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Reciprocal face-to-face communication between rhesus macaque mothers and their newborn infants

Pier Francesco Ferrari^{1,2}, Annika Paukner², Consuel Ionica², and Stephen J. Suomi²

¹ Dipartimento di Biologia Evolutiva e Funzionale, via Usberti 11A, Università di Parma, 43100, Parma, Italy

² Laboratory of Comparative Ethology, Eunice Kennedy Shriver NICHD, NIH, Bethesda, MD 20892-7971, USA

Summary

Human mothers interact emotionally with their newborns through exaggerated facial expressions, speech, mutual gaze, and body contact, a capacity that has long been considered uniquely human (1–4). Current developmental psychological theories propose that this pattern of mother-infant exchange promotes the regulation of infant emotions (4–6) and serves as a precursor of more complex forms of social exchange including perspective-taking and empathy. Here we report that in rhesus macaques, mother-infant pairs also communicate intersubjectively using complex forms of emotional exchanges including exaggerated lipsmacking, sustained mutual gaze, mouth-mouth contacts, and neonatal imitation. Infant macaques solicit their mother's affiliative responses and actively communicate to her. However, this form of communication disappears within the infant's first month of life. Our data challenge the view that the mother-infant communicative system functions in order to sustain proximity and that infants are simply passive recipients in such interaction. Thus, emotional communication between mother and infant is not uniquely human. Instead, we can trace back to macaques the evolutionary foundation of those behaviors that are crucial for the establishment of a functional capacity to socially exchange with others.

Results

In humans, mothers and infants engage in intense emotional communication characterized by mutual gaze, facial expressions (e.g. smile), body contact (e.g. hand-body contacts, kisses, etc.), and play (1–4). Further studies in the last three decades paved the way to the development of intersubjectivity theory (1–3,5) proposing that newborns are sensitive to their mother's facial expressions, body movements, and voice, and that they are capable of and motivated to mutually engaging with her in an intersubjective game involving different sensorimotor modalities (4–5). Infants are therefore not simply passive subjects that respond to and learn from the mother's solicitation, but are also capable of soliciting mother's affiliative responses and actively communicating to her, thus demonstrating the capacity to exchange emotions and purposes. For years these capacities were considered to be basically unique to humans (7), although perhaps shared, to some extent, with chimpanzees (8–11). Early pioneering studies in macaques (e.g. 12–15) rarely reported these types of mother-infant interactions. When observed, they were considered to be related to separation episodes (16,17) relegating first forms of mother-infant communication mainly within the tactile-sensory domain (18). In

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contrast to this view, evidence of neonatal imitation in macaques (20) has demonstrated that some forms of intersubjectivity can be present at birth in this species. However, these kinds of interactions in macaques are not commonly reported in naturalistic contexts. We therefore investigated the possible occurrence of mother-infant intersubjective exchanges and sought to verify whether their possible presence at birth could be related to communicative functions.

We studied 14 rhesus macaque mother-infant pairs for the first 2 months of the infants' life. We used focal-animal sampling to record all mother-infant pairs. Each focal pair was observed 1–3 times a day for 15 minutes sessions for infants' first 23 days of life (6 days/week). Three additional sample collections were made on three different days when the infants were approx. 4 and 8 weeks old for a total of 110 hours of observation.

We observed frequent visual contact between mother and their infants. More specifically, mutual gaze was more frequent between infants and mothers than between infants and other individuals ($F_{1,13}=45.27$, $p<0.0001$; see figure 1a and an example in figure 2). There was also a tendency to increase mutual gaze with infant age ($F_{1,13}=2.67$, $p<0.07$), but there was no interaction between these two factors. Mutual gaze between infants and the mothers was more frequent in the second and third week of life and decreased after 2 months.

