Frans B. M. de Waal
Jennifer J. Pokorny

Research on nonhuman primates has produced compelling evidence for so-called reconciliation and consolation, that is, postconflict contacts that serve to repair social relationships and comfort distressed individuals, such as victims of aggression. Although it is difficult and perhaps impossible to demonstrate forgiveness explicitly among nonhuman primates, inferences can be drawn from the behavior these animals use to repair social damage. Their behavior can be seen as an evolutionary precursor to conflict resolution and forgiveness in human societies.

ASSUMPTIONS ABOUT FORGIVENESS AND RECONCILIATION

The best known behavioral mechanism that allows primates to repair social damage caused by hostilities is *reconciliation*. Reconciliation is defined as a friendly reunion between former opponents: The reunion supposedly serves to return the relationship to normal levels of tolerance and cooperation. An early anecdote of this behavior is Köhler's (1925) description of the need for "forgiveness" in a juvenile chimpanzee.

> The little creature, which I had punished for the first time, shrank back, uttered one or two heartbroken wails, as she stared at me horror-struck, while her lips were pouted more than ever. The next moment she had flung her arms round my neck, quite beside herself, and was only comforted by degrees, when I stroked her. (p. 261)

Apes seem to perceive a conflict with those close to them as a threat to the relationship and try to control the damage with affectionate behavior. Although the environment of hand-reared apes is obviously unnatural, human influence does not appear to explain the phenomenon. As we will see below, nonhuman primates have many forms of contact behavior that seems to serve to repair disturbed relationships.

Forgiveness \ Reconciliation	Yes	No
Yes	Internal process of forgiveness and reconciliation	Forgiveness without reconciliation
No	Reconciliation without forgiveness—often a truce	No forgiveness and no reconciliation

FIGURE 2.1. Possible combinations of reconciliation (a social process between two parties) and forgiveness (an internal process with an offender in mind). After Park and Enright (2000).

When discussing forgiveness, it must be remembered that reconciliation is not forgiveness. It is possible to reconcile with an opponent without actually forgiving the individual. Likewise, it is possible to forgive another without ever formally reconciling (see Figure 2.1). The process of forgiveness occurs when individual A has been wronged in some way by individual B, resulting in A having negative emotions toward B. A then attempts to cope with the situation and overcomes these negative feelings, which usually requires changing one's perception of the other individual. Forgiveness implies acceptance of the situation and the other individual.

Because forgiveness is an internal process to which we have no access in nonhuman primates, if it exists at all, and reconciliation is an externally visible social process, the comparison is difficult to make. Suffice it to say that what the two have in common is some emotional switch, which when turned moves the attitude toward another individual from aggressive and/or fearful to friendly, perhaps even affectionate. This switch is truly remarkable and not something anyone expected to find in animals (Rowell, 2000). It is unlikely that this switching mechanism evolved independently in several species, especially closely related ones. We must assume that if we share it with our close relatives, it derives from the same source: the first group-living mammals perhaps, which arose many millions of years before we appeared on the planet.

REVIEW OF THE LITERATURE

The Need to Preserve Relationships

From an evolutionary perspective, benefits of cooperation are most evident in relationships with a reproductive function, such as male–female and mother–offspring relationships.

Relationships also produce benefits not immediately related to reproduction, however, such as when two individuals protect one another against attack, tolerate one another around resources, provide vigilance against predators, or cooperate during intra- or intergroup competition. It is of course assumed here that cooperative tendencies evolved because they paid off in the long run in terms of survival and reproduction.

Kummer (1978) defined the benefits that individual A provides to B as A's value to B. Any individual will try to improve this value: B will select the best available A, predict A's behavior, and modify A's behavior to its own advantage. In other words, B will invest in the relationship with A. Although most of B's investments may not lead to quick profits, such as immediately useful actions by A, they may help cultivate a relationship that is beneficial to both A and B over the long haul. A good example of such investment is social grooming. One primate may groom another for over an hour without any immediate return favor. After the session, the two will simply part company, each going its own way. There are indications that grooming is altruistic in that it entails costs for the groomer, such as reduced time available for other activities and reduced attention to potential danger, whereas it provides benefits to the groomee in terms of hygiene and a calming effect. Why would one individual provide services to another—grooming is one of the most common activities in primate groups—if not to foster future beneficial exchanges?

