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The Evolution of Primate Attachment

Beyond Bowlby's Rhesus Macaques

Masako Myowa and David L. Butler

Abstract

Bowlby's theory of attachment has been hugely influential, yet his proposal and its subsequent support derives heavily from research involving rhesus macaques, the most extensively studied nonhuman primate in attachment research. Does his theory apply to other primates? A substantial amount of data concerning primate (including human) child care now challenges Bowlby's original proposal, particularly as it relates to the notion of the mother being the sole continuous care-and-contact provider: caring can be shared by various individuals, the father can serve as the primary attachment figure, and infants can form multiple attachments. This chapter focuses on the phylogenetic history of attachment among primates, identifies features of attachment that are shared or which differ between humans and nonhuman primates, and considers the possible cognitive, social, and ecological factors associated with these similarities and/or differences in attachment among primates. Current evidence suggests that the human attachment system appears to be uniquely characterized by (a) social interactions based on combined visual, tactile, and auditory modalities, (b) the use of positive cognitive empathy, and (c) certain contextual elements typically contained in human social environments.

Background

The attachment relationship between parents and their infant is an important part of the evolutionary heritage of mammals, and is particularly prominent in many primates within which a lifelong propensity for such a bond has also evolved. According to Bowlby's and Ainsworth's classic conception, common manifestations of attachment are (a) an infant's selective preference for its mother, (b) displays of agitation or distress by an infant upon maternal

separation, and (c) the attenuation of such agitated or distressed states by the mother through her presence and/or soothing skills (Bowlby 1969, 1973; Ainsworth 1972). Although these characteristics are widely (and perhaps incorrectly) accepted in relation to primate development, particularly for humans, important questions remain unanswered concerning primate attachment more generally, which may have possible implications for our current understanding of human attachment: What is the phylogenetic history of attachment among the many species of primates (and not simply monkeys and/or apes) (Figure 3.1)? Are humans unique in any or all major aspects of attachment? What are the possible cognitive, social, and ecological factors associated with these similarities and/or differences in attachment among primates?

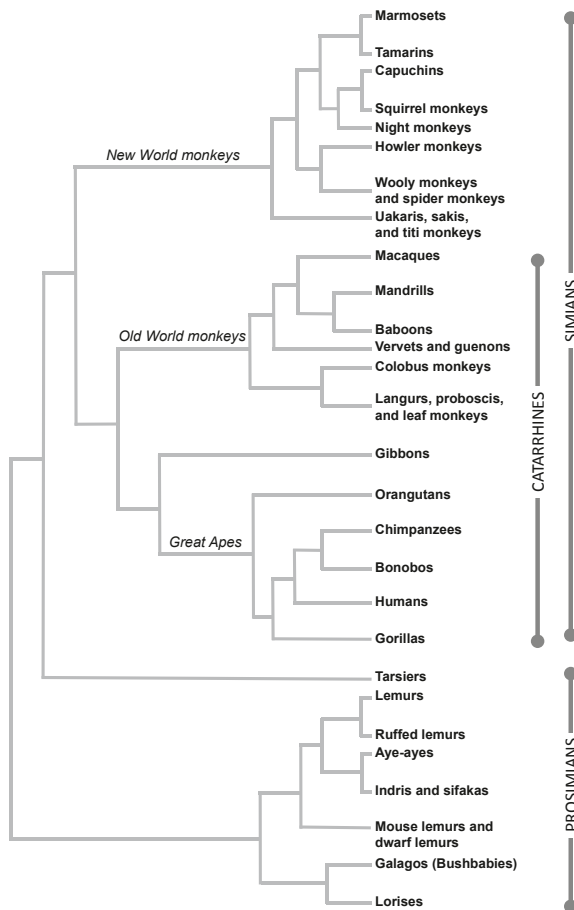


Figure 3.1 Classification of living primates mentioned in the text (Hrdy 2009). As this figure makes clear, the evolution of attachment must be considered (both generally and in more specific detail) in all primates, not simply in one or two species of monkeys or apes.

