



Maternal encouragement of infant locomotion in pigtail macaques, *Macaca nemestrina*

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Abstract. This study investigated whether pigtail macaque mothers encourage their infants' independent locomotion by increasing distance from them and displaying a retrieval signal, the pucker face. Fifteen mother–infant pairs living in a large captive social group were focally observed during the first 12 weeks of infant life. Mothers puckered to their infants only when out of contact with them, and the pucker was followed by reduction in distance by the mother or the infant. The pucker was significantly associated with an increase in distance initiated by the mother, and mothers that frequently puckered to their infants were also those that frequently left them. Multiparous mothers puckered to their infants more than primiparous mothers. The infant's initiative in reducing distance after the pucker increased with its age, and the latency of its response gradually decreased in the first 6–7 weeks of life. Infants that received more puckers from their mothers spent less time in contact with them and approached and left them more frequently than infants that received fewer puckers. The evidence is insufficient to assess unequivocally whether developmental changes in infant responses to the pucker reflect social learning or maturation of motor skills.

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In recent years, there has been a growing interest in social transmission of information in animals (Whiten 1989; Galef 1992; Tomasello et al. 1993). Social information transfer can take different forms and be broadly categorized as active or passive. Active information transfer, also referred to as instruction or teaching, differs from passive forms of information transfer such as local enhancement or imitation, because it requires the active participation of an individual in the role of 'instructor' (King 1991; Caro & Hauser 1992). Although observational learning and local enhancement are not uncommon in animals, the question of whether animals engage in active information transfer is still debated (Tomasello et al. 1993).

In a recent review of putative cases of teaching in animals, Caro & Hauser (1992) noted that most if not all of these cases involve parent–offspring interactions. Among the best known examples are mother cats, *Felis catus*, teaching their kittens

hunting techniques (Ewer 1969) and mother chimpanzees, *Pan troglodytes*, assisting their infants in nut-cracking activities (Boesch 1991). Several authors have also suggested that primate mothers encourage their infants to walk independently, to follow or climb on, through complex behavioural sequences involving the use of communicative signals. The typical sequence, as observed in a number of cercopithecine monkeys and chimpanzees, involves the mother placing her infant on the ground, moving a few steps away from it, and displaying facial expressions (e.g. lip-smacking, teeth-chattering or pucker; Redican 1975), gestures (e.g. extending one arm towards the infant) and body postures (e.g. presenting the hindquarters) that serve a retrieval function; mothers have occasionally been seen walking backwards bipedally while supporting the infant with one hand (Maestriperi 1995a; Maestriperi & Call, in press).

Unfortunately, all reports of these interactions in primates are qualitative and anecdotal, and the notion that the mother may encourage the behaviour of her infant is based on the subjective impression of a human observer rather than on quantitative evidence. One exception is provided

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by a recent study of rhesus macaques, *Macaca mulatta* (Maestriperi 1995b). Quantitative observations of early interactions between mothers and infants strongly suggested that reproductively experienced macaque mothers actively encouraged their infants' independent locomotion, that maternal encouragement was sensitive to infant competence, and that encouraged infants displayed some locomotor skills earlier in life than they would have without maternal encouragement.

The aim of the present study was to evaluate quantitatively whether early mother-infant interactions involving the display of a specific visual signal, the pucker face, can be considered instances of maternal encouragement of infant behaviour in the pigtail macaque. Several authors have hypothesized that pigtail macaque mothers use the pucker face, also referred to as len (Bobbitt et al. 1964), flehmen face (van Hooff 1962), protruded lips face (van Hooff 1967), and jaw thrust (Kaufman & Rosenblum 1966), to regulate proximity and contact with their infants (Jensen & Gordon 1970; Castell & Wilson 1971; Jensen et al. 1973; Bolwig 1980). In particular, Jensen & Gordon (1970) showed, through an analysis of behavioural sequences, that the pucker was likely to be followed by a reduction in distance by the infant and that if the infant did not approach its mother, she was likely to repeat the gesture (see also Bolwig 1980).

Although some authors who described sequences of mother-infant interactions involving this signal in pigtail macaques suggested that the mother was actually encouraging her infant to walk independently or perhaps teaching the meaning of the signal (Jensen et al. 1973; Bolwig 1980), they did not support this impression with quantitative data. To argue that these interactions qualify as encouragement, one has to show that the display of the pucker is consistently preceded by the mother breaking contact with her infant and increasing distance from it. If the pucker serves a retrieval function, mothers should not consistently increase the distance from their infants and then display the signal to re-establish contact unless some process of encouragement is involved. In fact, if no encouragement is involved, the display of the pucker should occur regardless of whether the mother or the infant increased the distance. If anything, the pucker should mainly occur after the infant initiates an increase in distance, because a young infant is less experienced

than its mother in evaluating the potential risks associated with separation from its mother (e.g. risk of kidnapping and harassment from other group members: Maestriperi 1993a, b, 1994a, b, c). Therefore, an infant may be expected to break contact with or increase distance from its mother at inappropriate times, and its mother could solicit contact or reduction of distance by puckering.