The most pervasive and effective cooperation within primate groups is the formation of alliances: Two or more individuals band together against a third. For example, a male attacks a juvenile, and the mother rushes to the juvenile's aid at considerable risk to herself. Or two males together overthrow the reigning alpha male, after which one of the victorious males becomes the new alpha. These kinds of cooperation are critically important to primates: Social rank and sometimes life depend on it. Consequently, they need to get along with others, even with their competitors. Maintenance of valuable relationships despite occasional conflicts of interest is a critical requirement of group life.

Reconciliation Behavior

Initially, reconciliation research contrasted and compared expectations concerning the effect of aggressive behavior on social relations. Two hypotheses existed, the first one being traditional in the extensive aggression literature of the 1960s and 1970s and the second one formulated on the discovery that chimpanzees often reunite following aggression.

Dispersal Hypothesis. Losers of aggressive incidents are expected to avoid winners. The notion of aggression as a spacing mechanism was based on experience with territorial species and the observation that many animals use aggression to maintain what Hediger (1941) termed *species-typical individual distances.* This hypothesis would predict reduced contact following aggression.

Reconciliation Hypothesis. Individuals are expected to "undo" the damage that aggression inflicts on valuable social relationships. Such a tendency would be expressed in increased contact following aggression and special reassuring and appeasing gestures during these contacts.

In support of the second hypothesis, de Waal and van Roosmalen (1979) were the first to demonstrate that aggression leads to increased contact. Former opponents in the chimpanzee colony of Arnhem Zoo (the Netherlands) were found more often within 2 meters of one another after than before a conflict. Moreover, the chimpanzees engaged in intensive body contacts following conflict, such as kissing and embracing (see Figure 2.2) and preferred such contact with former opponents rather than with individuals who had not been involved in the previous conflict. Interopponent contacts constituted 30% of all postconflict contacts, compared with a random expectation of 5.6%. These results demonstrated a pronounced conciliatory tendency in the chimpanzee, later confirmed by reports from the wild.

Following these findings, de Waal and Yoshihara (1983) developed a controlled methodology to look at reconciliation in a relatively intolerant primate, the rhesus macaque. This new method compared the postconflict observation (PC) with a matched control observation (MC). The MC was usually taken the following day, during the same time of day to control for any diurnal or seasonal behavioral differences. If affiliative contact occurs only in the PC and not in the MC, these individuals are said to be attracted. If contact occurs during the MC and not during the PC, these individuals are said to be dispersed. Therefore, there is a direct comparison between rates of contact following aggression and matched baseline periods (see Figure 2.3). Rather surprisingly, it was found that rhesus macaques also follow peacemaking strategies, although not to the same degree as chimpanzees.

Since then, the PC-MC method has become a staple of research on postconflict behavior across species. Some changes have been made, such as controlling for distance

FIGURE 2.2. Kiss on the mouth by a female to a male chimpanzee. This is a behavior often used between former opponents as a conciliatory gesture. Photograph by Frans de Waal.

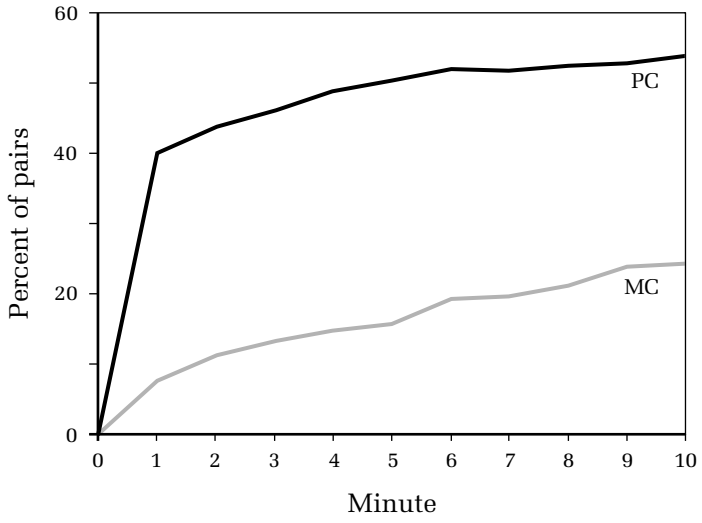

FIGURE 2.3. Primates show a dramatic increase in body contact between former opponents during postconflict (PC), as compared with matched-control (MC) observations. The graph provides the cumulative percentage of opponent pairs establishing friendly contact during a 10-min time window following spontaneous aggressive incidents in a zoo group of stump-tailed macaques.

