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The Mother–Offspring Relationship as a Template in Social Development: Reconciliation in Captive Brown Capuchins (*Cebus apella*)

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Mother–offspring (MO) relationship quality was investigated to determine its influence on the development of reconciliation—affiliation between opponents shortly after a fight—because it influences what distressed youngsters learn about calming down. Data were longitudinal and cross-sectional observational samples of 38 MO pairs of monkeys across 24 months. An MO relationship quality index (RQI) classified each pair as secure or insecure. Reconciliation emerged in infancy. Secure youngsters had an appeasing conciliatory style, and insecure youngsters had an agitated conciliatory style. Conclusions are that reconciliation develops from the attachment behavior system and MO RQI is related to the particular conciliatory style youngsters develop by affecting how aroused they are by conflict and the subsequent socializing they seek to calm down.

During the past 2 decades, social and political scientists and particularly primatologists have shown an increasing interest in investigating cooperation, peace, and conflict management and resolution. The discovery that several species of apes, baboons, and macaques exchange conciliatory gestures and thus reconcile a significant proportion of their conflicts has led to the use of nonhuman primates as models in the investigation of a number of dimensions of conflict resolution.

Most studied among the behavioral mechanisms of primate peacemaking is a behavior called reconciliation, the exchange of friendly behavior between those involved in a fight (former opponents) shortly after the fight (de Waal & van Roosmalen, 1979). Reconciliation takes place under a number of circumstances in both human and nonhuman primates. Its presumed functions vary with the species and researchers' interpretations (Kappeler & van Schaik, 1992; Silk, 1996; Watts, 1995), but most primatologists agree that reconciliation functions to repair relationships that have been damaged by conflict between the social partners (de Waal & Aureli, 1997). Reconciliation reduces the likelihood of further attack (long-tailed macaques, Aureli & van Schaik, 1991), restores characteristic levels of tolerance between social partners (chacma baboons, Cheney & Seyfarth, 2000; long-tailed macaques, Cords, 1992), and serves the more general social function of reducing the anxiety engendered by conflict in both aggressor and recipient (Barbary macaques, Aureli, Das, & Veenema, 1997).

As a common social strategy in nonhuman primates (Aureli & de Waal, 2000), reconciliation is particularly likely between individuals that, through other behaviors, show a strong mutual interest in maintaining their relationship (de Waal, 2000). The importance of reconciliation as a mechanism of tension reduction and relationship repair is demonstrated when opponents' rates of autonomic arousal, measurable through behavioral indicators like self-scratching and shivering (Maestripieri, Schino, Aureli, & Troisi, 1992), drop after opponents reconcile (Aureli & van Schaik, 1991; Aureli, van Schaik, & van Hooff, 1989), but not when one opponent has friendly contact with an individual other than the former opponent (Aureli et al., 1989; Das, Penke, & van Hooff, 1997).

The occurrence of conciliatory behaviors like reconciliation in many species suggests that the mechanisms of conflict management are natural phenomena that maintain group integrity and function as critical components of social life (Aureli & de Waal, 2000). As such, it is essential to understand the factors that affect the development of reconciliation. The developmental perspective emphasizes how new behavior emerges and attains its adult form. It carries the assumption that certain aspects of behavior are influenced by events that occurred earlier in ontogenesis; that is, the individual's history (Gottlieb, 1983).

Two behaviors raised questions about the possible role of infant attachment mechanisms of arousal modulation in the development of reconciliation. One behavior had to do with the behavior of infants. Compared with adults, infants must develop the autonomous ability to modulate their own arousal levels (Kraemer, Ebert, Schmidt, & McKinney, 1991; Reite & Field, 1985; Wiener, Lowe, & Levine, 1992) and often require actual physical contact to resume homeostasis when distressed (Harlow & Zimmerman, 1958; Mason, 1965). The manner in which distressed infants seek physical contact has been elegantly comprehended by attachment theory (Bowlby, 1969) as secure and insecure (Ainsworth, Blehar, Waters, & Wall, 1978) patterns of contact. The other behavior that raised questions about the role of infant attachment had to do with

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reconciliation itself and the way it is accomplished. Reconciling opponents, distressed by their altercation, preferentially seek each other out and often make actual physical contact following conflict: That is, reconciling opponents also show patterns of contact. A probable source of the variation in these patterns of conciliatory contact is arousal modulation behavior related to emotional state (Aureli & Smucny, 2000), which in the developing youngster involves its mother or caretaker.

This report is about the influence of mother–offspring (MO) relationship quality on the development of reconciliation. The research is based on the argument developed below that, whether human or nonhuman primate, what an infant learns from his mother about behaving when he is distressed becomes part of his psychobiology (Hofer, 1987) or self-organization (Field, 1985) and is one of the most enduring consequences of the MO relationship (Sroufe & Fleeson, 1986).

Data from research on a number of disparate human and nonhuman behaviors indicate that mothers are vital regulators of their infant's development (human attachment, Ainsworth et al., 1978; depression, Field, 1984; bereavement, Hofer, 1984; human separation studies, Field, 1985; nonhuman separation studies, Kraemer, 1992; Reite & Field, 1985). It has been suggested that a human mother or caretaker promotes or delays the infant's psychobiological development by the extent to which she or he matches or opposes the infant in social interaction. For example, Spangler, Schieche, Ilg, Maier, and Ackermann (1994) conducted research on infant cortisol, a stress hormone, during mother–infant play. Mothers of infants in the study were rated as sensitive or insensitive. Then, their infants' behavior and cortisol levels were studied during MO play sessions. At 3 months of age, infants with insensitive mothers showed more negativity and higher levels of cortisol when playing with their mothers than infants with sensitive mothers did during their play sessions. At 9 months of age, however, infants with insensitive mothers showed the same negativity and elevations of cortisol when *anticipating* a play session with their mothers. These and other data (e.g., Sander, Stechler, Burns, & Julia, 1970) suggest that human infants synchronize with the characteristics of social interaction they experience most often and eventually establish their optimal range of arousal (Hebb, 1949) with respect to it.