Lipsmacking by adult monkeys always coincided with mutual gaze. Furthermore, infants received more lipsmacks from their mothers than from other individuals ($F_{1,13}=39.45$, $p<0.0001$; see figure 1b). The frequency of lipsmacking increased with infant age ($F_{1,13}=3.35$, $p<0.001$), and there was a significant interaction between infant age and social partner (mother or other adult $F_{1,13}=2.69$, $p<0.007$). Paired comparisons showed that the increase in lipsmacking directed at infants by their mothers significantly increased from the first days of life until the third week of life, after which it returned to baseline levels. Lipsmacking declined dramatically at the end of the infants' first month of life and was almost absent by the end of the second month. Further regression analysis indicated that the frequency of mother-infant mutual gaze not involving lipsmacking predicts the amount of lipsmacking the infants receive from their mothers ($F=91.12$, $p<0.0001$).

The methodological approach used in the present study did not allow us to report precisely the rich sequences of behavioral patterns that mothers displayed towards their infants. However, some of these patterns seem to be common and worthy of reporting here. Two patterns of lipsmacking in particular appeared to be specific to mother-infant interactions; we never observed them between adults. In the first pattern, the mother held the infant and actively searched for the infant's gaze, sometimes holding its head and gently pulling it towards her face (see video 1 in supplemental material). In the second pattern, the infant was physically separated from the mother on the ground or on a perch. The mother moved her face towards the infant's face to a distance of 20–40 cm, and sometimes lowered the head and bounced it in front of the infant's face (see an example in figure 3 and supporting video 2 and 3; see supplemental material for further details).

Infants started to separate from their mothers on the third day (3 out of 14; see figure 1b white dots). By day 6, half of the infants were observed to have physically separated from their mothers. By day 12 almost all infants (13/14) had at least one physical separation. Starting from the second week of life, infants started to separate for longer distances and outside their mother's arm reach. In the second month of life, their time of physical separation from their mothers had significantly increased, and often they could remain outside their mother's immediate vicinity. We found no association between the frequencies of lipsmacking a mother directed at her infant and the number of infant separations (within arm reach, $F_{1,12}=2.53$, $p>0.1$; outside arm reach, $F_{1,12}=0.65$, $p>0.1$; see supplemental figure 1A and B). Similarly, we found

no association between the first day the infant separated from the mother and the frequency of lipsmacking the mother directed at her infant ($F_{1,12}=1.79$, $p>0.1$).

In several cases we were able to observe both mother and infant during these interactions, and we recorded all instances in which the infant responded to the mother's lipsmack with similar gestures. Lipsmacking responses were most frequent between days 3 to 11, and infants were more likely to respond to the mother than to other individuals ($F_{1,13}=13.75$, $p<0.003$; see figure 4a). After day 11, infants' responses became less frequent despite the fact that infants received more lipsmacks from their mothers.

Finally, infants initiated lipsmacking more frequently toward their mothers than toward other females in the enclosure ($F_{1,13}=15.78$, $p<0.002$). Although this behavior was relatively infrequent, we observed that it became more common after the first week of life and then declined after the first month of life (see figure 4b).

By observing 6 mother-infant dyads in semi-free ranging conditions (at the LCE field station) we were able to confirm the presence of these patterns of behavior under more natural conditions, and we video recorded some of these displays (see details in supplemental material; see examples of these patterns in the supplemental video material).

Discussion

It has often been implicitly assumed that mutual gaze and facial communicative exchanges are uniquely human features and that they reflect the rich and complex mother-infant interactions that in humans last for years (7). Human mothers talk to their babies, smile at them, and solicit their babies in a playful way that is promoted by intense mutual gaze (1,5,6). To a lesser extent, chimpanzees also seem to possess some of these competencies (18,19). It has been proposed that this affective communication system plays an important role in regulating preverbal infant emotions and developmental cognitive structuring (4–6). Our study revealed that macaque mother-infant interactions are characterized by exaggerated lipsmacking at infants and touching their faces with the mouth, which resembles the empathic ritualized human 'motherese' and the intense body contact that human adults typically establish with their infants (e.g. face-to-face contact, hand-body touch, kiss etc.). Previous studies of mother-infant interactions in macaques (12–15) rarely reported such emotional facial communication. When observed, it was considered to be an infrequent phenomenon related to infant separation from the mother (15,16) and becoming more frequent with infant age. However, our data show no correlation between mother lipsmacking and mother-infant separation. Furthermore, a significant number of lipsmacks (159 out of 734; 21.67%) were performed while the mother and infant were in ventral-ventral contact. Together, these data suggest that the function of mother lipsmacking in the first weeks of infant development is not related to re-establishing body contact or maintaining proximity. Instead, mother-infant mutual gaze and the communicative exchanges we observed clearly promote the opportunity for early emotional communication and are likely to play a pivotal role in infants' emotional development.