Attachment Styles and Their Variability across Primates

Contrary to the prevailing notion of “cupboard love” advocated until the 1960s (i.e., that the mother was simply a food source for her infant), Bowlby (1969) proposed that the primary function of the mother was as a source of security and tactile comfort for the infant. He conceived of the attachment system as a strong mother-infant bond that had evolved as an adaptation to ensure survival and healthy development of the infant. Importantly, however, his proposal as well as its subsequent support drew heavily from research on rhesus macaques, the nonhuman primate most extensively used to study attachment (Hinde and Spencer-Booth 1971a; Hinde 1991). From this limited scope, Bowlby and many others inferred that humans and other primates alike retained the abilities for attachment because it had originated and descended from an earlier common ancestor (i.e., homological evolution). An explosion of new data concerning primate (including human) child care has since challenged Bowlby’s original homological proposal, particularly as it relates to the concept of the mother being the sole caregiver. Indeed, as described below, primate evidence now indicates that (a) among primates, caring can be shared by various individuals; (b) in some species, the father serves as the primary attachment figure; and (c) primate infants can form multiple attachments.

It is now known that many individuals among New and Old World monkeys (see Figure 3.1) serve as alloparents (Kohda 1985). Furthermore, “sharing caring” is exhibited by prosimians, such as lemur mothers (*Lemur catta* and *Varecia rubra*) who, when foraging, allow their infants (often twins) to be cared for by the father and another lactating mother, who may even feed hungry infants in the mother’s absence (Pereira and Izard 1989; Vasey 2007). Similarly, galagos (*Galago senegalensis*) and mouse lemurs (*Microcebus murinus*) have aunts and grandmothers that can spontaneously lactate and nurse offspring (often twins) (Eberle and Kappeler 2008; Kessler and Nash 2010). Clearly, these examples show that the mother is not the exclusive attachment figure among many primates. Why is this so?

In most primate species, males are present year-round in the same social group as females with whom they have mated. Most primate species, however, have a multimale/multifemale system of mating (see Hawkes et al., this volume). This makes it difficult to identify who has fathered any given child and may contribute to why fathers in many species do not (knowingly) provide care for their young. To compensate for this lack of fatherly input, mothers may rely on other (often related) females, juveniles, and adolescents, all of whom may be eager to practice their mothering skills (see below for further discussion on the potential function of alloparenting). Callitrichid primates, marmosets, and tamarins provide exceptions to this, as they live together in large family units within which the mother, father, and older siblings all care for infants by, for example, carrying them and performing other childcare roles immediately after birth (Kostan and Snowdon 2002; Washabaugh et al. 2002; Mills et al.

2004; Mota et al. 2006). The evolutionary backdrop to this behavior includes multiparous reproduction (i.e., twins) in many marmosets (other primates are typically uniparous reproducers) and the difficulty of individually transporting and caring for multiple offspring, especially newborns (Saito et al. 2008; see Figure 3.2). For example, a newborn marmoset weighs approximately 10% of its mother's weight, and marmosets usually give birth to twins or triplets.

Although fathers may not typically play a major role in rearing their own young, it is important to acknowledge that child-rearing does occur in conjunction with the assistance of other individuals including the father (see above) and that, beyond these duties, fathers themselves can assume the role of the primary attachment figure. For instance, in titi monkeys (*Callibebus moloch*), a New World species characterized by monogamous and biparental relationships, infants seem to show an attachment bias toward their father. Indeed, despite being nutritionally dependent on the mother for the first 8–12 weeks of life, an infant spends 70–90% of its time being transported by the father (Fragaszy et al. 1982). Interestingly, young titi monkeys continue to exhibit a preference for their father when they are no longer dependent on either parent for food or transport (Mendoza and Mason 1986). This has been demonstrated in the selective approaches that 6-month-old infants take toward their fathers when simultaneously presented with their mother and father in a Y-shaped maze (Mendoza and Mason 1986). Between the age of 3–5 months, infants exhibit a greater stress response when separated from the father than from the mother (Hoffman et al. 1995). Similarly, cotton-top tamarins between the age of 9–20 weeks (and which are already independent) exhibit an attachment bias toward fathers rather than mothers, as indicated by their running to the father



Figure 3.2 Transport of offspring marmosets (*Callithrix jacchus*) by the father, with the mother nearby. Photo used with permission from Toni Ziegler.

when presented with a fearful situation (Kostan and Snowdon 2002). Quite clearly, the care of infants extends beyond the mother and can include several other individuals. In some instances, infant care and/or attachment may primarily involve the father. Does this suggest that infants are capable of forming multiple attachments rather than just one?