Similarly, a range of data suggest that nonhuman primate mothers regulate the development of their infants' altricial psychobiological systems during social interaction with them (Kraemer, 1992; McKenna, 1990a, 1990b, 1990c). Decades of nonhuman primate developmental research on MO separation clearly demonstrate that the extent to which an infant does not have a mother or caretaker available to help it regulate its psychobiologic systems (e.g., via brief or permanent separation) is the extent to which those systems develop abnormalities (Clarke, 1993; Harlow & Harlow, 1969; Kraemer, 1992; Suomi, 1982). Maternal deprivation, even brief or graded (Rosenblum & Paully, 1984), is among the most serious insults the developing youngster can sustain in terms of damage to social and neurobiological systems that organize emotional responses to stress (Kraemer, 1985; Kraemer et al., 1991).

Theoretically, mothers in intact MO pairs promote their infants' psychobiologic development when they synchronize with the infant during social interaction because adults' endogenous rhythms are more stable than infant rhythms and interaction allows infants to match a stable rhythm more often (Field, 1985). Predictability in social relationships leads to greater behavioral organization (e.g., Insel, Scanlan, Champoux, & Suomi, 1988) and psychobiological stability in human children (Bretherton, 1985; Kraemer et al., 1991; Reite & Field, 1985). The result is that securely attached MO pairs typically involve psychologically healthy mothers and socially competent children (Main & Weston, 1981). In contrast, among humans, infants of unpredictable mothers typically exhibit poorly developed psychobiological organization (Field, 1987) and apparently learn to modulate their own arousal levels less completely (Field, 1984).

Because reconciliation is an arousal- or tension-regulating behavior, our main hypothesis was that MO relationship quality provided a template that guided the development of the infant's arousal-coping strategies and development of reconciliation. The prediction was that capuchin youngsters would show different types of MO relationships on the basis of the kind of physical contact they experienced with their mothers and would in turn develop different conciliatory styles contingent on their experience. We evaluated capuchin MO relationships, divided youngsters into two groups of high- and low-quality relationships, and compared their conflict and reconciliation behavior with adults other than their mothers (to avoid the potential circularity of comparing MO baseline behavior to MO reconciliation behavior). Developmental stage should also influence how much physical contact a distressed youngster needed to calm down after a conflict, so other factors being equal, we expected infants to show more postconflict physical contact than juveniles. Assumptions of the current research were that youngsters' behavior was influenced by the need to modulate their arousal states, that conflicts were distressing to them, and that physical contact calmed them down.

Brown capuchins were good models for this investigation. They are long-lived (up to age 45 years, Nowak, 1999), and they have one of the largest mammalian encephalization quotients (remaining neural mass after corrections for body mass), prolonged immaturity, and distinct phases of social maturity (Welker, Höhmann-Kröger, & Doyle, 1992). Development is highly social (Byrne & Suomi, 1995; Welker, Becker, Hohmann, & Schafer-Witt, 1990), mothers and infants exhibit a mutual, unusually intimate attachment (Fragaszy, Baer, & Adams-Curtis, 1991), and adults reconcile after fights (Verbeek & de Waal, 1997).

Method

Subjects

Subjects were brown capuchins (*Cebus apella*) at Living Links, Yerkes Primate Center, Emory University, Atlanta, Georgia. The monkeys were housed as two large groups ($n = 14$ monkeys and $n = 16$ monkeys at the start of the study). Each group lived in its own indoor–outdoor mesh enclosure, 30.9 m^2 and 25.2 m^2, respectively. The outdoor section was about a third of the available space in the cage. Inside, enclosures were outfitted with polyvinyl chloride shelves, swings, and wood shavings as substrate. A heavy plastic liner between the two enclosures allowed only acoustic contact between the monkeys. The monkeys had ad libitum monkey chow and water and received produce once a day. They had full access to both indoor and outdoor areas except during observation, when they were locked inside to ensure all animals were equally visible during sampling. All the monkeys were individually identifiable. Within each social group, MO pairs and siblings were the related monkeys.

Because this was a 2-year developmental study, the composition of the study groups changed from births that occurred during the study. One group increased from 14 (2 adult males, 4 adult females, 4 immature females, and 4 immature males) to 18 monkeys from the birth of 4 males. The other group increased from 16 (2 adult males, 5 adult females, 1 immature female, and 8 immature males) to 21 monkeys from the birth of 5 males. Of the total 26 youngsters (< 5 years old) in the two groups of monkeys, 2 infants born late in the study were excluded. To be included in the study, monkeys had to be at least 3 months old because social behavior was our research focus and capuchins aged under 3 months mostly cling to their mothers and react to social overtures rather than initiate social interaction. Of the 26 total youngsters, 24 youngsters were included in this study as focal animal subjects—those aged 3 months–5 years old (males, $n = 19$; females, $n = 5$) from 9 mothers.

Because focal subject youngsters changed developmental stages over the course of the 2-year study and we were studying their conflict-related behavior, we divided them into the three developmental stages to ensure that all youngsters in the same developmental stage were in a similar phase of weaning from the nipple (weaning is a source of conflict). We divided youngsters by visual inspection of monthly nursing rates according to the following criteria. Infancy was characterized by consistently high nursing rates. Weaning began with the first substantial drop in nursing rates, continued until nursing stopped, and was characterized by variability in nursing rates. Juvenescence was marked by the absence of nursing. The 24 youngsters were divided into infants ($n = 12$), weanlings ($n = 10$), and juveniles ($n = 16$) for a total of 38 MO pairs in the study. Fourteen of the 38 MO pairs contributed data to two or three developmental stages: 6 monkeys were both infants and weanlings in this study; 8 were both weanlings and juveniles; and 4 of these were infants, weanlings, and juveniles during the 2-year timeframe of the study.

Design and Procedure

We conducted our pilot study from October 1993 to May 1994 to develop the ethogram (Weaver, 1999) and combined longitudinal and cross-sectional sampling procedures (for observational sampling procedures, see Lehner, 1979; Martin & Bateson, 1986). The majority of ethogram events ($N = 70$) were social, defined as 2 monkeys in the same group that came within an arm's length distance of each other. These were *approaches,* monkeys within an arm's length of each other without further interaction; *outcomes,* social interactions < 15 either initiated (*overture*) or received (*response*) by the focal monkey; and *durations,* social interactions > 15 (defined as behavioral states in this study). Remaining ethogram events were nonsocial, self-directed behaviors including scratching, tail shivering, body shaking, urine washing, and yawning. Body shaking was defined as a full body shiver. Tail shivering involved a rapid, small-amplitude shudder of the (sometimes piloerect) tail in any position.