between former opponents by starting the MC observation only when that distance is similar to the distance at the start of the PC. Others have imposed a time limit on the observation following a conflict, because reconciliation often occurs within the first few minutes. This may be conservative in that some contacts outside this time may function as reconciliation. However, long observations by nature lead to higher chances of contact. These methods also allow one to determine how likely it is for reconciliation to occur with the group (kin vs. nonkin) or species as a whole. Veenema and colleagues (Veenema, Das, & Aureli, 1994) introduced a method to use these observations to measure reconciliation frequencies between different individuals and determine their conciliatory tendency. This is calculated by subtracting the number of dispersed pairs from the number of attracted pairs and dividing by the total number of PC-MC pairs.

Following these methods, similar results have subsequently been reported for a variety of other macaque species, as well as for gorillas, bonobos, golden monkeys, vervets, mangabeys, baboons, and so on. Most of these studies were conducted in captivity, but reconciliation has also been demonstrated in wild primates. In most species studied thus far, affiliative contact between former opponents is more likely during the first few minutes after a conflict, and postconflict attraction is selective. The contact increase does not occur indiscriminately with all possible partners but specifically between recent opponents. For reviews of the literature, see Aureli and de Waal (2000) and de Waal (2000).

According to both the data on captive chimpanzees and descriptions of chimpanzees in the wild, reconciliation in this species involves distinct behavior patterns, such as embracing, gentle touching, and mouth-to-mouth kissing. In fact, chimpanzee opponents kiss one another 10 times more often during the first postconflict contact than during subsequent contacts. Not all primates show a similar behavioral distinction between first postconflict and other contacts, but stump-tailed macaques use another conspicuous behavior pattern rarely observed outside the reconciliation context—the "hold-bottom ritual," in which one individual, usually the recipient of aggression, presents the hindquarters, and the other clasps the presenter's haunches (see Figure 2.4). This ritual occurs in more than 30% of first postconflict contacts, a 20-fold increase compared with control contacts.

The kiss of chimpanzees and the hold-bottom ritual of stump-tailed macaques require high levels of intimacy and coordination. They assist the reconciliation process by making both the context and meaning of the contact more explicit. This is in contrast to the implicit reconciliations of some other species, such as the rhesus macaque, which often reestablish relationships through a brief, inconspicuous brushing contact that is quite meaningful, given the risks involved in mere proximity in this short-tempered species.

Reconciliation serves as a heuristic label for these contacts: It generates ideas about their function, such as that they repair social relationships or reduce social tension. The validity of this label has been confirmed experimentally. Cords (1992), for example, carried out experiments indicating that reconciliation restores tolerance between former opponents. Following an aggressive incident between macaques, the monkeys were presented with two drinking nipples, side by side, from which they could obtain a sweet drink. The monkeys drank together more readily if reconciliation had taken place than without reconciliation. Observational studies of both macaques

FIGURE 2.4. Hold-bottom by a dominant male (right) to a subordinate, which is a specific conciliatory gesture among stump-tailed macaques. Photograph by Frans de Waal.

and chimpanzees confirm that reconciliation reduces the chances of further aggression: The frequency of renewed attack is reduced following reconciliation. These results support the hypothesis that reconciliation restores the relationship between former opponents.

Both macaques and chimpanzees follow what seems a general rule among primates, that is, reconciliation aims to restore the most valuable relationships. In macaques, in which matrilineal kin relationships are particularly valuable, related individuals reconcile conflicts more often than do unrelated individuals. In the chimpanzee, males form stronger bonds than females, and male conflicts are more often reconciled than female conflicts. This general rule, the Valuable Relationship Hypothesis, is reviewed by van Schaik and Aureli (2000) and de Waal (2000), and can be summarized by predicting that reconciliation will be most common between partners that stand most to lose, were conflict to continue.