Infant macaques, similar to human infants, are able to respond to their mothers' lipsmacking by lipsmacking back at them. These behaviors are reminiscent of the neonatal imitative responses that we reported under more controlled conditions in nursery-reared infant macaques (20,21) and might reflect the involvement of specific neurobiological mechanisms committed to intersubjective exchange (22). Furthermore, our findings suggest that infants are not merely the recipients of such exchanges. We observed that, even in the first days after birth, infants actively solicit their mothers to interact by spontaneously lipsmacking at them. Thus, similarly to humans and chimpanzees, infant macaques possess the ability to communicate in an intersubjective modality where behavioral synchronization and facial expression are the basic

elements of emotional exchange. We suspect that the lack of such early communicative exchanges might influence infant emotional development. This hypothesis is supported by research on humans showing that ineffective face-to-face communication and mutual exchanges between mother and their newborns deeply impact infants' emotional development (6).

Surprisingly, such intense emotional exchanges between mother and infant macaques dramatically decrease after the first month of life. The reason for this decrease could be due to several changes in infant development occurring at this stage. Infant rhesus macaques are highly mobile after their first month of life, and the periods of physical separation from their mothers increase accordingly (13,23). This phenomenon reflects not only the maturation of the skeleto-motor system but also important changes of psychological development, such as increased interest in their same-age peers within the colony. Thus, both the maturation of the infant skeleto-motor system and its psychological development seem to have a profound impact on mother-infant interactions.

In sum, our results clearly demonstrate that humans are not unique in showing emotional communication between mother and infant. Instead, we can trace the evolutionary foundation of those behaviors that are considered crucial for the establishment of social exchange with others to macaques. Mutual gaze, neonatal imitation, infant gestures, and exaggerated facial gesturing by mothers are distinctive signs in macaques, as well as in humans, of interpersonal communication and perhaps even a mutual appreciation of others' intentions and emotions.

Experimental procedures

The subjects were 14 mother-infant rhesus macaque pairs (*Macaca mulatta*). Seven infants were male and seven were female, all being reared by their biological mothers (aged between 6 and 12 years; 3 were primiparous). All animals were born at the Laboratory of Comparative Ethology's (LCE) primate facilities at the National Institute of Health Animal Center near Poolesville, MD and were housed in social groups containing 8–10 adult females (including the infant's mother), one or two adult males, and other similar-aged infants. Monkeys were housed in indoor-outdoor enclosures measuring $2.44 \times 3.05 \times 2.21$ m-indoor; and $2.44 \times 3.0 \times 2.44$ m-outdoor (see details in supporting material).

The frequencies of the following infant behaviors were recorded: mutual gaze between infants and their mothers or other individuals, infant lipsmacking at the mother or other individuals, mother or other individuals lipsmacking at infant, infant lipsmacking in response to mother's or other individuals' lipsmacking (see supplemental material for detailed description of behaviors and statistical analysis). The infant had to look at the gesture of the performing individual in order for lipsmacking at infant to be scored. We also recorded the frequency of separation of infant from the mother, classified as either within or outside an arm's reach (see supplemental material).

All testing was conducted in accordance with regulations governing the care and use of laboratory animals, and had prior approval from the Institutional Animal Care and Use Committee of the *Eunice Kennedy Shriver* National Institute of Child Health and Human Development.