Let us consider this in relation to infant transfer patterns from one caretaker to the next, which usually occurs smoothly when the future caretaker takes the infant from the back of the current caretaker. Potential nonmother caretakers appear highly motivated to carry infants (Schradin and Anzenberger 2003; Zahed et al. 2008). Infants themselves may also facilitate transfers by doing so spontaneously (Tardif et al. 2002). The fact that infants experience such passive and active forms of contact with nonmother individuals relatively soon after birth suggests that infants can form multiple and varied styles of attachment with their various caretakers (Maestripieri 2003). While these examples indicate that alloparenting and multiple attachments are likely evident in many primates, whether and how such interactions involve qualitative differences in attachment between the infant and their various caregivers—particularly among great apes—remains to be investigated.

With this outline of some of the similarities and differences in attachment among primates, which contradict Bowlby's claims, we will now consider factors which might be important to explain such patterns.

Variations in Sensory Modalities Related to Attachment among Primates

It is possible that the unique characteristics of parent-infant bonds relate to their social interactions and are based on the sensory modalities used. From an early age, Old World monkey infants develop the ability to recognize a primary caretaker through various modalities. For example, within two weeks after birth, long-tailed macaques can differentiate their mother's nipples from those of other females (Negayama and Honjo 1986). In addition, at least some Old World monkey infants have shown a visual ability to recognize a primary caretaker. Surprisingly, Japanese macaque infants reared by human caretakers preferred looking at their surrogate human mothers compared to other humans after only three hours of visual experience with human faces (Yamaguchi et al. 2003). This indicates that the development of this species' ability to discriminate caregivers from noncaregivers may rely on visual as well as tactile information (as evident in their clinging-embracing behavior described below).

Recent research has also shed light on the use of visual information by apes in their early social interactions. Using the preferential looking method, one of us (MM) investigated developmental changes in infant visual face recognition in species representative of small and great apes: One gibbon (*Hylobates agilis*) and three chimpanzees (*Pan troglodytes*); (Myowa-Yamakoshi and Tomonaga

2001a). As shown in Figure 3.3, both gibbon and chimpanzee infants were able to distinguish visually each of their caregiver's faces from other faces very shortly after birth. More specifically, although the gibbon had witnessed human faces for only 2 weeks, he showed a general preference for human-type faces (particularly that of the primary human caregiver) rather than a gibbon face. In contrast, chimpanzees began to show a preference for their biological mother's face at around 4 weeks of age. It is important to emphasize that the amount of face-to-face interaction encountered by chimpanzees (i.e., mutual gaze between mothers and infants) has been found to be less than is typically experienced by humans, in terms of the duration of mutual gaze events and the amount of maternal looking (Bard et al. 2005). When reared in such human environments, chimpanzees might begin to recognize the faces of their primary caregivers earlier by accumulating more visual experience with them (the effects of human enculturation are discussed more below).

Although there are cultural differences, visual exchanges involving gazing and facial expression play a significant role in forming and enhancing parent-infant interactions for humans. For example, during social interactions, some human caregivers draw attention to themselves using several facial expressions in an "exaggerated" mode, such as raising their eyebrows and opening their mouths wider. Infants appear attracted to such changeable and attractive faces. As a possible basis for this type of interaction, human infants seem to be hardwired for visually orienting toward the faces of other individuals. For example, human newborns are sensitive to and prefer looking at stimuli-resembling faces. They also look longer at faces that exhibit direct as opposed to averted gazes (Batki et al. 2000; Farroni et al. 2002). Moreover, human newborns react to facial gestures made by others, by appearing to imitate actions

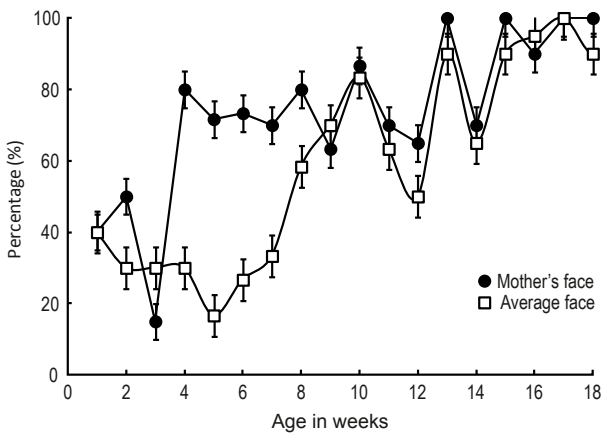


Figure 3.3 Developmental change expressed as a mean percentage of the tracking scores for a mother's face (●) versus average face (□) for each week of age, plus standard error.