An experimental investigation of this hypothesis was carried out by Cords and Thurnheer (1993), who trained pairs of macaques to cooperate during feeding, thus enhancing their interdependence. Reconciliation following conflict increased dramatically once a partner had become useful for obtaining food, thus confirming the idea that reconciliation occurs in proportion to the value of the relationship.

Interspecific variability in aggressiveness and peacemaking tendency makes it possible to expose members of a given species to a social environment with dramatically different rates of these behaviors. This can be done by housing them with another species. If reconciliation is a learned social skill, one expects such a manipulation to affect postconflict behavior. This prediction was examined by de Waal and Johanowicz (1993), who exposed rhesus monkeys—a species with low levels of reconciliation—to a highly conciliatory species, the stump-tailed macaque. Both species belong to the genus *Macaca*.

Juveniles were housed in mixed-species groups of seven monkeys each for a period of 5 months. Following this period, they were observed for 6 weeks in groups of conspecifics only. Control rhesus monkeys, matched in age and sex to the experimental subjects, went through the same procedure without contact with another species (i.e., in all-rhesus groups). Initially, individuals of different species lived somewhat separate lives, sleeping and huddling in separate subgroups, but by the end of the 5-month period, they were fully integrated and highly tolerant of each other.

Compared with the control experiment, the main result of the manipulation was a three- to fourfold increase in the proportion of fights followed by reconciliation. Rhesus monkeys who had lived with the kinder, gentler species apparently had learned peacemaking skills. This difference emerged gradually during the co-housing phase but was sustained following removal of the "tutor" species (see Figure 2.5). The experimental setup did not include a control group of stump-tailed monkeys and hence did not allow investigation of whether the tutors had learned to be more aggressive and less conciliatory and after the co-housing stage.

This result, which shows that reconciliation can be modified through environmental manipulation, has important implications. It shows that primate peacemaking is not