Observations of interactions in 6 mother-infant pairs of semi-free-ranging rhesus monkeys

In order to assess the presence of these behaviors under more naturalistic conditions, we also followed six mother-infant pairs living in the LCE's 5-acre outdoor field station at the NICHD. These pairs were observed twice a week (15 minutes for each observation), and mother-infant behaviors were recorded during these observations (see supplemental material).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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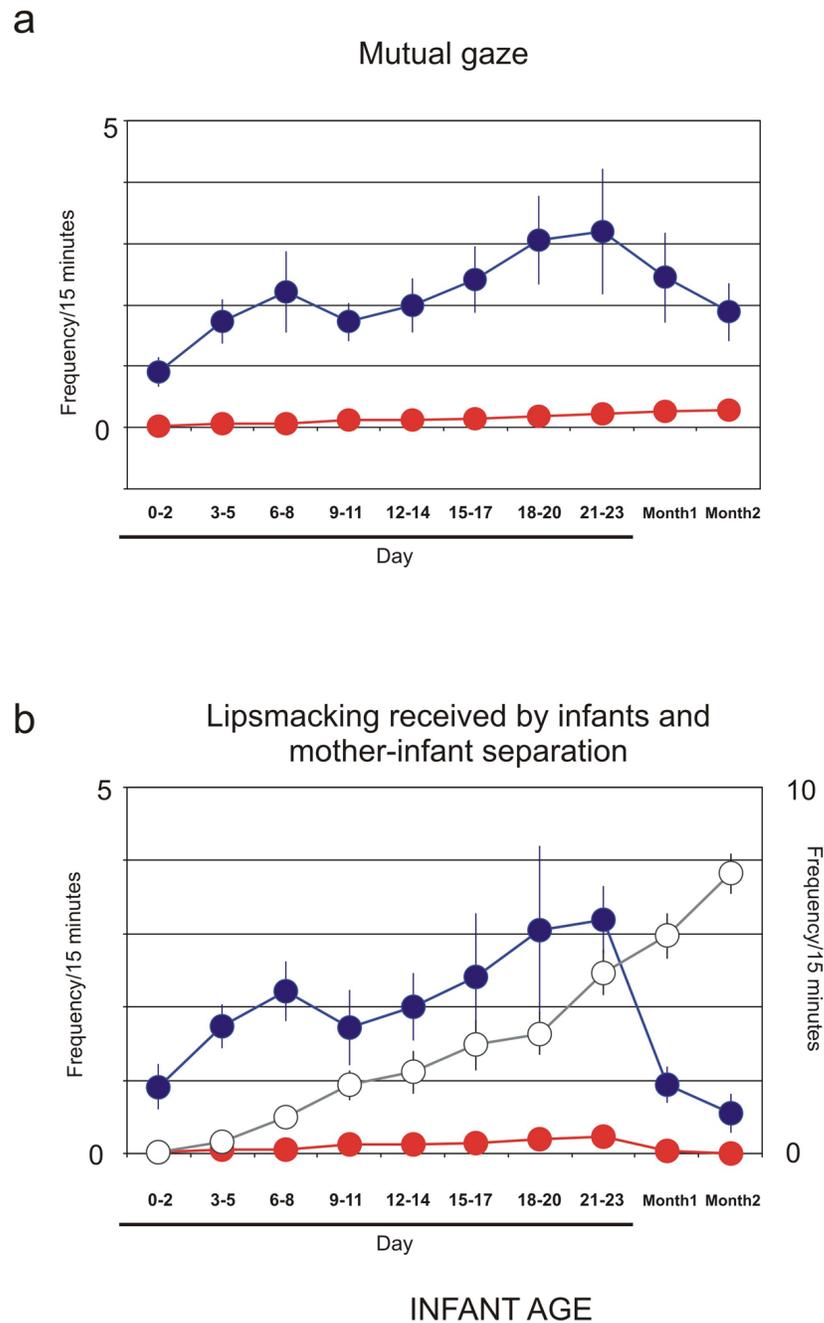


Figure 1.

1a. Frequency (means \pm SEM) of mutual gaze between mothers and infants (blue) and between other females and infants (red) during the infants' first two months of life. 1b. Frequency of lipsmacking (means \pm SEM) directed at infants by mothers (blue) and other females (red) during the infants' first two months of life. White dots show the frequency (means \pm SEM) of infants' physical separation from their mothers outside mother's arm reach.



