Current Biology 19, 1768–1772, November 3, 2009 ©2009 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2009.08.055

Report

# Reciprocal Face-to-Face Communication between Rhesus Macaque Mothers and Their Newborn Infants

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## 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 via 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 have paved the way toward 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 mutually engaging with her in an intersubjective game involving different sensorimotor modalities [4, 5]. Infants therefore are not simply passive subjects that respond to and learn from the mother's solicitation but are also capable of soliciting the 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 primarily to the tactile-sensory domain [18]. In contrast to this view, evidence of neonatal imitation in macaques [19] 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 in 15 min sessions one to three times per day for the infant's first 23 days of life (6 days per week). Three additional sample collections were made on three different days when the infants were approximately 4 and 8 weeks old, for a total of 110 hr of observation.

We observed frequent visual contact between mothers 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 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 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 predicted the amount of lipsmacking that the infants received 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 toward their infants. However, some of these patterns seemed 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 toward her face (see Movie S1 available online). In the second pattern, the infant was physically separated from the

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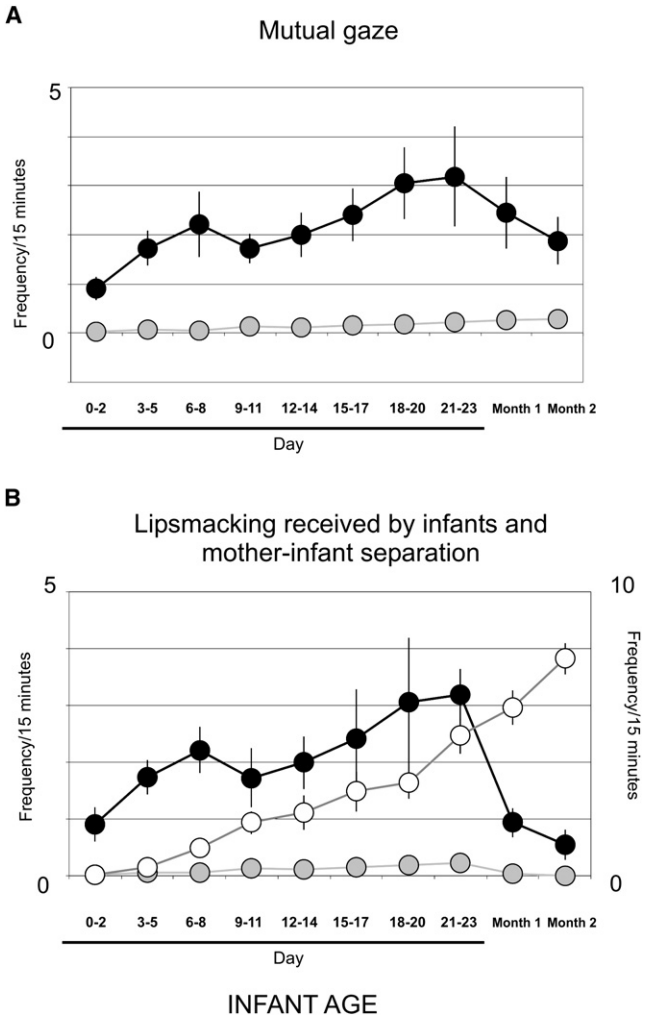


Figure 1. Mother-Infant Mutual Gaze and Mother Lipsmacking in Relation to Infant Age and Physical Separation from Mother

(A) Frequency (means ± standard error of the mean [SEM]) of mutual gaze between mothers and infants (black) and between other females and infants (gray) during infants' first 2 months of life.

(B) Frequency of lipsmacking (means ± SEM) directed at infants by mothers (black) and other females (gray) during infants' first 2 months of life. White circles show frequency (means ± SEM) of infants' physical separation from their mothers outside of the mother's arm reach.

