THE FORM AND FUNCTION OF RECONCILIATION IN PRIMATES

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■ **Abstract**   Sociality is favored by natural selection because it enhances group members' access to valued resources or reduces their vulnerability to predators, but group living also generates conflict among group members. To enjoy the benefits of sociality, group living animals must somehow overcome the costs of conflict. Nonhuman primates have developed an effective mechanism for resolving conflicts: They participate in peaceful postconflict (PC) reunions with former opponents. These peaceful PC interactions are collectively labeled reconciliation. There is a broad consensus that peaceful contacts among former opponents relieve stressful effects of conflict and permit former opponents to interact peacefully. Primates may reconcile to obtain short-term objectives, such as access to desirable resources. Alternatively, reconciliation may preserve valuable relationships damaged by conflict. Some researchers view these explanations as complementary, but they generate different predictions about the patterning of reconciliation that can be partially tested with available data. There are good reasons to question the validity of the relationship-repair model, but it remains firmly entrenched in the reconciliation literature, perhaps because it fits our own folk model of how and why we resolve conflicts ourselves. It is possible that the function of reconciliation varies within the primate order, much as other aspects of cognitive abilities do.

MAKING AMENDS

Conflict is a common consequence of group living. Sociality is favored among primates by natural selection because it enhances group members' access to valued resources (Wrangham 1980, 1987) or reduces their vulnerability to predators (van Schaik 1983, van Schaik & van Hooff 1983), but group living also generates competition and conflict among group members (Isbell 1991, van Schaik 1983, van Schaik & van Hooff 1983). To enjoy the benefits of sociality, group living animals must somehow overcome the disruptive effects of competition and conflict.

Many species of nonhuman primates have developed an effective mechanism for resolving conflicts. Although disputes seem likely to drive antagonists apart, conflict often has the opposite effect. For example, a female baboon who has just attacked a lower ranking female may subsequently approach her former victim

and grunt softly to her (Castles 1998, Gore 1994, Silk et al. 1996). Experimental and observational evidence indicates that these grunts reassure the victim that the conflict has ended (Cheney et al. 1995) and facilitate peaceful interactions among former opponents (Cheney & Seyfarth 1997, Silk et al. 1996). In a wide range of primate species, former opponents are much more likely to interact peacefully or sit together in the minutes that follow conflicts than they are at other times. The behaviors that constitute these peaceful postconflict reunions are collectively labeled reconciliation.

Reconciliation has now been documented in more than two dozen species of nonhuman primates (Aureli & de Waal 2000b), as well as in feral sheep (Rowell & Rowell 1993), domestic goats (Schino 1998), spotted hyenas (Hofer & East 2000), and bottle-nosed dolphins (Samuels & Flaherty 2000). Reconciliation occurs in all major taxa within the primate order, including prosimians, monkeys, apes, and humans, and has become a major focus of empirical and theoretical work in primatology over the last two decades.

THE FUNCTION OF RECONCILIATION

Reconciliation may be favored by natural selection because it settles conflicts swiftly and unambiguously. This might be useful because agonistic interactions have abrupt beginnings but quite indefinite endings. A conflict may end after one episode of aggression, or it may continue and even escalate to a more dangerous level. The recipient of aggression may submit, retaliate, or recruit support from powerful allies. This uncertainty makes the period following conflict stressful for both aggressors and their victims (Aureli et al. 1989, Aureli & van Schaik 1991, Das et al. 1997). Uncertainty also precludes further contact among former opponents because it is risky to reestablish contact when the intentions of former opponents are uncertain.

Reconciliatory behaviors, such as female baboons' grunts, may be signals that inform the recipient that the current conflict is over and the actor's intentions are now benign (Silk 1996, 1997). Signals of nonaggressive intent may be favored by selection because they enable former opponents to coordinate their interactions (Silk 1997). Imagine that a conflict takes place between two female monkeys. The aggressor does not intend to continue fighting; she would like to be groomed. The victim aims to avoid further aggression and would rather groom her former aggressor than retaliate against her. In this situation, it is important for females to be able to signal their intentions because there is real uncertainty about what will happen next. If no signals that convey this information are given, both parties may be wary of each other and reluctant to approach. If dishonest signals are given neither will benefit. For instance, if the aggressor signals that her intentions are nonaggressive and then resumes her attack, the victim will flee, and there will be no grooming. Similarly, if the victim signals peaceful intentions and then retaliates, the aggressor will either fight or flee, but will not groom. If grooming is more beneficial than fighting at this juncture, then both parties benefit from sending truthful signals

about their peaceful inclinations. Since there is no incentive for deception, these signals are expected to be inexpensive and inconspicuous (Silk et al. 2000).

Alternatively, reconciliation may be adaptive because it preserves the quality of valuable social bonds. De Waal & van Roosmalen (1979) originally chose the term reconciliation to describe peaceful postconflict reunions among captive chimpanzees because it was their subjective "impression that such body contacts have a calming effect and serve an important socially homeostatic function" (1979:65). This "homeostatic function" was hypothesized to be important because it preserves the cohesion of social groups by reducing the disruptive effects of conflict. In more recent formulations of this model, the emphasis has shifted from the maintenance of group cohesion to the preservation of valuable[1] social relationships among individuals (e.g., Cords 1988; de Waal 1989, 1993; de Waal & Aureli 1996; Kappeler & van Schaik 1992). Peaceful contact among former opponents is favored by natural selection because it contributes to the stability of social bonds, which ultimately enhances reproductive fitness.

Some workers have argued that the benign-intent and relationship-repair models are complementary, not alternative, explanations of why reconciliation occurs (de Waal 2000, Cords & Aureli 1996). According to this view, the long-term effects on social relationships may be incidental, albeit advantageous, side effects of reconciliatory behavior: "The habit of reconciling conflicts might make social partners get along better over the long run by increasing a dominant's tolerance of the subordinate, and by decreasing chronic stress in the subordinate. Repeated occasions in which partners communicate their common interest in each other by reconciling after conflict may increase the predictability of their interaction patterns, and hence their ability to interact in adaptive ways" (Cords & Aureli 1996:45).