such as tongue protrusion and mouth opening (Meltzoff and Moore 1977, 1983; cf. Oostenbroek et al. 2016). Such early competencies in face perception may help infants to establish face-to-face interactions with their caregivers following birth. Do other primates show such face-to-face tendencies?

During their first three months of life, chimpanzee mothers and infants, both in the wild and in captivity, also engage in face-to-face interactions through mutual gazing, although there is no evidence that a chimpanzee mother exhibits exaggerated facial expressions toward their infants as humans do (e.g., van Lawick-Goodall 1968; Bard 1994). In contrast, several Old World monkey mothers (i.e., rhesus and Japanese macaques) seldom look into the eyes of their infants; direct eye contact, in general, has negative connotations in these species and is often interpreted as a threat (e.g., Emery 2000). Nonetheless, a recent study has reported reciprocal face-to-face interactions (e.g., sustained mutual gaze, mouth-to-mouth contacts, lipsmacking) between rhesus macaque mothers and newborn pairs (Ferrari et al. 2009). Additionally, newborn apes and perhaps macaques share at least some of the features exhibited by humans in relation to face perception. Like humans, gibbons, chimpanzees, and Japanese monkeys all discriminate between face-like and nonface-like patterns, as indicated by their preferential looking shortly after birth (Myowa-Yamakoshi and Tomonaga 2001a; Kuwahata et al. 2004). Moreover, gibbons and chimpanzees are also sensitive to faces with open rather than closed or averted eyes, and they pay attention to the gaze of other agents (Myowa-Yamakoshi and Tomonaga 2001b). Finally, chimpanzee and rhesus monkey neonates appear to imitate several human gestures (Figure 3.4; Myowa 1996; Myowa-Yamakoshi et al. 2004; Ferrari et al. 2006; Bard 2007). As for how enhanced survival and/or reproduction may be enabled through this, we tentatively postulate as follows.

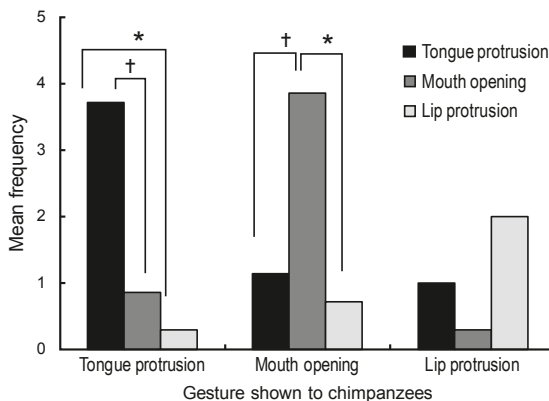


Figure 3.4 Frequencies of the three gestures (tongue protrusion, mouth opening, and lip protrusion) exhibited between one and eight weeks of age (data obtained from Pal, a chimpanzee). The x-axis represents the facial gestures shown to the chimpanzee; * $p < .05$; † $p < .10$.

Hardwired competencies involving face perception that are observed in catarrhine (i.e., Old World monkey and ape) infants may help them form face-to-face interactions with caregivers after birth. In particular, the attention that an infant gives to the caregiver via direct gaze may, in turn, trigger the caregiver to provide greater attention to the infant (particularly via the sharing of positive empathy; see below). This may ultimately create increased opportunities for receiving care (Myowa-Yamakoshi et al. 2005). Still, in terms of eye gazing in humans, we acknowledge that there are strong cultural differences which may impact infant interaction; for example, some Australian Aboriginal people believe that it is disrespectful to look another person, particularly elders, in the eyes. Cultural differences involving face-to-face interactions and subsequent variations in attachment are a topic worthy of future investigation.