Observations were made by Ann Weaver (interobserver reliability tests were not run) at a small table about 2 m from the front of each enclosure. Data were typed into a laptop computer in real time in a form that could be analyzed with UNIX software and downloaded after each session for later analysis. Baseline, conflict, and postconflict data were collected from June 1994 to June 1996 during 2–4-hr observational periods conducted several times weekly. Observation periods were divided into two segments, 2–3 hr of baseline behavior sampling preceded by 1 hr of behavior sampling (Altmann, 1974) for conflict. Altmann defined behavior sampling as a technique used for rare but significant events (like conflict) in which data collection begins when the behavior of interest begins. The database had a total of 774 baseline focal animal samples (20 min each) and 591 conflict samples, roughly divided evenly among the focal monkeys.

Baseline data were 20-min focal animal samples (Altmann, 1974) involving all-occurrence recording of the focal subject's behavior as initiator–behavior–recipient; self-directed behaviors did not have a recipient. Data on infants, weanlings, and juveniles were analyzed separately by developmental stage. The behavior of each focal subject was analyzed separately by (a) individual social partners or (b) social partner class (mother, unrelated adults, and peers). Approaches, outcomes, and self-directed behaviors were rendered into hourly rates; we corrected for differing numbers of available partners in social partner classes by dividing each focal subject's total frequency of a behavior by the total observation hours on the subject and then by the total number of partners per social partner class. A select number of behavioral events analyzed as hourly rates were also documented for duration (contact sitting, grooming self, grooming other, nursing, and playing). Duration data were analyzed as mean duration of all bouts recorded on the focal subject per developmental stage.

From baseline samples, we derived a quantitative measure called the MO relationship quality index (RQI) for each MO pair per developmental stage (yielding an RQI for all 38 MO pairs in the study) with the following formula: relative affiliation rate/relative agonism rate. Affiliation was the combined hourly rate of mother grooming youngster and youngster grooming mother. Agonism was the combined hourly rate of four events (low-level threats, protest begging, avoidance, and distress without cause) that mother and youngster aimed at each other. The four agonistic events were given descriptive (mnemonic) names and objective definitions as follows. A low-level threat was a minor menacing gesture aimed at a conspecific that gave a neutral response in return. Protest begging was a trilling vocalization given while eyebrow flashing or staring at the social partner. Avoidance was an increase in interanimal distance by one animal moving away or leaning away. Distress without cause was a brief (< 15 s) high-pitched yelp or screech for no observable reason. Relative measures were derived by dividing each individual's hourly rate by the mean rate of all individuals in the same developmental stage. In each developmental stage, youngsters were divided as above or below the median MO RQI. Youngsters whose MO RQI values were above the median were labeled *secure,* and youngsters whose MO RQI values were below the median were labeled *insecure,* following Weaver and de Waal's (2002) extensive analysis showing that the labels secure and insecure are valid and reliable descriptors of the two types of relationships. In subsequent analyses, we compared the behavior of secure youngsters with the behavior of insecure youngsters. For example, using one-tailed predictions of behavior based on attachment theory, we tested the prediction that secure youngsters played with unrelated adults more than insecure youngsters played with unrelated adults.

Conflicts were defined as occurring when a youngster clearly received aggression from another monkey or gave distressed vocalizations of at least 15 s duration during social interaction. Such youngsters became the focal subject (Altmann, 1974), and a conflict sample was collected immediately, starting with the identity of the aggressor, the intensity of the attack, the focal subject's identity, the real-time duration in seconds of subject's distressed vocalizations, their response to the aggressor, and the context in which conflict occurred. Aggression intensity was a numeric value: 1 = intimidating behavior; 2 = lunge; 3 = grab and release, light slap, or mock bite; 4 = chase; 5 = aggressive biting and hair pulling; and 6 = fierce or sustained biting. Response-to-aggressor events were curling (a lateral reclining posture with limbs retracted), follow aggressor, flight from aggressor, and vocalizing at aggressor (barking, hoarse cries, screaming, or warbling). Contexts were interest-in-infant behavior, food interest, grooming, mobbing, nursing requests, object interest, play, redirected aggression, support, and unknown. We calculated hourly conflict rates per opponent class (mother, unrelated adults, and peers) and mean values for aggression intensity, occurrence per conflict for each response-to-aggressor event, and duration of distressed vocalizations. Conflicts with distressed vocalizations lasting over 1 min were labeled *tantrums.* Context data were mean proportions of the total number of conflicts.

This report pertains to a specific subset of conflict behavior sampled during the study: conflicts between unrelated adults as aggressors and youngsters as recipients of adult aggression. We further restricted the data by analyzing only the conflict and reconciliation data on youngsters with at

least five conflicts with unrelated adults, in keeping with similar restrictions in statistical tests requiring a minimum of 5 data points (e.g., chi-square; Siegel & Castellan, 1988). This resulted in an analysis of 23 of the 38 youngsters in the three developmental stages of this study ($n = 23$ youngsters in conflict and reconciliation analysis). We tested the one-tailed prediction that insecure youngsters threw more tantrums than secure youngsters. The tantrum measure was derived by combining hourly dyadic tantrum rates at mother, unrelated adults, and peers and was regressed on relationship quality and developmental stage.

Conflicts were defined as ending when the focal animal stopped vocalizing for at least 15 s and were sampled with the postconflict–matched control (PCMC) method (de Waal & Yoshihara, 1983). When conflict ended, we immediately began collecting a postconflict focal animal sample, the PC sample, that documented the focal subject's behavior; we used the same format for sampling PC behavior as for baseline samples but collected 5 min samples (instead of 20 min samples). To determine if reconciliation occurred, we compared the behavior of opponents in the PC sample with their behavior under baseline conditions and obtained a corrected conciliatory tendency (CCT; Veenema, Das, & Aureli, 1994) for each youngster in each developmental stage. The CCT compares the latency to opponents' first contact in the PC sample with their latency to contact under baseline conditions (MC, or matched control, sample). In this study, MC samples were drawn from the first 5 min of the recipient's baseline focal animal sample collected closest in time before the conflict occurred. Opponents that made contact earlier in the PC than in the MC sample were attracted pairs (*a*), those that made contact later in the PC than in the MC sample were dispersed pairs (*d*), and those that made contact at the same time or did not make contact were neutral pairs (*n*). The CCT formula is $(a - d)/(a + d + n)$. When a Wilcoxon signed-ranks comparison indicates that significantly more opponent pairs behave as attracted pairs than as dispersed pairs, the species is considered to reconcile.