All interactions between two individuals contribute incrementally to the history of events that define their relationship (Hinde 1983), so peaceful reunions after conflicts will inevitably, but indirectly, influence the nature and quality of social bonds. But this does not necessarily mean that natural selection has favored the evolution of reconciliatory behaviors *because* they enhance long-term social bonds. This is an important distinction because the selective forces that favor the evolution of signals of benign intent may be quite different from the selective forces that shape the evolution of social bonds among females. The distinction also becomes meaningful when we consider how reconciliation is patterned in nature. The two

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[1]In this context, value is defined in terms of reproductive fitness. According to evolutionary theory, natural selection is expected to favor the evolution of behaviors that enhance the fitness of individuals. Altruistic behaviors, which enhance the fitness of others and reduce the fitness of the actors, can evolve via kin selection (Hamilton 1964) or reciprocal altruism (Trivers 1971). Kummer (1978) suggested that the same logic applies to evolutionary forces shaping the formation and maintenance of social relationships. Animals are expected to selectively invest in relationships from which they gain benefits that exceed their costs, and work hardest to cultivate relationships from which they derive the greatest profits. Again, benefits and costs are defined in terms of their effects on reproductive fitness.

models generate different predictions about the frequency of reconciliation across species, groups, and dyads (Silk 1996, 1997, 2000). Thus, the empirical record holds important clues about the function of these interactions.

Alternative Strategies for Resolving Conflicts

It is important to emphasize that reconciliation is not the only tactic that primates use to resolve conflict. Redirected aggression provides another means for reducing the stressful consequences of conflict in some species. After conflicts, monkeys sometimes initiate aggression against third parties who were not involved in the original dispute (Watts et al. 2000). Male baboons who characteristically redirect aggression tend to have lower levels of basal glucocorticoids, hormones secreted in response to stress, than males who do not do so (Ray & Sapolsky 1992, Sapolsky & Ray 1989, Sapolsky 2000, Virgin & Sapolsky 1997). It is not entirely clear why redirected aggression has this effect, but it may be linked to the fact that monkeys are able to reduce uncertainty about subsequent events by redirecting aggression (Aureli & van Schaik 1991). Long-tailed macaques who redirected aggression to third parties during postconflict periods were less likely to become the targets of further aggression themselves than monkeys who did not redirect aggression or reconcile with their former opponents. Redirected aggression and reconciliation were equally effective in protecting the victim against further harassment from former aggressors. This was directly reflected in change in rates of some self-directed behaviors. Monkeys that redirected aggression or reconciled conflicts peacefully scratched themselves less often than monkeys who did not reconcile or redirect aggression (Aureli & van Schaik 1991).

In some species, reconciliation apparently does not occur at all. Red-bellied tamarins, ring-tailed lemurs, and white-faced capuchins all live in cohesive social groups, but apparently do not reconcile after conflicts (Schaffner & Caine 2000, Perry 1995, Kappeler 1993).

Measuring Reconciliation

Reconciliation is a functional label, like affiliation or aggression, not a descriptive one, like grooming or biting (Cords 1993, de Waal & van Roosmalen 1979). In ordinary English, reconciliation refers to the settlement of conflicts or inconsistencies and the restoration of peaceful or amicable relations,[2] a meaning that is embodied

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[2]De Waal (2000) writes "According to my English dictionaries, 'reconciliation' refers to the reestablishment of close relationships and the settlement of conflict" (p. 21). However, the closeness of relationships does not figure prominently in definitions of 'reconciliation' in at least two major dictionaries. The *Random House Dictionary* defines reconcile as: "(1) To render no longer opposed, bring to acquiescence or acceptance; (2) to win over to friendliness, cause to become amicable; (3) to compose or settle (a quarrel, dispute, etc.); (4) bring into settlement or harmony; make compatible or consistent." (There are a number of additional definitions that are used in religious contexts.) The *Oxford English Dictionary* lists a number of definitions that are related to conflict resolution: "(1) To bring a person

in both of the working models described above. The use of this term is justified if we can demonstrate that nonaggressive interactions after conflicts enable former opponents to settle disputes and restore peace (Silk 1998). Despite this, most studies of reconciliation have relied on an operational definition of the behavior, and it is "assumed that behavior that fits the prescribed criteria of operationally defined reconciliation does actually function to restore, or at least improve, the relationship between former opponents after aggressive conflicts" (Cords 1993:256).

Studies that make use of operational definitions of reconciliation rely on comparisons between the sequence and timing of events that occur after conflicts and the sequence and timing of events that occur at other times (Veenema 2000). This is done by comparing events during a specified period of time after conflicts (the postconflict period) with events observed during a control period [the matched-control (MC) period]. Control samples are generally matched for time, activity, and sometimes for proximity among former opponents. In the PC-MC method, for example, former opponents are said to be "attracted" if they make contact during the postconflict period but not the MC period, or if they make contact earlier in the postconflict period than in the MC period (de Waal & Ren 1988). The timed-rule method (Aureli et al. 1989) is based on the fact that former opponents often make initial affiliative contact very early in the postconflict period, whereas first contacts are more evenly distributed through MC observations. Reconciliation is thus defined as any affiliative contact among former opponents that occurs during the interval in which the two distributions are disjunct (Figure 1).

Some studies have developed explicitly functional assays of reconciliation. For example, Cords (1993) investigated how nonaggressive postconflict interactions among captive long-tailed macaques influence their tolerance of one another at drinking bottles. After conflicts, monkeys were normally less willing to drink in close proximity to higher-ranking opponents. But monkeys who made physical contact, sat together, or exchanged friendly signals with their former opponents were more tolerant of their former opponents while drinking than monkeys who did not participate in these kinds of behaviors. Thus, these peaceful postconflict interactions were apparently effective in reconciling former opponents. Similarly, free-ranging female baboons who grunted to their former opponents after conflicts were more likely to subsequently interact peacefully and less likely to harass or supplant their former opponents than females who remained silent after conflicts (Figure 2). Thus, postconflict grunts were interpreted as reconciliatory signals that facilitated peaceful interactions among former opponents (Silk et al. 1996).