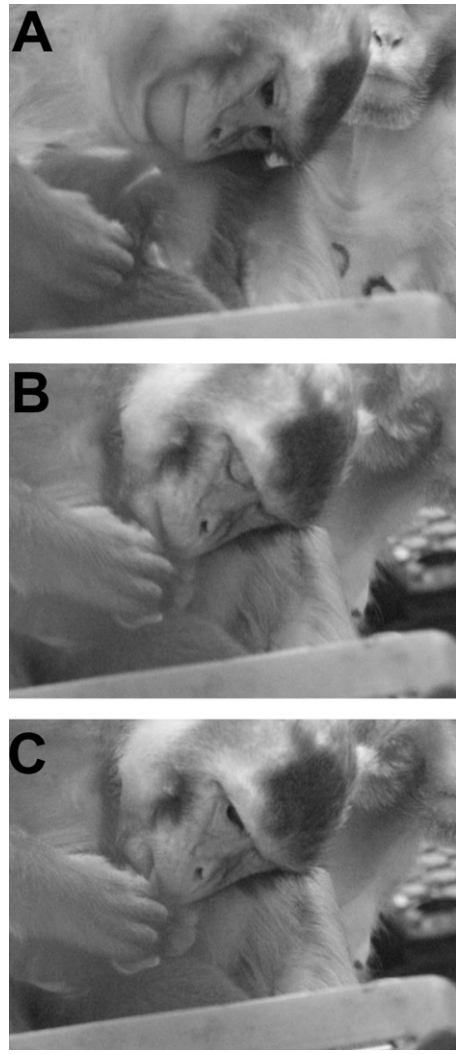


Figure 2. Captured and Cropped Still Frames Illustrating Maternal Behaviors toward Infants

Images are from Movie S1.

(A) Mother pulls infant's head and stares at him. Infant is ~10 days old.

(B) Mother lipsmacks at infant's orbital area.

(C) Mother licks at infant's orbital area.

mother on the ground or on a perch. The mother moved her face toward the infant's face to a distance of 20–40 cm and sometimes lowered her head and bounced it in front of the infant's face (see example in Figure 3 and Movies S2 and S3; see Supplemental Experimental Procedures for further details).

Infants started to separate from their mothers on the third day (3 of 14; see white circles in Figure 1B). By day 6, half of the infants were observed to have physically separated from their mothers. By day 12, almost all infants (13 of 14) had at least one physical separation. Starting in the second week of life, infants started to separate for longer distances and move outside their mother's arm reach. In the second month of life, the infants' 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 frequency 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 Figures S1A and S1B). Similarly, we found no association between the first day the infant separated from its 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 and 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

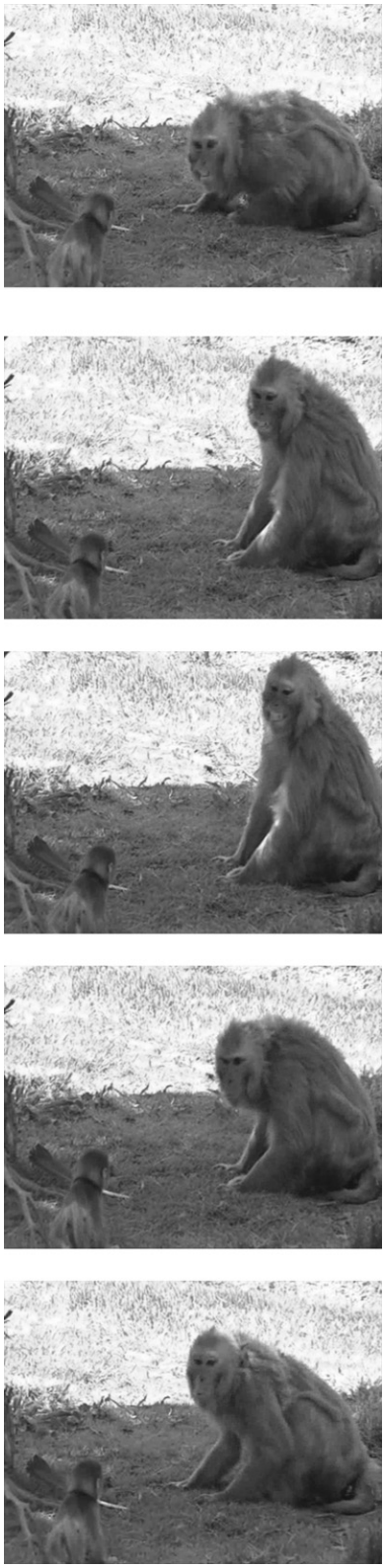

Figure 3. Captured and Cropped Still Frames Illustrating a Mother Lipsmacking at Her Infant

Images are from Movie S2.
Infant is 6 days old. Note that the mother's head is bouncing up and down and that her facial expressions are alternating between teeth chattering and lipsmacking (bottom image).