To study how youngsters used physical contact with opponents following conflict, we defined reconciliation more specifically as the most physical of six behaviors exchanged between opponents any time during the PC sample (from most to least physical): grooming, oral–genital contact, sitting in contact, sitting an arm's length distance apart, walking by at arm's length, and giving a facial signal from arm's length. In this case, aggressors were always unrelated adults. Reconciliations that involved grooming, oral–genital contact, and contact sitting were analyzed together as *direct reconciliations* and considered potentially comforting. Remaining reconciliations (accomplished when opponents sat, walked by, or gave a facial signal from an arm's length distance) were labeled *indirect* and not considered directly comforting. Reconciliations were subdivided by who made the contact; that is, youngster-initiated and aggressor-initiated reconciliations (Y Init and Ag Init, respectively, in the figures). Unreconciled conflicts were conflicts that were not followed by contact between the opponents.

We used nonparametric statistics (Siegel & Castellan, 1988) with a significance level of $p < .05$ because (a) we couldn't be sure that observational data were normally distributed and (b) we considered nonparametric statistics to be more conservative (on the basis of the ranks of the data rather than the actual data points) in dealing with obvious confounds such as the pseudoreplication problem inherent in any developmental study in which the same youngsters are sampled longitudinally but are too few in number to be analyzed separately as repeated measures. Tests were one-tailed unless stated otherwise because we tested specific predictions from attachment theory. We analyzed data by comparing proportions of the total conflicts; for example, reconciled versus unreconciled conflicts, youngster- versus adult-initiated reconciliations, and direct versus indirect reconciliations. Proportions within developmental stages were statistically evaluated with Wilcoxon signed-rank tests (T^+ = total plus ranks), across MO RQI values with Mann–Whitney *U* statistics, and across developmental stages with Kruskal–Wallis analyses of variance (*KW*). We looked for the effects of developmental stage and MO RQI on conflict and reconciliation with a multiple regression by assigning each developmental stage with a number (1 = infancy, 2 = weaning, and 3 = juvenescence). We calculated a per minute rate of all self-directed behaviors and compared them across three conditions: before reconciliation, after reconciliation, and in unreconciled conflicts to see if they were affected by reconciliation. We expected them to decrease after reconciliation. Finally, we used Spearman rank-order correlations between rates of self-directed behaviors during conflict and under baseline conditions to test the prediction that the two behaviors correlated positively.

Results

Unrelated Adult–Youngster Conflict

For the 23 focal animal subjects that met our five-conflict minimum criterion, a total of 268 unrelated adult–focal youngster conflict samples were collected. Table 1 shows the distribution of subjects by developmental stage and MO RQI. The small number of subjects per cell meant we analyzed behavior by developmental stage and MO RQI separately rather than by individual developmental stage and MO RQI category. Secure capuchins (i.e., youngsters rated as securely attached to their mothers) played with adults twice as much as did insecure capuchins (i.e., youngsters rated as insecurely attached to their mothers; $U = 110.5$, $z = 2.05$, $p = .02$, number of secure subjects [n_S] = 19, number of insecure subjects [n_I] = 19; secure, $M = 0.96$ play bouts/hr, $SD = 1.04$; insecure, $M = 0.45$ play bouts/hr, $SD = 0.57$).

Conflicts between youngsters and unrelated adult (nonmother) aggressors occurred in all three developmental stages. Of the 132 possible adult–youngster opponent pairs, 62.9% were observed at least once and none contributed disproportionately to the data set. Focal youngsters' developmental stage was not related to the level of aggression intensity they received from unrelated adult opponents (*KW* = 2.18, *df* = 2, *ns*; infancy, $M = 1.32$, $SD = 0.31$; weaning, $M = 1.51$, $SD = 0.52$; juvenescence, $M = 1.68$, $SD = 0.53$), which was uniformly low. Nor was focal youngsters' developmental stage related to the mean duration of their distressed vocalizations (*KW* = 0.08, *df* = 2, *ns*; infancy, $M = 68.2$ s, $SD = 48.1$; weaning, $M = 57.4$ s, $SD = 58.4$; juvenescence, $M = 64.7$ s, $SD = 43.45$).

Developmental stage was associated with an increase in only one response-to-aggressor event, hoarse cries (*KW* = 9.22, *df* = 2, $p = .02$; infancy, $M = 0.09$ hoarse cries/conflict, $SD = 0.09$; weaning, $M = 0.23$ hoarse cries/conflict, $SD = 0.20$; juvenescence, $M = 0.49$ hoarse cries/conflict, $SD = 0.25$). Developmental

Table 1
Number of Focal Youngsters Used in Analysis of Conflict Behavior Between Youngsters and Unrelated Adults by Developmental Stage and MO RQI

	MO RQI		
Developmental stage	Secure	Insecure	Total
Infants	3	2	5
Weanlings	4	4	8
Juveniles	7	3	10
Total	14	9	23

Note. MO RQI = mother–offspring relationship quality index.

stage was also significantly associated with the context of conflicts. Unrelated adult–infant conflicts occurred when infants showed interest-in-infant behavior ($KW = 8.49$, $df = 2$, $p = .02$; infancy, $M = .66$, $SD = .23$; weaning, $M = .44$, $SD = .38$; juvenescence, $M = .15$, $SD = .14$). Juveniles' conflicts occurred in the context of aggressor support (i.e., other monkeys joined the original aggressor against the juvenile; $KW = 10.56$, $df = 2$, $p = .01$; infancy, $M = .03$, $SD = .06$; weaning, $M = .03$, $SD = .05$; juvenescence, $M = .12$, $SD = .05$) and unknown contexts ($KW = 6.90$, $df = 2$, $p < .05$; infancy, $M = .00$, $SD = .00$; weaning, $M = .03$, $SD = .05$; juvenescence, $M = .10$, $SD = .12$).