These two studies have also examined the effectiveness of particular kinds of signals in resolving conflicts. In long-tailed macaques, proximity is as effective in

again into friendly relations to or with (oneself or another) after an estrangement; (2) to win over (a person) again to friendship with oneself or another; (3) to set (estranged persons or parties) at one again; to bring back into concord, to reunite (persons or things) in harmony; (4) to bring (a person) back to, into peace, favour, etc . . . (7) to conciliate, recover (a person's favour, etc.); to gain credit, (9) to adjust, settle, bring to agreement."
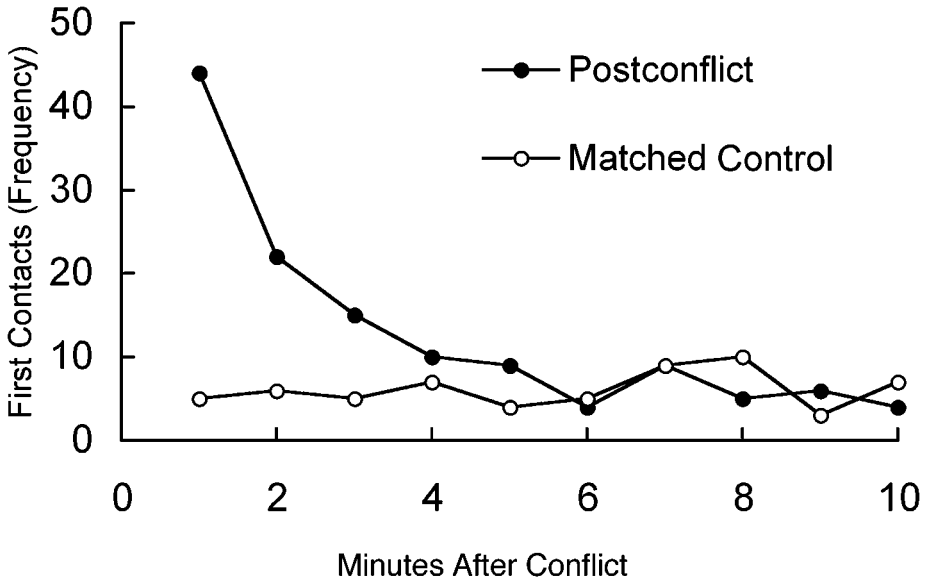
Figure 1 Among captive long-tailed macaques, the frequency of nonaggressive contacts between former opponents (*solid circles*) peaks in the first few minutes after conflicts and then declines to baseline levels. When no conflicts occur (*open circles*), the rate of nonaggressive contacts is uniformly low. (Adapted from Aureli et al. 1989, Figure 1.)

restoring tolerance among former opponents as are more intimate forms of contact (Cords 1993). Proximity maintenance also plays an important role in reconciliation among rhesus and stump-tailed macaques (Call et al. 1996, 1999). Among baboons, however, proximity alone is not sufficient to resolve conflicts: Females must grunt to their former opponents. Field experiments in which reconciliation is simulated by playing the aggressor's tape-recorded grunt to her former victim indicate that grunts by former aggressors are sufficient to reconcile conflicts, even in the absence of any other behavioral cues (Cheney & Seyfarth 1997).[3]

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[3]A number of studies report the sequences of behaviors observed during postconflict and MC observations, attempting to determine whether specific behavioral elements were characteristic of the initial postconflict contact between former opponents. In some species, certain behaviors are more likely to occur earlier in postconflict periods than later in postconflict periods or during MC periods (e.g., de Waal & van Roosmalen 1979, de Waal & Yoshihara 1983, de Waal & Ren 1988, Ren et al. 1991). These studies have two shortcomings. First, they do not examine the efficacy of different types of behaviors in facilitating subsequent affiliation and tolerance or inhibiting further aggression. Second, vocalizations are not included in most of these analyses, although they may play a role in facilitating peaceful postconflict reunions.
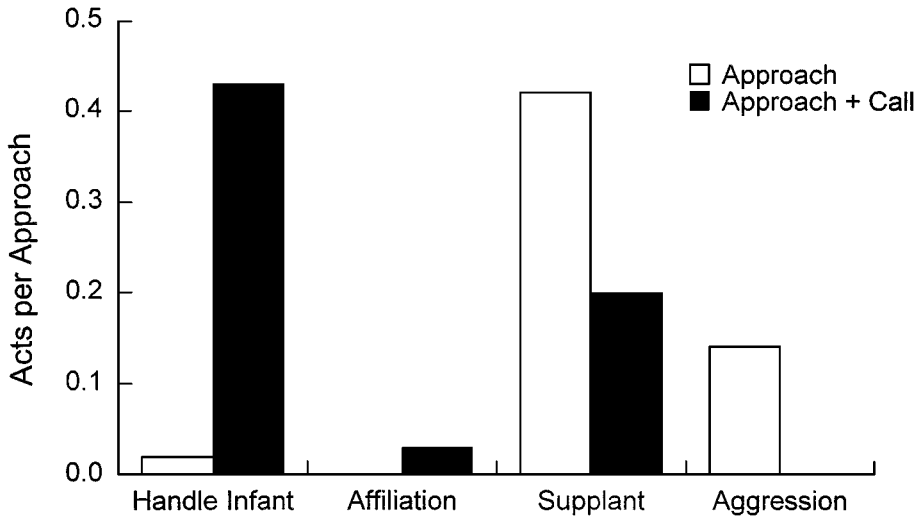
Figure 2   When female baboons approach and grunt to their former opponents during the postconflict period, they are more likely to handle their former opponents' infant and less likely to supplant their former opponents than if they approach and remain silent. (Adapted from Silk et al. 1996, Figure 2.)

FIRST-ORDER EFFECTS OF RECONCILIATION

For primates, conflict is stressful. The heart rates of female rhesus macaques increase sharply after conflicts and remain elevated over baseline levels for several minutes (Smith et al. 1986 cited in Aureli & Smucny 2000, Smucny et al. 1997). Rates of self-directed behaviors, including scratching, yawning, and body shaking, which are associated with physiological measures of stress, also increase after conflict and remain elevated for several minutes (Aureli 1992, 1997; Aureli & van Schaik 1991; Aureli et al. 1989; Castles & Whiten 1998b; Das et al. 1998). Stress is an adaptive short-term response to crises because it produces a set of physiological responses that facilitate rapid responses to danger (Sapolsky 1998, 2000). However, prolonged activation of the stress response is quite debilitating.