Moving past the role of vision (particularly face-to-face) in social interaction and attachment, what about touch? For macaque and ape infants, continuous physical contact is evident as of birth: infants cling to their mother's hair to be safe from predators, to be fed, to build a secure attachment with their mothers, and to learn socially from their mothers. Prosimian (e.g., *L. catta*) and New World monkey (e.g., *Saguinus oedipus* and *Callithrix jacchus*) infants also exhibit continual physical contact by clinging to their caregiver's hair. Yet despite this similarity, and in contrast to Old World monkeys and apes, prosimian and New World monkeys do not generally tend to embrace their infants; the infants themselves are responsible for clinging to the caregiver during feeding and transportation. The mother-infant relationship characterized by such a clinging-embracing (ventro-ventral) bond, especially observed in macaques and apes, might thus be related to the intense emotional connection between them. If so, such a characteristic may be a unique and crucial aspect of the catarrhine attachment system. As research continues, it will be important for future researchers to consider whether interspecies differences in clinging-embracing behavior among and within catarrhines are associated with potential differences in attachment. For instance, although chimpanzee mother-infant pairs are in physical contact via clinging-embracing 24 hours a day for the first three months of an infant's life (Matsuzawa 2006), and humans generally tend to engage in skin-to-skin contact, there appears to be considerable cultural differences among humans as to the amount and style of clinging-embracing which may be related to external factors such as work, on-demand nursing, and weaning (Diamond 2012). More specifically, human infants raised in WEIRD (western, educated, industrialized, rich, and democratic) societies may spend time in a playpen and sleep in rooms separate from caregivers, whereas infants raised in traditional cultures may spend considerable time being carried around by the caregiver and share the same room (if not bed) with their parents while sleeping. It is estimated, for example, that for 90% of the time during the first year of life, !Kung infants engage in skin-to-skin contact with the mother and other caregivers, an amount of time that greatly exceeds the experience of WEIRD infants (Diamond 2012). Determining the extent to which human

cultures do vary in this regard, particularly among traditional hunter-gatherer societies and for children of different ages, needs to be a priority for future research.

Finally, in addition to the visual and tactile modalities, it seems likely that many humans also frequently use vocal sounds in parent-infant interactions. More specifically, human infants cry very frequently, and they gradually begin to use their cries to attract the parent's attention. In at least some (i.e., Japanese and Western) cultures, parents often reply vocally to their infants instead of actually embracing them (Takeshita et al. 2009). Whether and how such vocal interactions occur in other cultures and in other primate infant-parent dyads, and the relationship (if any) between such interactions and styles of attachment, remains to be systematically identified (for discussion on face-to-face communication between rhesus macaque mothers and their newborn infants through lip smacking, see Ferrari et al. 2009).

Primate Attachment in Relation to Alloparenting, Cognitive Autapomorphies, and (Ecological and Social) Context

Having considered the role that sensory modalities play in differentiating attachment among primates, we turn to the role of the human mind itself, as this is likely to be a major force behind the unique style of human attachment. Over the last few decades, an explosion in comparative psychological studies has uncovered not only what appears to differentiate the cognitive abilities of apes from other primates, but also what appears to be unique human capacities, such as “nested scenario building” (i.e., open-ended imagination, or stated differently, the ability for recursively reflecting on different situations) and our “urge to connect” with other minds (e.g., Suddendorf and Whiten 2001; Suddendorf 2013; Butler and Suddendorf 2014). Indeed, when combined, these unique abilities may even be responsible for transforming animal communication into human language, habitual behavior into cultural traditions, problem-solving into abstract reasoning, and empathy into morality (Suddendorf 2013). How do these (or other) human autapomorphies (i.e., traits unique to one species) contribute to attachment? As one possibility, we propose that the evolution of human alloparenting is related to the evolution of other specific aspects of social cognition that appears to be unique to humans. Before discussing this, we will set the stage by considering the presence and function of alloparenting among primates in general, with particular emphasis on one of our closest living relatives: the common chimpanzee.