MO RQI was unrelated to aggression intensity ($U = 42.5$, $z = 1.07$, *ns*, $n_S = 13$, $n_I = 9$; secure, $M = 1.59$, $SD = 0.39$; insecure, $M = 1.44$, $SD = 0.49$) and the context in which conflict occurred. During conflict, insecure youngsters showed a marginal tendency to have longer bouts of distressed vocalizations ($U = 37.0$, $z = 1.44$, $p = .07$, $n_S = 13$, $n_I = 9$; secure, $M = 52.7$ s, $SD = 31.5$; insecure, $M = 79.8$ s, $SD = 50.4$), but they had significantly more vocalized response-to-aggressor events per conflict than secure youngsters had (one-tailed $U = 17.5$, $z = 1.72$, $p < .05$, $n_S = 14$, $n_I = 9$; secure, $M = 0.19$ vocal bouts/conflict, $SD = 0.13$; insecure, $M = 0.54$ vocal bouts/conflict, $SD = 0.29$). Young insecure capuchins threw significantly more tantrums than secure capuchins, $F(2, 34) = 7.14$, $p = .003$, $r = .56$, $r^2 = .31$ (developmental stage, $pr = -.43$, $t = 2.77$, $p = .009$; MO RQI, $pr = -.34$, $t = 2.09$, $p = .04$; secure, $M = 0.02$ tantrums/hr, $SD = 0.02$; insecure, $M = 0.04$ tantrums/hr, $SD = 0.02$).

Unrelated Adult–Youngster Reconciliation

There was a significant tendency for youngsters and unrelated adults to reconcile. The infant CCT of 50% with unrelated adults was significantly higher than the weanling CCT of 25%, $\chi^2(1, N = 22$; 12 infants and 10 weanlings$) = 9.8$, $p < .01$, and the juvenile CCT of 28%, $\chi^2(1, N = 16$ juveniles$) = 3.9$, $p < .05$. Table 2 presents proportions of reconciled conflicts by developmental stage and MO RQI and shows that juveniles were the only class of youngsters that did not have significantly higher proportions of reconciled than unreconciled conflicts with adult aggressors.

In youngster-initiated reconciliations, multiple regression revealed that developmental stage and MO RQI accounted for a highly significant 50% of the variance and that each of these two independent variables contributed significantly after correction for the other, $F(2, 22) = 9.88$, $p = .001$, $r = .71$, $r^2 = .50$ (developmental stage, $pr = -.60$, $t = 3.32$, $p = .003$; MO RQI, $pr = -.53$, $t = 2.79$, $p = .01$). In adult-initiated reconciliations, developmental stage and MO RQI accounted for a highly significant 44% of the variance and each independent variable again contributed significantly after correction for the other, $F(2, 22) = 7.67$, $p = .003$, $r = .66$, $r^2 = .44$ (developmental stage, $pr = .12$, $t = 0.54$, $p = .59$; MO RQI, $pr = .66$, $t = 3.85$, $p = .001$). Developmental stage and MO RQI accounted for a nonsignificant 23% of the variance in unreconciled conflicts, $F(2, 22) = 2.27$, $p = .07$, $r = .48$, $r^2 = .23$.

These findings are illustrated in Figures 1 and 2. Figure 1 shows that youngsters (white bars) initiated fewer reconciliations with unrelated adults as they aged and that adult initiative (black bars) was not affected by youngsters' developmental stage. Figure 2 shows that insecure youngsters initiated more reconciliations (white bars) with adults than secure capuchins initiated but adults initiated more reconciliations (black bars) with secure than insecure youngsters.

Table 2
Mean Proportions and Standard Deviations per Individual Subject of Reconciled Conflicts Between Unrelated Adult Opponents and Youngsters by Developmental Stage and MO RQI in Immature Brown Capuchins

Developmental stage and relationship quality	Reconciliation			
	M	*SD*	T^{+} [a]	*n* [b]
Developmental stage				
Infancy	.71	.14	10.0*	5
Weaning	.71	.19	33.5**	8
Juvenescence	.59	.17	38.5	10
Relationship quality				
Secure	.68	.16	96.5***	14
Insecure	.63	.21	29.5*	9

Note. Reconciliations refer to 5-min postconflict periods in which former opponents had friendly social interaction. MO RQI = mother–offspring relationship quality index.
[a] Wilcoxon T^{+} statistic (total plus ranks) comparing the proportion of reconciled conflicts (listed) with the remaining proportion of unreconciled conflicts (postconflict periods in which former opponents failed to have social interaction) for a total of 1.00. Those marked with an asterisk indicate a significantly higher proportion of reconciled conflicts compared with unreconciled conflicts. [b] *n* is the number of capuchin youngsters with 5 or more conflicts with unrelated adult opponents.
* $p < .05$. ** $p < .01$. *** $p < .001$.

Infants and weanlings initiated significantly more direct reconciliations than juveniles did ($KW = 8.09$, $df = 2$, $p = .02$; infants, $M = .29$, $SD = .19$; weanlings, $M = .24$, $SD = .12$; juveniles, $M = .09$, $SD = .01$), and insecure youngsters initiated more direct reconciliations than secure youngsters did ($U = 33.5$, $z = 1.87$, $p = .03$ $n_S = 14$, $n_I = 9$; insecure, $M = .24$, $SD = .12$; secure, $M = .14$, $SD = .16$).

Secure youngsters curled and followed the aggressors significantly more than insecure youngsters did (one-tailed $U = 29.0$, $z = 1.85$, $p = .03$, $n_S = 14$, $n_I = 8$). Figure 3 shows that secure youngsters showed 2.5 times as many occurrences of curling and following response-to-aggressor events during reconciled conflicts (black bars) than during unreconciled conflicts ($T^{+} = 72.5$, $z = 1.89$, $p = .02$, $n = 14$), whereas occurrences among insecure youngsters did not differ ($T^{+} = 17.5$, $z = 0.59$, *ns*, $n = 9$).

Figure 4 illustrates that insecure youngsters vocalized significantly more during reconciled conflicts (black bars) than during unreconciled conflicts ($T^{+} = 25.0$, $p = .03$, $n = 7$), whereas secure youngsters did not differ in vocal behavior ($T^{+} = 21.0$, *ns*, $n = 11$) in reconciled and unreconciled conflicts. In addition, insecure youngsters vocalized significantly more during reconciled conflicts than secure youngsters did (one-tailed $U = 23.5$, $z = 1.71$, $p < .05$, $n_S = 13$, $n_I = 7$).