Figure 2. Captured and cropped still frames (see video 1 of supporting materials) illustrating maternal behaviors toward infants. A. Mother is pulling her infant's head and stares at him. The infant is about 10 days of age. B. Mother is lipsmacking at infant's orbital area. C. Mother is licking at the infant's orbital area.



Figure 3. Captured and cropped still frames (see video 2 of supporting materials) illustrating a mother lipsmacking at her infant. Infant is 6 days old. Note that the mother's head is bouncing up and down and that facial expressions are alternating between teeth-chatter and lipsmacking (bottom figure).

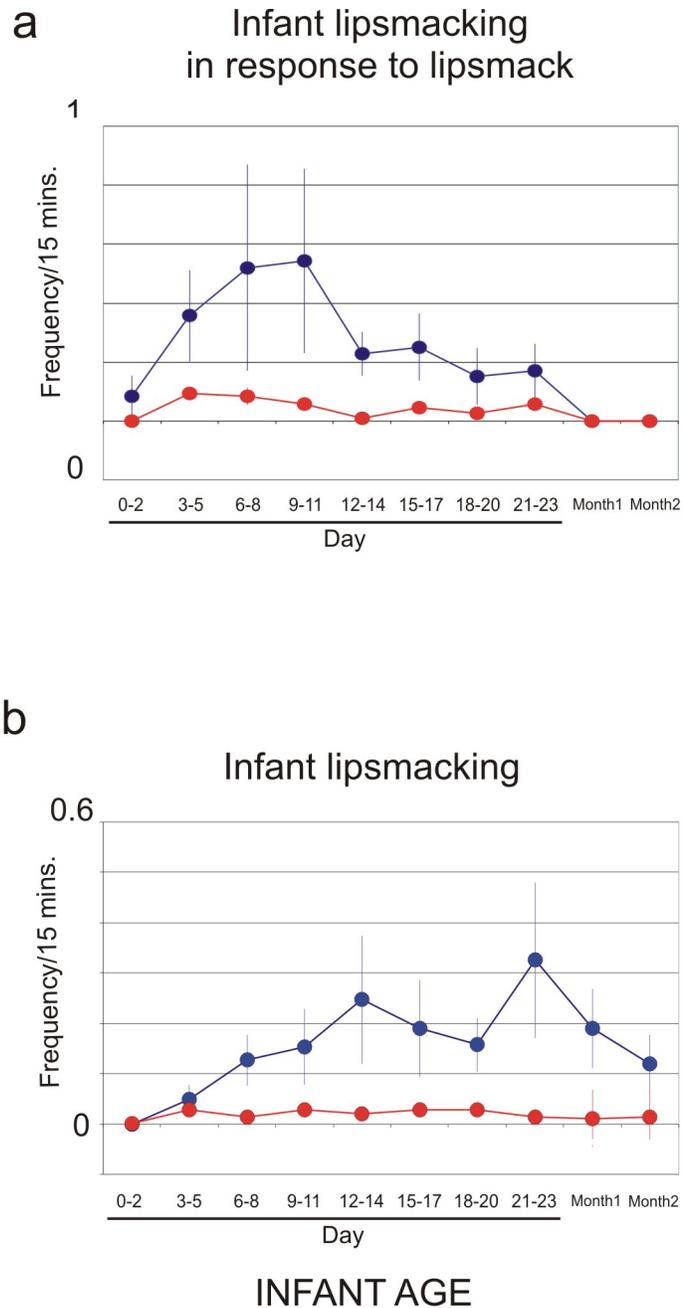


Figure 4.

4a. Frequency (means \pm SEM) of infants' lipsmacking in response to mother's lipsmack (blue) and other females' lipsmack (red) during the infants' first two months of life. 4b. Frequency (means \pm SEM) of infants' lipsmacking directed at the mother (blue) or other females (red) without prior lipsmacking by adult monkeys during the infants' first two months of life.