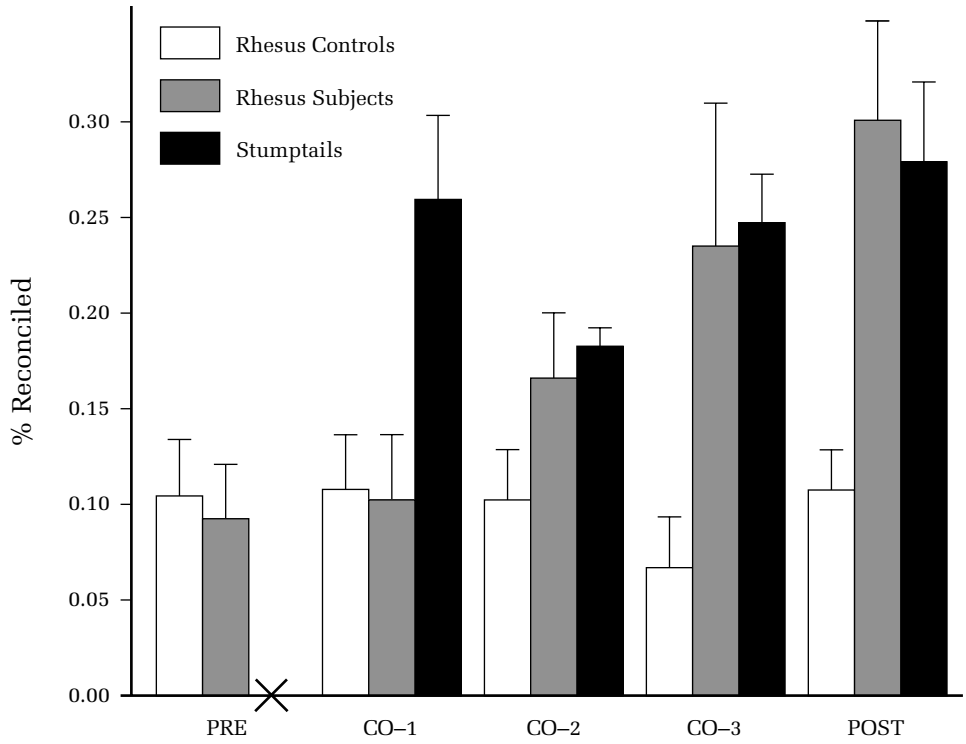

FIGURE 2.5. Mean (+ SEM) proportion per individual of aggressive conflicts followed within 3 min by a reconciliation initiated by the individual. During the pre- and postphase, subjects were housed with conspecifics only; no prephase data are available on stump-tailed monkeys. The 5-month co-housing phase has been divided into three equal parts (CO-1, CO-2, CO-3). The graph shows that rhesus experimental subjects, which lived during co-housing with stumptails, increased their reconciliation rate and maintained this high rate in the postphase, when they lived with other rhesus monkeys only. Adapted from de Waal & Johanowicz (1993).

some inflexible, "instinctive" pattern but is subject to learning. An instructive confirmation of this learning ability can be found in a study of a wild baboon troop that maintained exceptional peacefulness for over a decade as a result of a past incident (Sapolsky & Share, 2004). This flexibility is even more prominent in our own species.

Complexity and Cognition

Like all macaques, pig-tailed macaques form matrilineal societies in which female kin associate with and support one another. Apart from direct reconciliations between former combatants, Judge (1991) found that relatives of the victim tend to seek contact

with the aggressor. For example, a mother may approach and groom the attacker of her daughter in what appears to be a reconciliation "on her offspring's behalf" (p. 234). If such triadic reconciliation protects the victim's matriline against further hostilities, all of its members benefit, including the individual who went to contact the aggressor.

If monkeys sometimes reconcile "for" their matriline, the same mechanism could operate between groups. Intergroup relations tend to be hostile, but on a number of occasions, adult females of different free-ranging groups have been observed to come together for grooming. Several such contacts took place shortly after intergroup fights and involved the alpha females of both groups (Judge & de Waal, 1994). These contacts may serve to reestablish peace between groups.

The complexity of peacemaking interactions is even greater in chimpanzees. In this species, individuals act as though they know the meaning of reconciliation not only for themselves but also for others. The following are typical examples of the cognitive complexity of peacemaking in the Arnhem chimpanzee colony.

Third-Party Mediation. If, after a fight between them, two male rivals stayed in prolonged proximity without engaging in an actual physical reunion (an apparent deadlock situation), an adult female might initiate a grooming contact with one of the two. After several minutes of grooming, she would slowly walk to the other male, often followed by her grooming partner. If he failed to follow, she might return to tug at his arm. After the three individuals had been together for a while with the female in the middle, she would then get up and stroll away, leaving the males alone.

Deception. On six occasions, a dominant female who had been unable to catch a fleeing opponent was observed to approach this individual some time afterward with a friendly appearance, holding out her hand, only to change her behavior when the other came within reach. Reasons to regard the subsequent attack as the female's real intention are its timing (very sudden, without warning signals), the fact that all instances concerned victims capable of outrunning the aggressor, and the intensity of the punishment.

Strategic Reconciliation. Reconciliation may occur in a hurried fashion if continuation of the fight would harm the interests of both individuals. For example, in the years that the Arnhem colony was ruled by a coalition of Nikkie and Yeroen, the alpha male, Nikkie, could get in serious trouble during prolonged conflicts with his partner. A third male would begin an intimidation display, initially terrorizing the females and juveniles but later displaying closer and closer to the two quarreling males themselves. Nikkie was never observed to control the third male on his own. He would first approach his opponent, Yeroen, with a large grin, seeking an embrace. Only after reestablishment of contact with his partner would Nikkie go over to the third male to subdue him.

Control Role. In many primates, high-ranking males break up fights. This so-called control role is perhaps best developed in chimpanzees. Males who adopt this role move from the usual support of winners in fights to loser support and dissociate their

intervention tendencies from individual preferences. That is, they are the only group members to intervene in fights impartially. They may move with all hair on end between two combatants until they stop screaming, scatter them with a charging display, or literally pry locked fighters apart with both hands. In all of this, their main objective seems to be to put an end to the hostilities rather than to support one party or the other. The following description illustrates how Luit, within weeks of attaining alpha status in the Arnhem colony, adopted the role.