Peaceful contact among former opponents reduces stress levels. When female rhesus macaques make peaceful contact with their former opponents in the moments that follow conflicts, their heart rates rapidly decline to baseline levels. This effect is much more marked when females interact with their former opponents than when they interact with other group members or do not interact at all (Smucny et al. 1997). In long-tailed macaques and baboons, rates of self-directed behavior also decline rapidly to baseline levels after peaceful reunions with former opponents, whereas rates of self-directed behavior remain elevated for several minutes if former opponents do not reconcile (Figure 3; Aureli & van Schaik 1991, Castles & Whiten 1998b, Das et al. 1998).
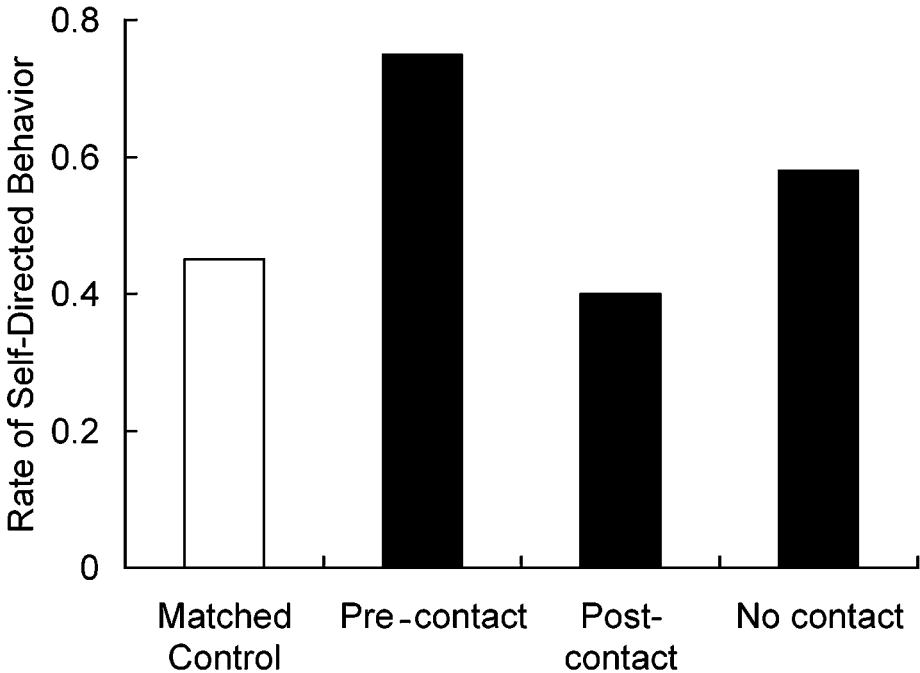
Figure 3   The rate of self-directed behavior by female baboons exceeds baseline rates during post-conflict periods in the minutes preceding peaceful contact and when no peaceful contact occurs. The rate of self-directed behavior falls to baseline levels during the postconflict period after peaceful contact occurs. (Adapted from Castles & Whiten 1998b, Figure 6.)

Further evidence in support of the hypothesis that reconciliation reduces stress because it alleviates uncertainty about subsequent events comes from a playback experiment conducted on free-ranging baboons (Cheney et al. 1995). This experiment took advantage of the fact that female baboons sometimes screamed when other group members attacked them, and victims of aggression sometimes redirected aggression toward lower ranking individuals. Thus, a female who heard the scream of a higher-ranking female might soon become the target of redirected aggression. To determine whether grunting during the postconflict period reduces females' anxiety about whether former aggressors would harass them, the investigators played tape-recorded screams of aggressors to their former victims (*a*) shortly after they had fought and the aggressor had grunted to her former victim, (*b*) shortly after they had fought but the aggressor had not grunted to her former victim, and (*c*) as a control, after a period of 45 minutes in which they had not interacted at all. Females reacted most strongly when they had fought, but the aggressor had not grunted to the victim. Females' responses after grunts had been given matched their responses when they had not interacted at all. Thus, the stressful effects of prior conflicts were remedied by grunts.

Uncertainty Makes Reconciliation More Likely

If the proximate function of reconciliation is to reduce stress that arises from uncertainty about the intentions of others, then we should expect conciliatory tendencies to vary in relation to the degree of uncertainty that exists. Several lines of evidence suggest that this is the case:

1. Conflicts that do not have clearly decided outcomes are more likely to be reconciled than conflicts with clear and unambiguous outcomes (Aureli et al. 1989, 1993; Kappeler 1993).

2. Dyads in which both partners give aggressive signals are more likely to reconcile than dyads in which one partner consistently submits to the other (Aureli et al. 1989).

3. Dyads that are close in dominance rank, and presumably have roughly equivalent competitive ability, tend to reconcile at higher rates than dyads that are more distantly ranked (Aureli et al. 1993, Judge 1991, Silk et al. 1996), and this effect is not entirely due to the fact that kin tend to occupy adjacent ranks (Judge 1991).

4. Reconciliation is more common when aggression is directed up the hierarchy (and contravenes the established dominance order) than when aggression is directed down the hierarchy (Judge 1991).

5. Interspecific comparisons among macaque species indicate that the likelihood of reconciliation is consistently linked to the likelihood that aggression will be directed up the hierarchy. For example, despotic rhesus and Japanese macaques reconcile at lower rates than more egalitarian stumptailed macaques (de Waal & Luttrell 1989, de Waal & Ren 1988). Similarly, the degree of symmetry in aggression is related to the tendency to reconcile among rhesus, long-tailed, Japanese, and Tonkean macaques (Figure 4) (Thierry 1986, 1990). Finally, comparisons of two groups of long-tailed macaques housed under very similar conditions suggest that despotic dominance styles are associated with lower levels of reconciliation than more egalitarian dominance styles (Butovskya et al. 1996).

6. Nonhuman primates reconcile after aggressive disputes, but they typically do not reconcile after naturally occurring disputes over food [4] (e.g., Castles & Whiten 1998a, Verbeek & de Waal 1997, Watts 1995, Aureli 1992). This may reflect the fact that disputes over food are unlikely to continue once the victim has relinquished the contested food item, and thus they produce little uncertainty and stress.

7. The severity of aggression has little consistent effect on the likelihood of reconciling (Castles & Whiten 1998a, Cords & Aureli 1993, de Waal &

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[4]In a number of experimental studies of reconciliation, disputes are provoked by offering a desirable food item to the subordinate member of a dyad (Cords 1988, Cords & Thurnheer 1993). In these cases, disputes are sometimes reconciled.
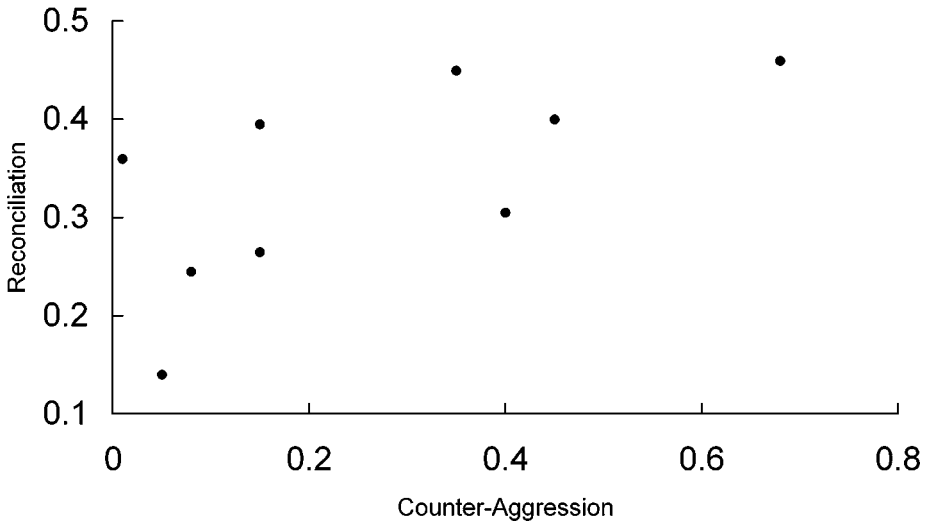
Figure 4   In macaques, the proportion of agonistic contests that involve aggressive signals by both parties is positively associated with the proportion of conflicts that are reconciled ($r = 0.70$, $n = 9$, 1-tailed $p = 0.02$). Data on rates of counter-aggression drawn from Thierry et al. 1997; data on rates of reconciliation drawn from Aureli & de Waal 2000b, Appendix A.