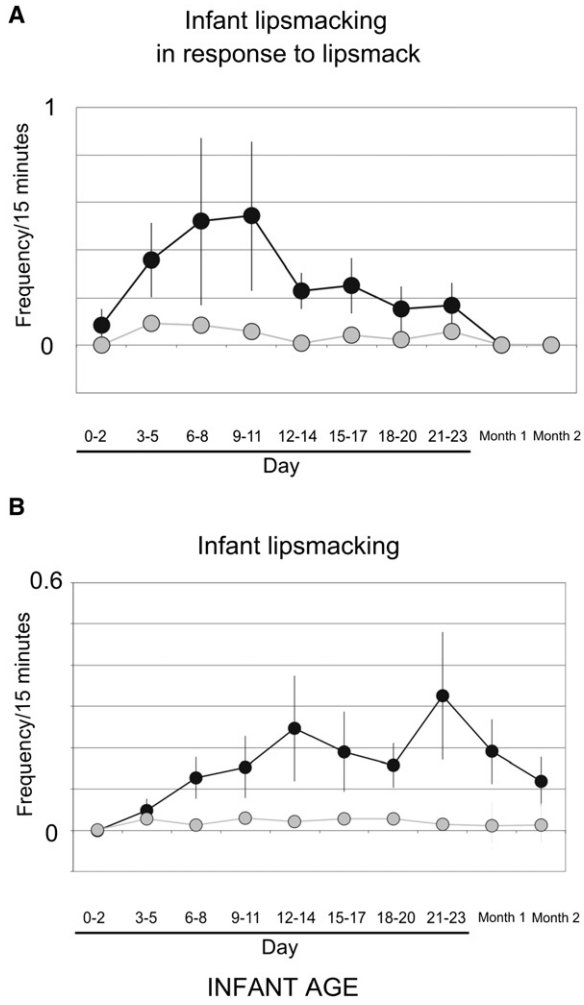


Figure 4. Infant Lipsmacking Responses and Solicitations toward Adults in the First Weeks of Life

(A) Frequency (means ± SEM) of infant lipsmacking in response to mother's lipsmacking (black) and other females' lipsmacking (gray) during infants' first 2 months of life.
(B) Frequency (means ± SEM) of infant lipsmacking directed at the mother (black) or other females (gray) without prior lipsmacking by adults during the infants' first 2 months of life.

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 Laboratory of Comparative Ethology 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 Experimental Procedures; see examples of these patterns in Movies S1–S3).

## 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, 20]. 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 infants' faces with the mouth, which resembles the empathic ritualized human "motherese" and intense body contact that human adults typically establish with their infants (e.g., face-to-face contact, hand-body touching, kissing, 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] that became 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 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 reestablishing 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 have reported under more controlled conditions in nursery-reared infant macaques [19, 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, similar 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 adversely influence infant emotional development. This hypothesis is supported by research in humans showing that ineffective face-to-face communication and mutual exchanges between mothers and their newborns substantially impact infants' emotional development [6].

Surprisingly, such intense emotional exchanges between mother and infant macaques dramatically decrease after the first month of life. 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 skeletomotor system but also important changes in psychological development, such as increased interest in their same-age peers within the colony. Thus, both the maturation of the infant skeletomotor system and its psychological development seem to have a profound impact on mother-infant interactions.

In sum, our results demonstrate that humans are not unique in showing emotional communication between mother and infant. Instead, we can trace the evolutionary foundation of those behaviors, which 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 (*Macaca mulatta*) pairs. Seven infants were male and seven were female; all were being reared by their biological mothers (aged between 6 and 12 years; three mothers were primiparous). All animals were born at the primate facilities of the Laboratory of Comparative Ethology (LCE) at the National Institutes of Health Animal Center near Poolesville, MD, and were housed in social groups containing eight to ten adult females (including the infant's mother), one or two adult males, and other similarly aged infants. Monkeys were housed in indoor-outdoor enclosures measuring 2.44 × 3.05 × 2.21 m indoor and 2.44 × 3.0 × 2.44 m outdoor (see details in Supplemental Experimental Procedures).

The frequencies of the following infant behaviors were recorded: mutual gaze between infants and their mothers or other individuals, infant lipsmacking at their mother or other individuals, mother or other individuals lipsmacking at infant, and infant lipsmacking in response to their mother's or other individuals' lipsmacking (see Supplemental Experimental Procedures 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 infants from their mothers, classified as either within or outside of arm's reach (see Supplemental Experimental Procedures).

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

### Observations of Interactions in Semi-Free-Ranging Rhesus Macaques

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 min for each observation), and mother-infant behaviors were recorded during these periods (see Supplemental Experimental Procedures).

### Supplemental Data

Supplemental Data include Supplemental Experimental Procedures, one table, two figures, and three movies and can be found with this article online at http://www.cell.com/current-biology/supplemental/S0960-9822(09)01690-X.

### Acknowledgments

This study was supported by the Division of Intramural Research of the NICHD, the National Institutes of Health, MIUR-COFIN 2007, and NeuroCom. We thank D. Stern and E. Palagi for valuable comments on an early draft of the manuscript.

Received: May 17, 2009
Revised: August 24, 2009
Accepted: August 25, 2009
Published online: October 8, 2009

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