> 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. I had never seen him act so impressively before. (de Waal, 1982, p. 124)

Distress Alleviation and Empathy

Postconflict contact between former opponents should be distinguished from postconflict contact by one of the participants in a fight with a bystander (i.e., an individual who had not been involved in the fight). Such contacts, especially when initiated by the bystanders themselves, cannot serve the same function as reconciliation (which is to repair a disturbed relationship). The most likely function of contact with bystanders is distress alleviation.

Sensitivity to the emotions of others emerges early in humans, such as when a nursery room with infants bursts out crying in response to the cries of one among them. This process, known as *empathic distress* or *emotional contagion*, provides the ontogenetic basis for cognitively more advanced responses to distress in which the actor understands the other's situation, distinguishes the other's distress from his or her own feelings, and acts out of genuine concern about the other's well-being. Hence, dependent on the precise mechanism involved, empathy, or the capacity to be emotionally affected by someone else's feelings, can be cognitively simple or complex.

An early study of chimpanzees found that affiliative contact between participants in a fight and bystanders occurred more often in the first minute following a conflict than in subsequent minutes (de Waal & van Roosmalen, 1979). Moreover, first-minute contacts included more embracing and gentle touching than did contacts during subsequent minutes. Contacts with bystanders were labeled *consolation*. Recent research confirmed these findings, demonstrating that it is particularly with victims of serious aggression that contact is made (de Waal & Aureli, 1996; see Figure 2.6). These are, of course, also the individuals expected to be most in need of comfort.

In macaques, in contrast, none of the studies addressing this behavior have thus far produced evidence for consolation. Despite various measures and statistical methods, the finding has been the same in four different species: Affiliative contact between recipients of aggression and bystanders does not occur more often following

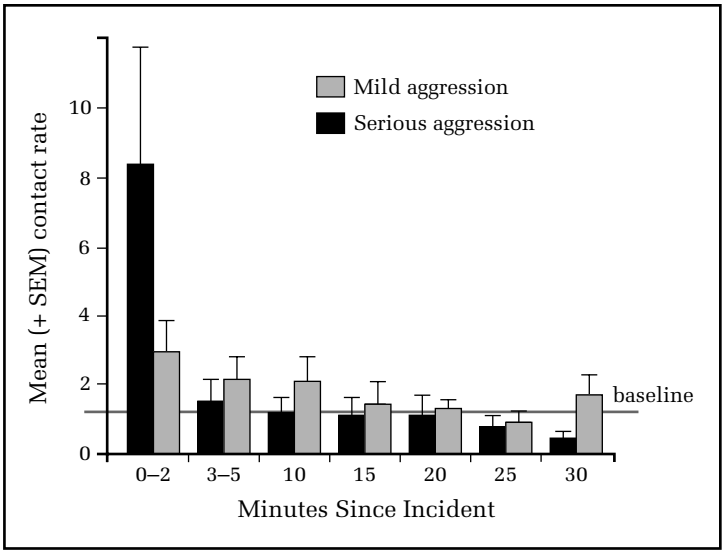

FIGURE 2.6. The rate with which third parties contact victims of aggression in chimpanzees, comparing recipients of serious and mild aggression. Especially in the first few minutes after the incident, recipients of serious aggression receive more contacts than baseline. Adapted from de Waal & Aureli (1996).

conflict than during control periods. Despite this lack of evidence, qualitative observations suggest that macaques do engage in consolation behavior, at least when very young. We have regularly seen infant rhesus monkeys being attracted to the screams of one among them (e.g., after punishment by an adult or after a fall), approach the vocalizer, and establish contact. Occasionally, this resulted in a pile of infants clambering over each other. Given this strong empathic distress response, why is there so little of it left at later ages?

One possible explanation is that association with the recipient of aggression is fraught with risk. In macaques, recipients of aggression continue to attract aggression in the period immediately following the aggressive incident. If this elevated chance of further aggression extends to bystanders who approach recipients of aggression, this is a risk with which bystanders need to reckon. Perhaps these risks are less important in a chimpanzee society with its looser and more tolerant hierarchy.