Alloparenting in Chimpanzees

There is limited data on observed chimpanzee births in the wild. Field researchers engaged in long-term studies of wild chimpanzees in Africa rarely get to

witness a birth because females will quietly leave the group and disappear a few days before going into labor. Like other nonhuman primates, chimpanzees give birth alone (Nishida et al. 2003). Although they return to the group afterward, it is unknown where they go or what they do while they are away. Researchers often tell of being surprised to see a female reappear suddenly with a newborn at her breast. After returning, chimpanzee mothers raise their children on their own. Even for a first child, a chimpanzee mother receives no instructions or direct assistance from anyone. Nonetheless, mothers do not appear to abandon their offspring. It is possible, although as yet unconfirmed, that a mother might return to the group alone and leave behind her newborn if, for example, it is weak at birth or because of a lack of breast milk.

Curiously, in the early period following birth, a mother seldom wants her infant to be touched by other group members, and thus alloparenting seldom occurs in wild settings (van Lawick-Goodall 1968; Nishida 1983; Goodall 1986). At around one year after birth, infants develop motor skills to move around on their own and can approach other familiar members of the group. They increasingly spend short amounts of time being looked after by individuals other than their mothers (i.e., short-term alloparenting). Such short-term (i.e., nonadoptive) alloparenting behavior has also been confirmed in several Old World monkeys such as baboons (Altmann 1980), vervet monkeys (Lancaster 1971), bonnet monkeys (Silk 1980), and patas monkeys (Muroyama 1994; Nakagawa 1995).

Many ethologists and primatologists argue on the basis of kin selection theory that there must be some sort of (reproductive) benefit to nonmothers who care for the young of others at a cost to themselves. The primary merits suggested have been the building of good social relationships with the child's mother and other members of the group (in the form of being groomed by others) and training for future child-rearing to ensure greater success with one's own child since first-time mothers are usually associated with lower infant survival rates. Regarding the latter possibility, Fairbanks (1990) found that in vervet monkeys (*Cercopithecus aethiops sabaues*), first-time mothers with high alloparenting experience raised 100% of their first offspring to maturity, whereas mothers with low alloparenting experience had less than a 50% survival rate for their first infants.

There are far fewer cases, however, of long-term alloparenting, i.e., adoption (operationally defined as any relationship between an adult and another individual's child in which the adult shows maternal-like behavior, e.g., food sharing, protection, for at least a two month period) (Boesch et al. 2010). Over the fifty years that chimpanzees have been observed in the wild, fewer than thirty instances have been reported (e.g., Goodall 1986; Nishida et al. 2003; Wroblewski 2008; Boesch et al. 2010). The majority of these were orphan situations where individuals under five years of age (i.e., not weaned) had lost their mothers. In 23 cases, 13 represented kin relationships (e.g., grandmothers, siblings, aunts) and ten involved adoption by nonkin members. Thus,

long-term alloparenting does occur among wild chimpanzees with both kin and nonkin members, including males. The occurrence of such long-term alloparenting by nonkin raises an issue that requires further consideration: What possible benefits accrue to the alloparent, beyond those observed for short-term alloparenting?

It is important to note that long-term alloparenting does not seem to occur when the biological mother is still alive. Still, we have evidence of full adoption by a grandmother (the mother's mother) in a case where the mother abandoned her child (Wroblewski 2008). Whether nonkin adopt another's offspring after maternal abandonment, however, remains to be confirmed.¹

Even though chimpanzees exhibit long-term alloparenting, and despite its potential benefits, why is it so rare? Recall that wild chimpanzee mothers seldom allow others to contact their infants within the first six months, indicating that it must be difficult for them to entrust their child to another individual. This is not to suggest that chimpanzees lack the psychological trait of trust (e.g., Engelmann and Hermann 2016). In fact, at the Primate Research Institute (Kyoto University), mothers allowed their children to be touched soon after birth by certain researchers with whom they had grown familiar over the years (Matsuzawa 2006). It is possible that captive settings might allow chimpanzee females to develop the characteristic of trusting other female individuals, as indicated by their more "bonobo-like" female coalitions that have been observed (e.g., de Waal 1998). It will be important to reveal further which factors may affect the development of trust toward other individuals in primates, and ultimately their relevance to alloparenting and attachment (see below).

Human Cognitive Autapomorphies and Alloparenting

Empathy is the ability to share and understand other people's moods through various forms of latent and unconscious transmission or high-order inferential cognitive processing. Merely being aware of another's distress or joy, for example, automatically elicits a similar response in us; this "emotional empathy" is mainly based on the mirror neuron system network (Shamay-Tsoory 2011). Further, deliberately "climbing into the shoes" of another person in an effort to imagine or feel their distress or joy, "cognitive empathy," is thought to be mainly related to mentalizing circuits (Iacoboni et al. 1999).