Ren 1988; but see Schino et al. 1998). Since mild conflicts can escalate into severe aggression and severe conflicts may continue for long periods, mild and severe aggression may be equally stressful even though they are not equally dangerous.

DISENTANGLING PROXIMATE AND ULTIMATE BENEFITS OF RECONCILIATION

The data reviewed to this point provide a compelling account of the short-term effects of reconciliation—reconciliation reduces uncertainty about the intentions of former opponents and thereby relieves stress that is associated with not knowing whether hostilities will continue. However, these data do not fully resolve functional questions about why reconciliation occurs. Does natural selection favor the evolution of reconciliation because it preserves valuable social bonds, as the relationship-repair model hypothesizes, or does natural selection favor reconciliation because it permits former opponents to resume peaceful contact as the benign-intent model suggests?

The relationship-repair model predicts that the value, security, and compatibility of a pair's social relationship will influence the likelihood that they reconcile. By contrast, the benign-intent model predicts that primates will reconcile to gain

short-term objectives, which may include access to favored partners or desirable resources. Below, I review evidence that is relevant to evaluating these predictions in an effort to weigh the plausibility of these two functional hypotheses. Readers will soon realize that this is not a straightforward exercise because the two models do not generate orthogonal predictions; multiple interpretations of the same observation are often possible. This means that evidence that supports one hypothesis does not necessarily disconfirm the other and vice versa.

Reconciliation Preserves Valuable Bonds

The relationship-repair model rests on the idea that reconciliation preserves valuable social bonds. This means that the likelihood that two individuals will reconcile is expected to vary in relation to the value of the pair's social relationship. It is difficult to test this prediction directly because we cannot assess the adaptive value of social relationships in quantitative terms. This problem is common to almost all studies of the adaptive function of social behavior in animals. Instead, researchers rely on what Grafen (1991) calls the phenotypic gambit, the assumption that the short-term benefits that individuals derive from social interactions are ultimately translated into long-term differences in fitness. Animals who are regularly supported in agonistic confrontations, protected from harassment, or allowed to share access to desirable resources are expected to gain short-term benefits that are ultimately translated into fitness gains (Cords & Aureli 2000, van Schaik & Aureli 2000). Thus, relationships with allies, protectors, and tolerant group members would be particularly valuable.

Some studies have reported associations between conciliatory tendencies and the frequency of affiliative interactions (see below), and cite these data as evidence that primates reconcile selectively with valuable partners. However, Cords & Aureli (2000) caution against conflating the value of social bonds with the compatibility of partners. They point out that "partners with whom one is especially friendly are often, but not necessarily, very valuable" (p. 187).

Comparisons of the rates of reconciliation among dyads within groups provide some support for the hypothesis that primates reconcile selectively with valuable partners. Thus, monkeys tend to reconcile at higher rates with kin (Schino et al. 1998; Koyama 1997; Call et al. 1996; Castles et al. 1996; Silk et al. 1996; Demaria & Thierry 1992; Judge 1991; Aureli et al. 1989, 1993, 1997; Cheney & Seyfarth 1989; de Waal & Ren 1988; York & Rowell 1988; de Waal & Yoshihara 1983) who are most likely to provide coalitionary support. These data suggest that the value of social bonds influences the tendency to reconcile, but this conclusion must be viewed with some caution. First, there is little evidence that the frequency of coalitionary support is directly linked to reconciliatory tendencies. Even if such correlations were established, conclusions about the causal processes underlying the correlations would not be justified. Monkeys may reconcile and support kin because they gain important inclusive fitness benefits from interacting with kin, generating a spurious correlation between coalitionary support and conciliatory tendencies (Hemelrijk & Ek 1991).

To my knowledge, only two studies have assessed the relationship between coalitionary support and reconciliation directly. In a study of juvenile macaques, Cords & Aureli (1993) monitored patterns of support in agonistic contests. Juveniles were equally likely to reconcile with monkeys that had previously supported them as with monkeys who had not done so.[5] Similarly, captive chimpanzees did not reconcile selectively with those that supported them most often (Preuschoft et al. 2002).

Evidence from great apes provides support for the idea that primates reconcile selectively with valuable partners. Thus, male chimpanzees, who rely on one another for coalitionary support (Boesch & Boesch-Achermann 2000, de Waal 1986, Goodall 1986), reconcile at higher rates than do females (de Waal 1986, Goodall 1986). Female gorillas selectively reconcile disputes with resident males, on whom they rely for protection from strange males (Watts 1995). However, there is no direct evidence linking support or protection and conciliatory tendencies in chimpanzees (Preuschoft et al. 2002) or gorillas, and alternative explanations cannot be ruled out.

In response to the difficulties of measuring the value of social relationships, Cords & Thurnheer (1993) designed an experiment in which they artificially manipulated the value of other individuals in the group and examined the subsequent effect on reconciliation. The study focused on seven pairs of female long-tailed macaques drawn from a large and stable captive group. In the first phase of the experiment, reconciliatory tendencies in each dyad were evaluated by the pair's behavior after conflicts were artificially provoked. In the second phase of the experiment, each pair was trained to perform a cooperative task in which access to a desirable food was contingent on their mutual tolerance. In the third phase of the experiment, the reconciliatory tendencies were evaluated again, using the same methods as in the first phase of the experiment. If reconciliation is influenced by the value of social bonds, then an increase in the rate of reconciliation was expected to be observed. Six of the seven dyads performed as expected; rates of reconciliation increased after monkeys had been trained to cooperate on the feeding task. It is not known whether the tenor of females' social relationships was altered when they returned to their social groups. Cords & Thurnheer (1993) concluded that their results were "consistent with the hypothesis that monkeys reconcile more often with a former opponent when that opponent is more valuable to them."