The alternative explanation is that chimpanzees achieve a higher level of cognition that allows a sharper distinction between self and other. It is generally recognized that the development of empathy in human children relates to this distinction, hence to the level of self-awareness of the child. Given that chimpanzees can recognize themselves in mirrors, whereas macaques cannot, it is possible that chimpanzees achieve a level of empathy that is simply not present in most other primates (Gallup, 1982).

Physiological Correlates

One finding from clinical observations is that forgiveness negatively correlates with anxiety. Those who have forgiven an opponent show a significant decrease in level of anxiety (Fitzgibbons, 1986). Anxiety studies have also been conducted on nonhuman primates, making use of a behavioral index. It was proposed by Schino and colleagues (Schino, Scucchi, Maestripieri, & Turillazzi, 1988) that anxiety can reliably be measured in nonhuman primates through certain self-directed behaviors, such as self-scratching. In fact, Aureli and van Schaik (1991) found that among long-tailed macaques, the levels of self-scratching increased among recipients of aggression soon after having been attacked. Aureli also showed that among Barbary macaques, not only the recipients of aggression but also the aggressors increased self-scratching immediately following a conflict (Aureli, Das, & Veenema, 1997). This anxiety may reflect generalized arousal following conflict or it may in fact be a result of the temporary uncertainty within the relationship between two individuals. Support of the later explanation came from the observation that scratching occurred more often after conflict between strongly affiliated individuals. Most importantly, the studies by Aureli indicate that reconciliation is very effective in reducing or eliminating arousal, as measured by self-directed behavior.

Heart rate studies support some of these conclusions. Heart rate was measured in captive rhesus macaques engaged in aggressive conflicts (Smucny, Price, & Byrne, 1997). The heart rate of both the aggressor and victim rose following an aggressive interaction, taking longer to drop back to baseline in the victim than the aggressor. If reconciliation occurred between two opponents, there was a significant reduction in the elevated heart rate, returning to baseline levels. Aureli and colleagues also looked at changes in heart rate associated with different interactions between individual rhesus macaques living in a group situation (Aureli, Preston, & de Waal, 1999). Subjects showed a significantly increased heart rate if approached by a dominant individual but no change if approached by kin or a subordinate. It was further found that heart rates dropped in individuals engaged in social grooming.

Another study looking at physiological aspects of emotional response in the chimpanzee was conducted by Parr (2001). In this experiment, chimpanzees were shown videos and images that were believed to cause an emotional reaction while recording changes in skin temperature. In humans, it has been shown that decreases in skin temperature are associated with negative emotional arousal. The stimuli presented contained images of a hypodermic needle or dart gun, scenes of unknown conspecifics being injected, and veterinarians threatening chimpanzees with the dart gun. The largest decreases in temperature were recorded when individuals were shown the needle or dart gun, as well as when observing conspecifics being injected. It is not possible from this study to determine whether these changes were due to the subject's own fear of those stimuli or whether they indeed were responding with empathy toward the individual in the images.

How Is Aggression Avoided?

One function of dominance hierarchies, as found in many animals, is to regulate access to resources so that individuals do not need to contest priority every time there is a potential for competition. Mostly, the subordinate withdraws, and the dominant obtains the resource. This way, aggression is avoided, and the relationship is not undermined. Loss of the resource by the subordinate may appear costly, but had this individual attempted to prevent the other from claiming the resource, it most likely would not have gained much more than injuries and a damaged relationship. Conformity to the dominance hierarchy through avoidance of dominants is an effective way of resolving routine disputes.

Apart from avoidance, the approach of a dominant individual can also elicit special gestures or facial expressions in the subordinate. Primates have evolved ritualized status signals. Well-known examples are the bared-teeth display of rhesus macaques and the pant-grunt of chimpanzees. These submissive displays are completely unidirectional (i.e., only one individual in a given pair shows these signals toward the other). The most likely function is appeasement in order to avoid harmful confrontation.

Social conflict can also occur under circumstances and for reasons that do not involve direct competition. As Mason (1993) points out, the most common source of conflict occurs when one individual expects some form of "satisfaction" from another but fails to achieve it. For example, one individual seeks to have sex with or groom another and is rebuffed. This type of conflict rarely leads to aggression but is resolved by a process of negotiation in which the participants exchange signals to increase the predictability of the other's future behavior and to facilitate the achievement of a common goal.