Both secure and insecure youngsters' rates of self-directed behavior (e.g., scratching) after a conflict ended but before reconciliation occurred correlated positively with their rates of self-directed behavior under baseline conditions ($r_s = .54$, $p < .01$, $n = 23$). However, insecure youngsters' mean rates of self-directed behaviors were significantly lower after reconciliation than before

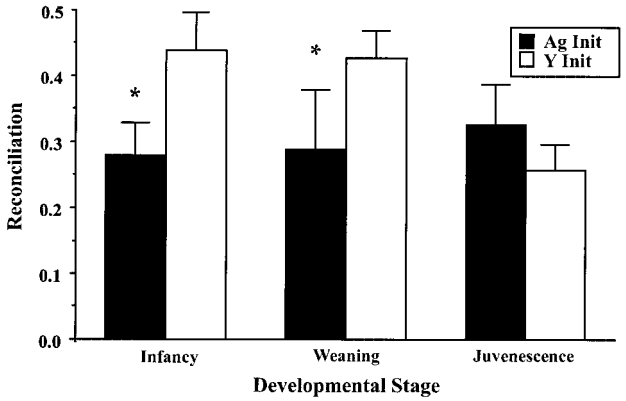

Figure 1. Mean (±*SEM*) of all individual subjects' proportions of reconciliations per developmental stage by the opponent that initiated the reconciliation, youngster-initiated reconciliations (Y Init) or unrelated adult-initiated reconciliations (Ag Init). Proportions are for reconciled conflicts only and do not add up to 1.0 because the remaining proportion of unreconciled conflicts is excluded from this figure. *$p < .01$.

($T^+ = 44.0$, $p = .004$, $n = 9$; see Figure 5), whereas secure youngster's self-directed rates did not differ significantly before and after reconciliation ($T^+ = 63.0$, *ns*, $n = 14$).

Discussion

These data allowed us to draw two major conclusions about the development of reconciliation. (a) Reconciliation emerges early in the behavioral repertoire of brown capuchins as a natural peacemaking mechanism. (b) Reconciliation with others in the group is affected by the quality of the relationship between a mother and offspring. The quality of relationship in an MO pair did not determine the existence of reconciliation in a developing youngster's social repertoire because a significant number of the conflicts involving both secure and insecure youngsters were reconciled. Rather, relationship quality was associated with how

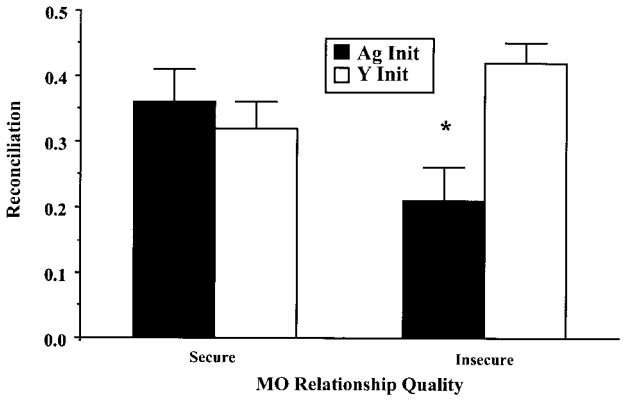

Figure 2. Mean (±*SEM*) of all individual subjects' proportions of reconciliations by mother–offspring (MO) relationship quality by the opponent that initiated the reconciliation, youngster-initiated reconciliations (Y Init) or unrelated adult-initiated reconciliations (Ag Init). Proportions are for reconciled conflicts only and do not add up to 1.0 because the remaining proportion of unreconciled conflicts is excluded from this figure. *$p < .01$.

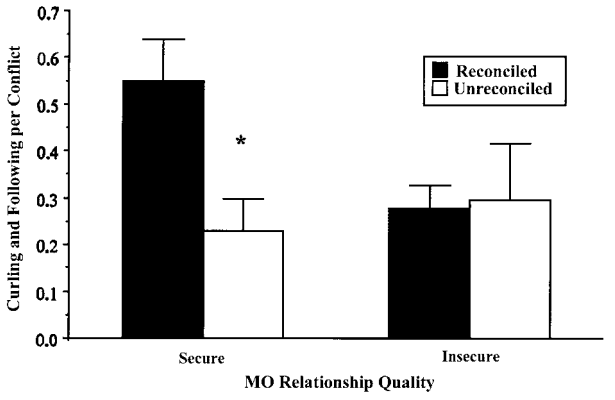

Figure 3. Mean (±*SEM*) occurrence per conflict per individual subject of youngsters' curling next to and following aggressors during conflict by the outcome of the conflict, reconciled or unreconciled. MO = mother–offspring. *$p < .05$.

reconciliations were accomplished; that is, the behavior that was involved. Secure and insecure youngsters used two distinct conciliatory styles in which emotions seemed to play a vital role. Our results suggest that by influencing the nature of negative arousal that youngsters experienced during early development, the quality of the MO relationship also influenced the amount of anxiety youngsters experienced when in conflict with adults (other than their mothers). The quality of the MO relationship was then indirectly related to the kind of social interaction youngsters sought, that is, the social interaction of reconciliation, to calm down and resume homeostasis after conflict.

Insecure Mother–Offspring Relationships and Youngsters' Conciliatory Style

In their MO relationships, insecure youngsters were distinguished from secure youngsters by high proportions of agonism compared to affiliation. Analysis of the nature of the two relationships (Weaver & de Waal, 2002) revealed that mothers and young-

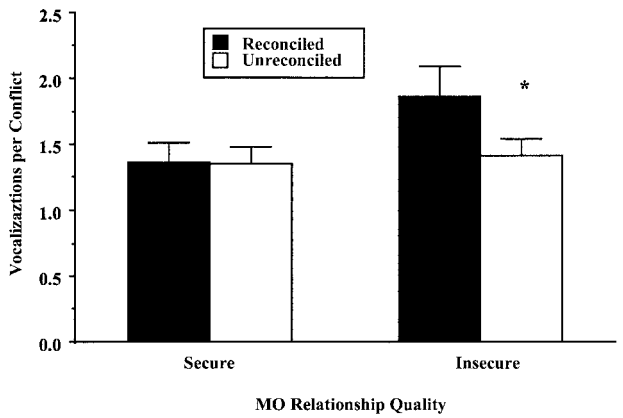

Figure 4. Mean (±*SEM*) occurrence per conflict per individual subject of youngsters' vocalizations (barking, screaming, and warbling) to aggressors during conflict by the outcome of the conflict, reconciled or unreconciled. MO = mother–offspring. *$p < .05$.