Reconciliation is Influenced by the Security of Social Bonds

The security of social bonds may also influence the benefits of reconciling (Cords 1988). Dyads that have valuable, but insecure, relationships are expected to be particularly motivated to reconcile because conflict is likely to be especially disruptive. By the same token, dyads whose relationships are valuable, but secure,

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[5]In this case, the categorical distinction between supporters and others may be problematic. A more fine-grained measure of alliance support, taking into account the amount and type of support provided, might generate different results.

should have little need to reconcile because their relationships are unlikely to be disrupted by conflict. This prediction has not been tested directly, partly because methods for measuring the security of social bonds have not been developed and validated (Cords & Aureli 2000). However, the theory of kin selection (Hamilton 1964) suggests that social relationships among close relatives will be particularly resilient because individuals can enhance their inclusive fitness when they help their relatives. Among kin, altruism is favored whenever the $br > c$, where $b =$ the fitness benefits gained by the recipient, $r =$ the degree of relatedness between the actor and the recipient, and $c =$ the fitness costs incurred by the actor.

If relationships among kin are less likely to be disrupted by conflict than relationships among nonkin, then it should require less effort to maintain bonds among them (Cords 1988). This prediction does not figure in recent writings about the pattern of reconciliation (e.g., Cords & Aureli 2000, de Waal & Aureli 1996), but the logic seems compelling. In all but one study, kin reconciled at least as often as nonkin did (Cords 1988). High rates of reconciliation among kin seem to contradict the predicted relationship between reconciliatory tendencies and the security of social bonds.

Reconciliation is Influenced by Compatibility

All other things being equal, compatible dyads are expected to reconcile at higher rates than others because they are more accessible to one another: "When the members of a dyad are in the habit of interacting in nonantagonistic ways in many contexts, it may be easier for them to engage in a friendly postconflict reunion because this is the sort of interaction they usually have with each other, and so it is a familiar course of action" (Cords & Aureli 2000). Compatibility is typically measured by the frequency of affiliative and agonistic interactions within dyads, but methods of assessing social bonds have not been fully standardized.

Compatibility is linked to reconciliation in a number of groups, as those with close and friendly relationships reconcile a greater proportion of their conflicts than those with hostile or weak relationships (Call et al. 1999, Schino et al. 1998, Castles et al. 1996, Cords & Aureli 1993, Aureli et al. 1989, de Waal & Ren 1988, de Waal & Yoshihara 1983). This result is not entirely due to the confounding effects of kinship[6] (Call et al. 1999, Schino et al. 1998, Cords & Aureli 1993, Aureli et al. 1989, de Waal & Yoshihara 1983).

Reconciliation Facilitates Short-Term Objectives

The benign-intent model suggests that primates reconcile primarily in order to obtain short-term objectives, such as access to a desirable resource or tolerance by a preferred partner. Preferences may be based on ephemeral features, such as

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[6]In some cases, the confounding effects of kinship are eliminated by examining the effects of relationship quality only among nonkin. In other cases, the effects of both kinship and relationship quality on conciliatory tendencies are examined in multivariate analyses.

reproductive status or possession of a valuable resource, or on more stable features, such as kinship.

Although many researchers argue that Cords & Thurnheer's (1993) experimental results provide compelling support for the relationship-repair model, the results are also compatible with the hypothesis that monkeys can learn to use reconciliation in an instrumental way to gain access to a valued resource. In Cords & Thurnheer's experiment, monkeys were allowed to feed on the desirable food item only if their partner fed simultaneously. If females anticipated being chased or attacked when they approached the feeding site or their partner, they might avoid coming close, thus preventing their partner from feeding. To avoid this undesirable outcome, both partners may benefit from communicating their intention to behave peacefully. Thus, monkeys may become more conciliatory to enhance prospects for tolerance, not because they came to value their relationships with their partners more highly.

Studies of captive chimpanzees suggest that they sometimes use conciliatory behaviors for instrumental purposes. Koyama & Dunbar (1996) found that rates of grooming and proximity were substantially elevated during the hour that preceded the regularly scheduled presentation of tightly clumped foods. After the food was presented, the chimpanzees spent the most time near the individuals that they had previously groomed and sat near. This suggests that they were "attempting to increase tolerance and facilitate co-feeding" (Koyama 2000).

Further evidence that primates may use reconciliation to gain strategic short-term objectives comes from studies of free-ranging baboons. Female monkeys are strongly attracted to infants, particularly newborns, and eager to handle them (e.g., Altmann 1980, Bauers 1993, Silk 1999). Although handling seems relatively benign in most cases, mothers respond warily when others try to handle their infants. Female macaques and baboons typically grunt as they approach new mothers, and these grunts facilitate infant handling (Silk et al. 2000). Female baboons reconcile selectively with the mothers of young infants (Silk et al. 1996). Moreover, the rate of reconciliation tracks changes in the rate of infant handling as infants mature. Females are most likely to reconcile conflicts with females whose infants they are most eager to handle (Silk 2000; Figure 5). These data suggest that females' decisions to reconcile were based on their motivation to obtain access to infants, not on the value of their long-term relationship with the mother.

RECONCILIATION IN *HOMO SAPIENS*

Reconciliation is an anthropomorphic concept (de Waal & van Roosmalen 1979), so it is not surprising that researchers have begun to delineate conflict resolution strategies in humans. Much of this work is explicitly based on de Waal's hypothesis that reconciliation repairs relationships that have been damaged by conflicts.