Humans are not the only animals capable of empathy. Along with our primate relatives, rats, dolphins, and many other animals are sensitive to the experiences of others, but mainly in regard to their feelings of distress (e.g.,

¹ Although we acknowledge an instance of chimpanzee adoption involving individuals known as "Gorilla" and "Roosje," documented by de Waal (1998), it is unclear whether maternal abandonment occurred.

Langford et al. 2006; Bartal et al. 2011). The phylogenetic origins of this restricted brand of empathy are thought to be directly linked to survival (i.e., an adaptation): animals may be better able to perceive quickly and take measures to avoid whatever it is that is threatening other group members. Although a small number of species (including orangutans) have shown evidence for emotional positive empathy (Davila Ross et al. 2008), we lack clear evidence that nonhuman animals are capable of cognitively empathizing with other individuals who show positive emotions, such as joy, pleasure, delight, or happiness (Myowa 2012). There are numerous theories as to why humans alone may have acquired this ability, but one interesting claim, relevant to our discussion on attachment, involves observed sex differences in empathizing, with more neurological activity being evident during empathy tasks in females (Baron-Cohen 2003). We assume that such a sex difference might be related to mother-infant pair bonding, especially in humans. With this in mind, it has been argued that mother-infant sharing of pleasurable emotions has been of paramount importance (either as an adaptation or a by-product) in the formation of human strategies for surviving the earliest stages of development (Myowa 2012).

Indeed, let us reconsider the evolution of human alloparenting in light of our possibly unique ability to empathize cognitively with the positive emotions of others. Humans show forms of long-term alloparenting irrespective of kin and nonkin members, as is evident in adoption and even large institutions for foster care (although we acknowledge that some instances of negative care do occur in such situations), whereas long-term alloparenting rarely occurs among chimpanzees and other catarrhine species. We assume that human alloparenting styles are unlikely to have grown solely out of the sharing of distress shown by others. In other words, it seems difficult to motivate others to participate in altruistic activities simply through the sharing of unpleasant emotions. On the other hand, a shared sense of comfort, joy, and achievement gained through the care of children serves as a positive mental reward to others who participate in the process. What at first appears to be an altruistic act, therefore, may be the result of pleasurable emotions derived from caring for children. It seems difficult to otherwise explain why only humans would make such an effort to raise children other than their own. Could it be that reinforcement through the evocation and sharing of pleasurable feelings played a role in the evolution of alloparenting? This is nothing more than guesswork at present (and extensive cross-cultural research is required), but one of the keys for understanding both attachment bonds and the establishment of alloparenting in humans is likely to be the cognitive function(s) of empathy. Similarly, further insights may be obtained by considering whether and how other human cognitive autapomorphies could influence attachment (e.g., mental time travel, theory of mind, nested scenario building, and our fundamental urge to connect with other minds).

Contextual Factors Related to Attachment and Alloparenting among Primates

While we believe that human cognitive autapomorphies, such as cognitive empathy for positive emotional states, are crucial factors related to the evolution of the human attachment system, attention must also be given to the role of context. What role does one's (ecological and/or social) environment play? A few observations are offered for consideration on this matter.

Recall that wild chimpanzees rarely appear to abandon their young. This stands in stark contrast to over 100 cases of birth with chimpanzees in captivity, where one out of every two mothers that give birth do not care for their infants (Matsuzawa 2006). What causes this abnormal attachment behavior? Over half of the chimpanzees kept in captivity in Japan live in groups of five or fewer members. This is quite different from the wild, where groups typically range from 20–100 members. Although caretakers and researchers are making efforts to increase captive group numbers, small groups mean that most captive chimpanzees do not have the chance to observe or interact directly with their own or other's offspring. This suggests that a lack of social learning opportunities during an early period in life may be one of the primary reasons why some captive mothers end up abandoning their offspring. Clearly, this indicates that a chimpanzee mother's attachment to her infant and her infant-rearing behavior are largely affected by habitat (for a discussion of other great apes and the effects of learning and experience in the development of good maternal skills observed within zoos, see Bard 2002; Abello and Colell 2006). What other evidence is there for enculturation influences?