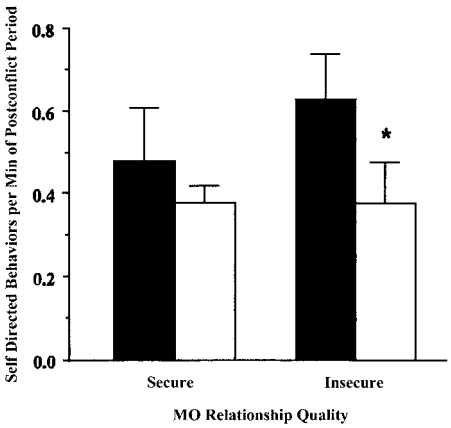

Figure 5. Mean (±*SEM*) of all youngsters' rates of self-directed behavior per minute during the 5-min postconflict period before (filled bars) and after (open bars) reconciliation by mother–offspring (MO) relationship quality. Before = mean arousal following conflict but before reconciliation; after = mean arousal rates following reconciliation. *$p < .01$.

sters in insecure relationships showed extensive approach–avoidance behavior and nearly 10 times more agonism than secure MO pairs. Insecure youngsters avoided their mothers over twice as often as secure youngsters avoided their mothers and squabbled at her 7 times more often than secure capuchins squabbled at their mothers. Mothers in insecure pairs avoided their youngsters and squabbled at them over 6 times more often than mothers in secure pairs avoided and squabbled at their youngsters. In general, insecure MO capuchin relationships were highly capricious, extremely tense, and strongly reminiscent of resistant attachments in human MO relationships (Ainsworth et al., 1978).

Similarly, data in this report revealed that insecure youngsters were highly agitated in conflict with adult monkeys other than their mothers but also showed strong conciliatory tendencies. Specifically, they showed higher rates of self-directed behaviors associated with autonomic arousal, were more likely than secure youngsters to flee from their opponents, tended to overreact by throwing more tantrums, and aimed more shrill and persistent vocalizations at adult opponents near them. Insecure youngsters showed strong conciliatory initiative in so far as they initiated significantly more reconciliations with unrelated adult opponents than these opponents initiated with them. When reconciling, these youngsters emphasized directly comforting physical contact and were conspicuously calmed by their conciliatory contacts. This behavior is notable considering that insecure youngsters had little contact with their own mothers following conflict with unrelated adults (Weaver & de Waal, 2001).

Insecure capuchins' active but agitated conciliatory style has three complementary interpretations that implicate their MO relationships as a template for it. First, reconciliation may have primarily served insecure youngsters themselves as comfort-seeking behavior. Insecure capuchins were highly aroused by conflict. In other nonhuman primate species, anxiousness itself promotes reconciliation in adults (Aureli, 1997) and juveniles (Cords, 1988). Whether or not their agitation may have served as an active coping strategy that forestalled excessive arousal (Levine & Wiener, 1988) while it reinstated contact (Coe, Wiener, Rosenberg, & Levine, 1985; Thierry, Steru, Chermat, & Simon, 1984), it resembled the behavior of insecure human youngsters. That is, according to Ainsworth and colleagues (1978), insecure human youngsters work harder to find calming contact when frightened or distressed because they are in greater need of an outside source of security then secure youngsters.

Another dimension of insecure capuchins' reconciliation behavior that suggests it was related to comfort seeking had to do with reinstating their most familiar range of arousal, that is, anxiety and unpredictability. Insecure youngsters may have shown such strong initiative in reconciling with unrelated adults because, as per their capricious MO relationships, interacting with larger frightening adults was among their most familiar social interaction. Approaching large adults that had just frightened them after a conflict (which results in reconciliation) may have created a familiar state (albeit of anxiety) in youngsters.

The second interpretation that implicates the insecure MO relationship as a template was reconciliation as relationship repair. That is, reconciliation may have primarily served insecure youngsters by helping them repair the damage that conflict caused to their relationships with unrelated adult aggressors. As indicated by their low MO RQI values, insecure capuchins' capricious MO relationships regularly gave youngsters the opportunity to deal with agonistic social interaction. Despite this, they were persistent about seeking interaction with their mothers (Weaver, 1999) and were correspondingly responsive to any friendly behavior their mothers extended to them (Weaver & de Waal, 2002). This means reconciliation was familiar and insecure capuchins were practiced at it. However, insecure youngsters seemed likely to have been uncertain of their relationships with unrelated adults (i.e., had low security in them in the sense of Cords & Aureli, 2000). For example, compared with secure youngsters, insecure youngsters rarely played with unrelated adults, behavior that raises the possibility that their relationships were not as well established. Such relationships may have required clear conciliatory gestures after conflict among capuchins like they do in long-tailed macaques youngsters, which also tend to reconcile with individuals about whom they are most uncertain (Cords, 1988, 1992; Cords & Aureli, 1993).

The third interpretation that implicates the insecure MO relationship as a template was similar approach–avoidance patterns in their MO relationships and in their behavior toward unrelated adult opponents. Following conflict, insecure youngsters emphasized vocal protest and flight but displayed some following and curling as well. Such ambivalence toward their opponents during conflict and reconciliation mirrored the ambivalence insecure youngsters showed during social interaction in their MO relationships. The ambivalence that insecure capuchins' showed toward their mothers and adult opponents is notable because it resembled similar behavior in insecurely attached human children: Resistantly attached children are ambivalent toward their mothers whether they interact with her at home (baseline) or during stressful laboratory conditions (Ainsworth et al., 1978).