Detailed studies of conflict resolution have been conducted on children in the United States and Europe (Butovskaya et al. 2000, Cords & Killen 1998, Schmitt & Grammer 1997, Verbeek et al. 2000). This body of work reveals a number
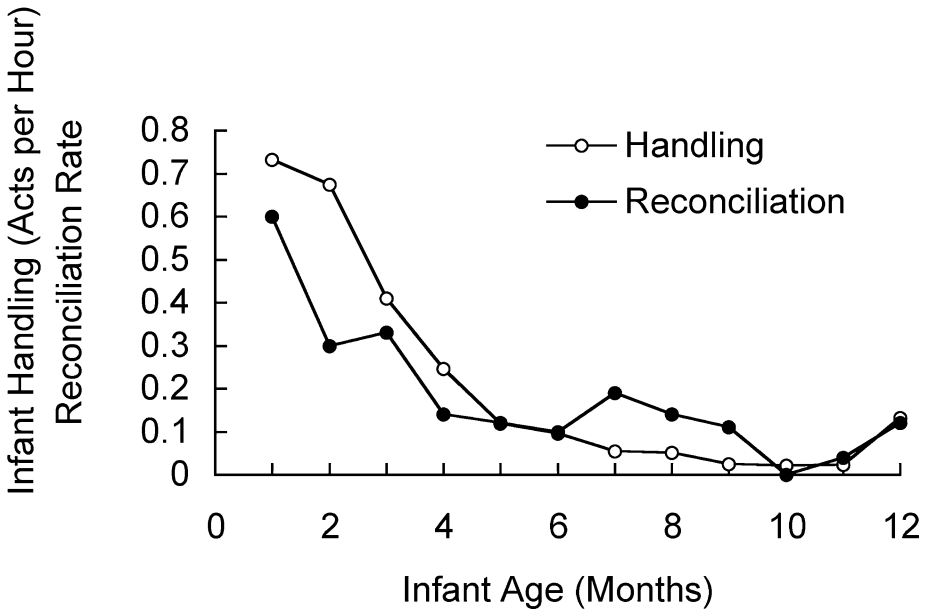
Figure 5 Among female baboons, rates of reconciliation with mothers closely track rates of infant handling. Females are most likely to reconcile with females when they have young, attractive infants. (From Silk 2000.)

of parallels between the reconciliatory behavior of children and other primates. Children often approach one another and make peaceful contact of some sort in the minutes that follow conflicts. The form and timing of these events is remarkably similar to the timing of peaceful postconflict contacts among monkeys (Verbeek 1996; Figure 6). Reconciliatory behaviors sometimes involve physical gestures, such as hugs or embraces, behaviors that are also seen among other primates. Reconciliatory behaviors by children also include verbal apologies, offers to share, and invitations to resume play. In other cases, "implicit" peacemaking strategies are inferred when children resume friendly play without any overt reference to the previous dispute.[7] Young children do not often attempt to mediate conflicts among their peers (Butovskaya et al. 2000), although they often intervene in conflicts on behalf of one of the disputants (Butovskaya et al. 2000, Verbeek et al. 2000).

Several studies have examined how the nature of children's relationships influences the likelihood of reconciling conflicts. In these studies, the quality of children's relationships is assessed by tabulating how often they are together or

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[7]Although "implicit" conflict resolution may seem to be an oxymoron, it is analogous to the elevated level of nonaggressive behavior seen soon after conflicts in many monkey species. Thus, engagement in peaceful interactions by former opponents is interpreted as a tactic for resolving conflicts.
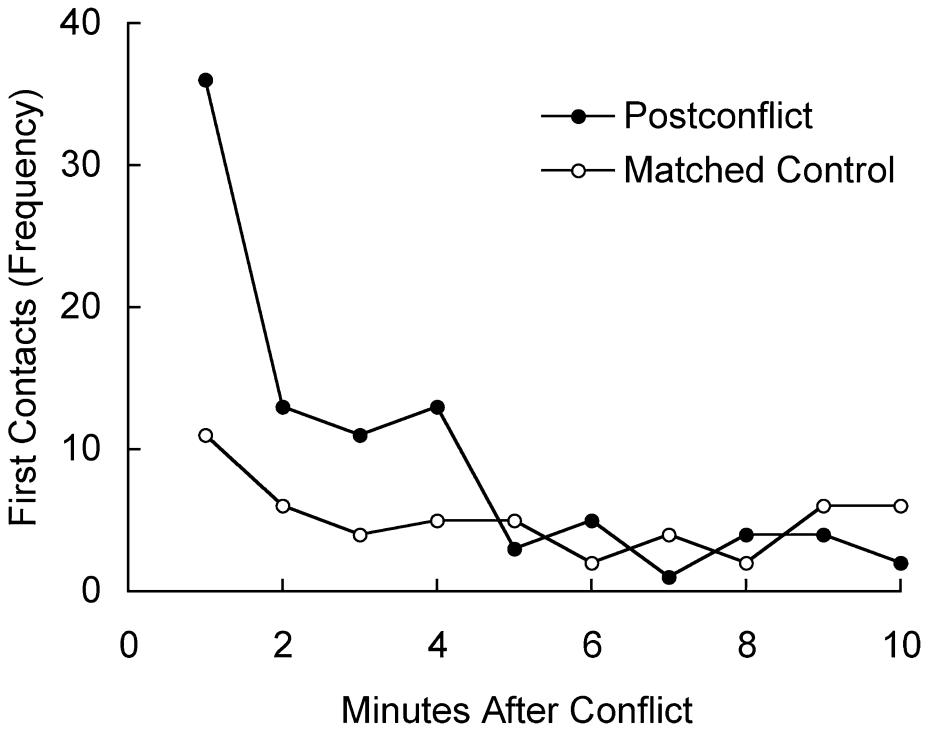
Figure 6   For human children, rates of friendly contact among former opponents peak in the minutes following conflicts and then fall to baseline levels. Note similarities in the course of postconflict interactions among macaques (Figure 1) and children. (Adapted from Verbeek 1996, Figure 3.1.)

how often they play. Friends spend more time together and play more than acquaintances, and acquaintances spend more time together and play more than "nonfriends." For children, Cords & Killen (1998) suggest that friendships, defined in this way, constitute valuable relationships: "Because friends are desirable social partners, and because there is much evidence that relationships with friends are important to children's development, it seems reasonable to take friends as an indicator of value measured in the currency of lifetime reproductive success."

In some studies, children reconcile less often with friends than with acquaintances or nonfriends, while in other studies friends reconcile more often. Drawing on a body of studies conducted by child psychologists, Cords & Killen (1998) conclude that children resolve conflicts with friends at higher rates than with nonfriends. Two studies using methods originally developed for studying conflict resolution in nonhuman primates present a different picture. Russian schoolchildren are nearly twice as likely to reconcile with acquaintances as with their friends (Butovskaya & Kozintsev 1999). When American children part after conflicts,

friends and acquaintances are equally likely to reconcile. However, friends are more likely to stay together after conflicts have ended than are acquaintances (Verbeek 1996, Verbeek et al. 2000).[8] Butovskaya et al. (2000) note that the results of these two studies "do not provide clear evidence that postconflict peacemaking specifically aims at restoring close relationships among children" (p. 253). It is not clear whether the discrepancy between the results cited by Cords & Killen and by Butovskya and her colleagues reflect differences in the methodologies used to assess conflict resolution or differences between the subject pools.