This process is more evident when individuals encounter one another for the very first time, as arranged in some introduction experiments. At the beginning, the encounter is characterized by mistrust and/or hostility, after which various signals help reduce the level of uncertainty and establish a relationship. This process of negotiation leads to the reduction of ambivalence and the achievement of common objectives or a compromise between the objectives of the two parties involved.

Sometimes negotiation is not successful, and one participant may attack the other. One of the most striking examples of overt aggression is when males compete over access to a mate. Among baboons, one male, alone or together with an ally, may attack another male who is in consort with an estrous female. However, nonaggressive tactics are also available to solve these competitive situations. Greeting rituals, in which one male gently touches or mounts another, are common during tensions among male baboons over sexual access to a female. When the number of estrous females is low, compared with the number of males, the chance of mating for an individual male is reduced. Interestingly, under these circumstances, the rate of male aggression stays the same but greeting rituals occur more often. This suggests that greetings decrease tension between males and lower the risk of intermale aggression through increased tolerance (Colmenares, 1991).

In captivity, primates have even more reasons to stop or prevent aggression than in the wild. This situation, with its reduced interindividual distances, offers an excellent opportunity to study conflict management capacities. A traditional view predicts that aggression increases under crowded conditions. Recent research on nonhuman primates has suggested an alternative view. Primates, and perhaps other animals as well, cope with high population density by conflict-avoidance strategies (de Waal, 1989). The way space restrictions affect social behavior varies per species and per situation, but the expected aggression increase under high-density conditions is often minimal and sometimes even reversed. In chimpanzees, it was found that during short-term crowding, the rate of agonistic behaviors was lower than during normal conditions (Aureli & de Waal, 1997). Under short-term crowding in rhesus monkeys, there was no significant increase in intense aggressive behaviors (Judge & de Waal, 1993). In fact, submissive behaviors such as avoidance actually increased under these conditions. Likewise, during long-term crowding, male rhesus monkeys increased grooming and huddling, but there was no increase in the rates of aggression (Judge & de Waal, 1997). This affiliation strategy probably functions to increase social tolerance and limit the potentially damaging effects of aggression.

NEW RESEARCH DIRECTIONS

Advances in technology may provide us with more direct insight into the underlying cognitive and possible emotional processes that are involved during conflicts and reconciliation. Brain regions have been identified in humans that appear to correspond to empathy and forgiveness processes. Through the use of functional magnetic resonance imaging (fMRI), it may be possible to present tasks to nonhuman primates, which may elicit similar responses, while monitoring the brain activity. If these regions are similar, more definite conclusions can be drawn as to the cognitive and emotional similarities and differences across species.

Another area for further research is the inclusion of data from wild populations. This process is currently well underway, with at least a dozen projects on wild primates either being published (e.g., Kutsukake & Castles, 2004; Wittig & Boesch, 2003) or ongoing. The rates of reconciliation are sometimes lower in the wild, but it is obvious that the principles of conflict resolution are essentially the same, meaning that we can gain a fuller understanding of the mechanisms and their evolution by combining controlled studies in captivity with detailed data from the field.

CONCLUSION

Nonhuman primates live in socially complex groups in which they rely for survival on other individuals. It is crucial to maintain cooperative relationships. Although there are competitive situations in which aggression may be inevitable, it is also essential to

repair the damage to ensure future cooperation. We have provided evidence showing that reconciliation and other forms of conflict resolution among nonhuman primates are widespread. Given the problem of determining the psychological underpinnings of these behaviors, we are unable to conclude that nonhuman primates do in fact forgive former opponents. However, studies have clearly shown that behavioral correlates of anxiety are significantly reduced following reconciliation between former opponents. In some species, such as the chimpanzee, the importance placed on maintaining relationships may be seen in the repertoire of behavior used specifically for reconciliation. However, the tendency to reconcile is not necessarily hard-wired and can be modified by the surrounding environment, as seen when species with differing conciliatory tendencies are brought together. Conflict resolution is a highly flexible process and, therefore, a social skill that takes into account the value of social relationships and the level of cooperation required for successful group life.

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