Secure Mother–Offspring Relationships and Youngsters' Conciliatory Style

In contrast, secure MO capuchin pairs mostly sat together quietly and groomed with a noticeable absence of strife and tension

(Weaver & de Waal, 2002). In general, secure MO relationships were characterized by highly positive physical contact and amiability founded on reliable maternal availability, predictability, and complementarity in interaction. A striking aspect was that secure youngsters responded affiliatively to both their mothers' affiliative initiatives and agonism (Weaver & de Waal, 2002), which suggested they were not intimidated by their mothers' agonistic acts. Nor did the amiable nature of secure MO relationships change as youngsters aged.

In terms of their conflict-related behavior, secure capuchin youngsters did not appear particularly aroused by conflict with unrelated adults (in contrast to insecure youngsters). For example, conflict failed to instigate significant elevations in their rates of self-directed behaviors. Secure youngsters were more likely to respond to their adult opponents by quietly curling near them or trailing behind them than by beleaguering them with shrill vocalizations. Perhaps correspondingly, adult opponents showed significantly higher tendencies to reconcile with secure youngsters than with insecure youngsters regardless of their age. In turn, secure youngsters reconciled with adult opponents at comparable rates and emphasized neither directly comforting nor indirect contacts when they reconciled.

Secure youngsters' appeasing conciliatory style mirrored the amiability of their MO relationships and implicated the secure MO relationship as a template for reconciliation in several ways. First, the way they emphasized curling and following during conflicts with unrelated adults was similar to the way they responded with affiliative behavior to their mothers' affiliative and agonistic behavior toward them. Curling is a form of self-comfort (Mason, 1965) and, as the antithesis of an aggressive capuchin overlord stance, is also an appeasement gesture. Appeasement gestures often forestall renewed attack among adult nonhuman primates (Aureli, Das, Verleur, & van Hooff, 1994). Both curling and following were nonagonistic behaviors that lacked noisy tensions and threats of renewed attack.

These behaviors in and of themselves may have also encouraged former aggressors to approach and reconcile, which would account for our finding that adult opponents reconciled with secure youngsters despite their stage of development. In several nonhuman primate species, adult–youngster social interaction is contingent on youngsters conforming to certain standards of behavior (e.g., Altmann, 1980; Barrett, Dunbar, & Dunbar, 1995; de Waal, 1993). In this study, adult opponents may have reconciled more with secure youngsters than with insecure youngsters because the former were more well-behaved in the context of conflict and reconciliation.

Second, these appeasing behaviors may have also promoted reconciliation from both unrelated adults and secure youngsters because, as implicated by significantly higher rates of play, secure youngsters had friendly relationships with several of the adults with whom they conflicted. Play is friendly behavior, and in other species, dyad partners that are friendlier to each other outside of the context of conflict also reconcile after conflicts more often (Call, Aureli, & de Waal, 1999; de Waal & Yoshihara, 1983). Moreover, social partners accustomed to interacting in several contexts are likely to find it easier to reconcile because friendly interaction is more characteristic of their relationships and approaches after conflict are less risky (Cords & Aureli, 2000). In the current study, the greater equivalency of conciliatory tendencies between unrelated adults and secure youngsters suggests they may have been more compatible than unrelated adults and insecure youngsters, with compatibility (Cords & Aureli, 2000) meaning more harmonious tenor in social relationships; in this sense of compatibility, social partners have more access to each other. In this respect, secure capuchins were dissimilar to juvenile long-tailed macaques, which tend to reconcile more among themselves with unfamiliar individuals (Cords, 1988; Cords & Aureli, 1993).

Third, we speculate that the curling or following behavior secure capuchins showed during reconciliation may have affected their mothers' behavior. Compared with shrill, persistent vocalizations, these behaviors are calm. They may have mitigated a mother's distress at the sight of her distressed youngster (Levine, 1983) and reduced her tendency to threaten adults that aggressed against her offspring. Adult opponents may have then been freer to approach and reconcile with youngsters. Compared with the agitated behavior of insecure youngsters, secure youngsters used an appeasing postconflict strategy based on placid posturing that defused conflict and repaired relationships by signaling the antithesis of retaliation and/or by eliciting adult opponents to approach through good behavior.

Homeostatic Perspective of Reconciliation

We speculate about a connection between the fact that reconciliation reduces the tensions created by conflict (Aureli & de Waal, 2000) and that it emerged early in the capuchin social repertoire (capuchin infant conciliatory tendencies were higher than those in the older age classes). One explanation is that reconciliation-like behavior emerged from coping mechanisms related to reinstating homeostasis; that is, youngsters' most familiar autonomic state. This perspective construes youngsters' behavior during conflict and reconciliation as adjustments to their fluctuating levels of arousal resulting from social interaction. Their respective conciliatory styles, appeasing and agitated, were the strategies each developed to reinstate homeostasis after being disturbed by conflict. From the perspective of resuming homeostasis, reconciliation initially developed as an arousal-control mechanism coincident with the onset of their independent mobility that enabled developing infants to participate in social interaction.

Youngsters' most familiar state of homeostasis was influenced by MO RQI and developmental stage. Low MO RQI values indicate insecure youngsters experienced a higher proportion of disorganizing or aversive periods of arousal during development than of smooth maternal intervention and tension-free episodes during development. This could account for their higher baseline and conflict levels of autonomic arousal, stronger initiative in instigating directly comforting reconciliations, and more obvious tension reduction from reconciliation. In conjunction with their youth and the unreliable availability of their mother to comfort them when they were distressed by conflict (Weaver & de Waal, 2001), insecure youngsters' capricious relationship history led to a greater need for contact comfort, which translated into greater conciliatory initiative and obvious tension reduction in them during periods of social strife.

When secure youngsters were distressed by conflict, the availability of their responsive and affectionate mothers (Weaver & de Waal, 2001) may have enabled them to respond to opponents the way they did. But secure youngsters also showed low baseline levels of autonomic arousal, did not appear to be as aroused by

conflict, showed conciliatory rates that did not differ from adults, and reconciled with less physical contact than insecure capuchins. From the homeostatic perspective, the consistent amiability of their MO relationships seems likely to have provided secure youngsters with a better-developed neurobiological (Kraemer, 1992) and psychological (Bowlby, 1969) model of an available and amiable mother. This may have enabled them to develop adult-like social skills earlier. In this respect, secure capuchin youngsters reflected the greater social maturity that characterizes securely attached human children (Grossmann & Grossmann, 1990). These findings suggest that future research investigate the association between MO RQI, conflict, and reconciliation in another species of nonhuman primate.

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