Fry (2000) draws on the ethnographic record to examine conflict resolution strategies in traditional human societies. Reconciliation tends to involve certain common elements in most cultures. These include gift giving or gift exchange; payment of restitution; food sharing; physical contact (i.e., kissing, shaking hands); appeasement postures and gestures; apologies and expressions of remorse and contrition; and mediation by third parties. Fry's review indicates that " . . . conflict resolution often focuses on restoring relationships and involves interested parties beyond the disputants themselves" (p. 347). Relationships that have important economic, social, or political utility are most likely to be reconciled.

Among young children, reconciliation is only weakly linked to friendship and rarely involves the intervention of third parties. In contrast, among adults reconciliation is consistently associated with the maintenance of relationships and frequently involves the intervention of third parties as mediators. This difference in the reconciliation behavior of children and adults may reflect the fact that young children have a limited ability to attribute knowledge, feelings, and intentions to others and to see things from another's perspective. These cognitive properties, collectively termed a theory of mind, are poorly developed in young children (Wellman 1990). De Waal & Yoshihara (1983) have argued that reconciliation does not rely on complex cognitive abilities. All that is needed is the ability to recognize individuals, remember past interactions, and a conciliatory disposition. However, " . . . if reconciliation is selectively employed to manipulate relationship quality, a 'Machiavellian' dimension is added to the cognitive challenge" (Castles 2000:189). To use reconciliation to preserve social bonds, individuals must exercise their conciliatory tendencies selectively. This selectivity is based on the likelihood that conflicts with certain partners in certain situations will have lasting, negative effects on the relationship. It is possible that children and adults may learn the contingencies between conflict and the impact on their relationships with others, or they may rely on innate proclivities to reconcile in certain situations and with certain partners. However, it seems more likely that the selectivity is based on

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[8]Schmitt & Grammer (1997) provide a brief description of the results of a study of conflict resolution among kindergartners. They report that "the probability of reconciliation does not co-vary with friendship, power, dominance, and rank in attention structure, whereas there is a strong and significant correlation with conflict intensity" (p. 99). The authors do not describe the methods that they used to conduct the study or provide details about the subjects of their study.

the ability to understand the impact of conflict on other individuals and requires at least some knowledge of others' minds (Silk 1998). Triadic interactions, including third party mediation, are cognitively demanding (Castles 2000, Tomasello & Call 1997). To mediate disputes among others, individuals must know something about their own relationship to the disputants and the disputants' relationship to one another.

WHAT IS THE MISSING LINK?

The relationship-repair model has been widely accepted in the literature (c.f. Aureli & de Waal 2000b), even though there are substantive reasons to question its validity when applied to nonhuman primates (and human children). The relationship-repair model may be compelling because it fits our own folk model of how and why we resolve conflicts. In daily life, we make frequent use of conflict resolution tactics such as apologies, and we are well aware of the deleterious effects of frequent, unresolved conflicts on our social relationships.

De Waal acknowledges that the relationship-repair model "rests on an anthropomorphic interpretation of animal behavior and as such comes with inevitable human connotations" (de Waal 2000). He defends the application of an anthropomorphic approach to the study of the behavior of monkeys and apes: "The decision making underlying much of what these animals do strikes the human observer as very familiar. Provided that it is based on intimate knowledge and translated into testable hypotheses, anthropomorphism is a very useful first step toward understanding a psychology similar to and almost as complex as ours" (De Waal 1989:25). Contemporary social scientists generally think of anthropomorphism in pejorative terms, but it can be a useful device when employed with caution: "Heuristic anthropomorphism, when pursued as an explicit strategy, is a straightforward example of the use of analogy in scientific hypothesizing, and demands the usual care in distinguishing positive, negative, and neutral correspondences between the two domains under comparison . . . care must be taken to distinguish the empirical and conceptual attractions of an analogy from the covertly anthropocentric attractions of mere familiarity" (Daston 1997:140).

De Waal's defense of anthropomorphism as a means of generating hypotheses about the behavior of other primates relies on the fact that monkeys and apes have "similar" psychologies. However, a considerable body of evidence indicates that there are important differences in the cognitive abilities of monkeys, apes, and humans (Povinelli & Eddy 1996, Tomasello & Call 1997). If mind-reading plays an important role in the development of reconciliatory strategies (Castles 2000, Silk 1998), then it is important to take into account how differences in theories of mind among monkeys, apes, and humans may influence the function of reconciliation. This does not mean that we cannot gain important insights about the evolutionary forces shaping conflict resolution in humans by studying other primates, but it

may limit the usefulness of our own intuition in understanding why other primates reconcile.

THE EVOLUTIONARY HISTORY OF RECONCILIATION

Reconstructing the functional origins of reconciliation is a perilous exercise because we can study only the end points of this process, the behavior of ourselves and other living primates. Writing about the difficulties of studying the evolutionary history of a trait's function, Povinelli & Eddy (1996) note: "When it comes to understanding the continuous chain of processes that have led to the evolution of a given biological system or structure, it is one thing to speak of precursors, foundations, or building blocks, but quite another to tackle the more difficult problem of function. Because we inhabit only a very narrow slide of evolutionary time, we are privy to only a thin cross section of the diversity it has produced. . . . Extinction, coupled with the imperfections of the fossil record, virtually guarantees that during a period of rapid evolutionary change we can never accurately identify the exact origin and subsequent elaboration of a given trait" (p. 184).

Although we cannot reconstruct the evolutionary history of reconciliation with great confidence, the empirical record provides some clues about how and when the function of reconciliation has been transformed over the last five million years (Silk 1998). Reconciliation may have initially evolved from signals that are used in a broad range of social situations to communicate information about intentions and subsequent events. Having little understanding of others' minds, monkeys use reconciliatory behavior to propitiate former opponents. These conciliatory efforts reduce uncertainty about whether hostilities will continue and facilitate peaceful interactions among former adversaries. Even though monkeys have little knowledge of their partners' minds, they can learn to use reconciliation instrumentally for strategic purposes. Apes, who may have a more powerful theory of mind than monkeys do, may use reconciliation for their own strategic purposes and may mediate disputes among others. Human children, who have not yet developed a powerful theory of mind, may use reconciliation primarily as a means to settle conflicts and reestablish contact with former opponents. As they grow older and develop a fuller knowledge of others' feelings, intentions, and knowledge, reconciliation acquires broader functions. It is used to mend and preserve relationships that have particular social, economic, or political value. Reconciliation often extends beyond the original parties in the dispute, involving consolation, mediation by thirty parties, and institutionalized remedies for conflict that are built into legal and judicial systems (Yarn 2000).

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