Tomasello et al. (1993) reported that enculturated chimpanzees developed more imitative abilities than mother-reared chimpanzees. Also, when young nursery-reared chimpanzees were exposed to a novel object, they exhibited gaze alternation between this object and the face of their primary caregiver, a phenomenon called human social referencing (Russell et al. 1997). Indeed, in day-to-day interactions between some human caregivers and infants, social turn-taking behaviors may play an important role in the formation of attachment. Recall our proposal that many human caregivers (in at least some cultures) attract attention to themselves by introducing infants to several "exaggerated" facial expressions, such as raising their eyebrows, opening their mouths wider, smiling, and often imitating the responses of the infants. In turn, infants may be attracted to the caregiver's changeable and attractive gestures and respond to them. Such socially responsive, turn-taking interactions (perhaps based on positive emotional empathy) may play a crucial role in attachment formation and may even increasingly enhance infants' cognitive abilities for things such as imitation (for further discussion on how caregiving practice may have influenced attachment, see van IJzendoorn et al. 2006). In any event, findings involving enculturated primates indicate that cognitive abilities related to attachment develop flexibly, depending on

extended exposure to varying rearing environments after birth. This point has been further reinforced by Bard et al. (2005), who found that mother and infant chimpanzees at a Japanese center (Primate Research Institute, Kyoto University) exhibited a higher rate of mutual gaze than those at an American center (Yerkes) (Figure 3.5). Compared to the latter, Japanese chimpanzees have established long-term relationships with human researchers in everyday life and are much more familiar with the human environment and the social ritualizations involved, such as active mutual gaze and joint attention. In other words, Japanese chimpanzees may have higher levels of human enculturation. These results suggest that there is flexibility in chimpanzees' development of mutual gaze and that infants learn group-specific patterns as observed in humans (Keller et al. 2004b). Finally, the possibility that enculturation can influence (and result in) alloparenting has actually been reported, albeit to our knowledge only once: alloparenting among captive lowland gorillas (*Gorilla gorilla gorilla*) while the mother is alive has been observed by Nakamichi et al. (2007), including when nonkin gorilla mothers mutually exchanged and reared their children. It is unknown whether this instance of alloparenting involved the form of 100% child care or was more restricted on a needs basis for the child.

Further longitudinal developmental, cross-cultural, and comparative studies are clearly needed to reveal the effects of socioecological experience and its relationship with species-specific biological foundations in the establishment of attachment between parent and infant pairs among captive and wild primates, including humans. For example, given that mothers in polyandrous-structured primate species show a tendency for having twins (e.g., titi monkeys), and that this seems to result in alloparenting involving the father, what possible relationships exist between attachment and other primate social structures:



Figure 3.5 Mutual gaze between mother and infant chimpanzees (*Pan troglodytes*) in the Primate Research Center of Kyoto University, Japan. Photo used with permission from T. Matsuzawa.

single mother and child, monogamous, polygynous, multimale/multifemale, and fission-fusion (for discussion of these types, see Kappeler 1997). We may similarly ask this question for humans, as they are the only primate to exhibit all of these structures (across rather than within cultures). A related issue is whether and how socioecological factors driving these differences in group structure also impact on attachment (e.g., food availability, group size, genetic relatedness of group members, dominance hierarchies, threat of infanticide). For example, does the threat of infanticide in chimpanzees contribute to the reluctance of wild chimpanzee mothers to disallow contact from other females during their infant's first six months? Is this exhibited by mothers of other primates affected by infanticide (i.e., gorillas and orangutans) or by those which are not, most specifically, gibbons and bonobos?

Human Attachment Summarized: What Is Shared and What Is Unique

Clearly, our understanding of primate attachment has progressed considerably since it was first outlined by Bowlby. Rather than being a uniform phenomenon among primates based on a homology, we know now that attachment varies across primates. Humans appear to be unique in relation to their combination of modalities used in forming attachments (i.e., large amounts of looking and the additional use of tactile and vocal cues), the use of positive cognitive empathy, and possibly certain contextual elements typically associated with human socioecological environments. More research is required to substantiate and potentially extend these claims. Nonetheless, it is time for researchers to adapt attachment theory to the extensive primate literature that has accrued since Bowlby's passing.

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