Whether the pucker is part of a process of maternal encouragement of infant behaviour is intimately linked to the question of whether the infant learns. For example, infants should reduce distance with their mothers more quickly after the pucker as they grow older, and infants receiving more frequent puckers from their mothers should respond more quickly and earlier in life. Infants that receive more puckers should also be more independent of their mothers, and, for example, spend less time in contact with them. Finally, if the tendency to encourage infant locomotion increases with maternal experience, as suggested in the study of rhesus macaques (Maestriperi 1995b), a similar association between maternal parity and tendency to break contact with and pucker to infants may be predicted for pigtail macaques as well.

METHODS

Subjects and Housing

Subjects were 15 pigtail macaque mother-infant pairs belonging to a large multi-male/multi-female social group housed in an outdoor compound measuring 25 × 25 m at the Field Station of the Yerkes Regional Primate Research Center in Lawrenceville, Georgia. The study was conducted from August 1992 to July 1993. At the beginning of the study, the group consisted of five adult males, one subadult male and 32 adult females. Sixteen females had one offspring older than 6 months. The group was formed in June 1991. All adult females were wild-caught and their genetic relationships were unknown. Because all females were captured in the same location, some of them may have been genetically related. When they arrived at the Yerkes Primate Center, the estimated age of the females based on dental condition ranged between 3 and 6 years. Because females were reproductively immature or at the beginning of their reproductive activity when

captured in the wild (about 1 year prior to their arrival at the Primate Center, and 2 years before the start of data collection), for analysis purposes the 16 females who had one previous offspring and gave birth again during the study period were considered multiparous; the females who had no previous offspring and gave birth during the study period were considered primiparous. The dominance hierarchy between adult females, as assessed by bared-teeth displays, unidirectional aggression and spatial displacements, was linear and remained stable throughout the study period (see Maestriperi 1994b, for information about age, parity, dominance rank of mothers and sex of infants). The monkeys were fed early in the morning with monkey chow, and a second time at 1500 hours with fresh fruit or vegetables. Water was freely available.

Procedure

Behavioural observations of mother–infant pairs started the day after the birth of the infant. I focally observed each mother–infant pair in four weekly 30-min observation sessions for the first 12 weeks of lactation (Martin & Bateson 1986). I observed subjects for 768 h (24 h for each mother–infant pair) and observation sessions were randomly distributed between 0800 and 1900 hours. During an observation period, all animals were locked out of the indoor housing area to provide constant visual access to the observer. All data were collected by the same observer using a portable computer (Radio Shack Model 102) programmed to allow the collection of true frequencies, durations and sequences of behaviour.

I defined the pucker as a gesture in which the lips are compressed and protruded, the forehead and ears pulled back, and the forequarters lowered to bring the jaw close to the ground. I recorded the number of times that mothers puckered to their infants, as well as the percentage of time that a mother–infant pair spent in contact, the number of contacts made and broken by mother and infant and the number of approaches and leaves made by mother and infant (Maestriperi 1994b). For analysis purposes, I summed the scores of contacts and approaches and those of contacts broken and leaves and referred to them collectively as ‘approaches’ and ‘leaves’. I also recorded the number and context of occurrence of maternal and infant vocalizations.

Statistical Analysis

I analysed data with non-parametric tests (Siegel 1956) and regression analysis (Pedhazur 1973). I used the Wilcoxon matched-pairs signed-ranks test (Z) for paired-samples comparisons and the Mann–Whitney test (U) for unpaired-samples comparisons. Data are presented as means \pm SES, even though means were not compared with these statistical procedures. I used Spearman’s rank order coefficient of correlation (r_s) for correlations and simple, polynomial and step-wise multiple regression to analyse associations between a dependent variable and one or more independent variables. Tests were two-tailed unless I tested a specific prediction, where I used a one-tailed test. Probability of ≤ 0.05 was considered statistically significant.

RESULTS

I observed 214 maternal puckers during the first 12 weeks of infant life. Mothers puckered to their infants only when not in physical contact with them. Puckers were not accompanied by maternal vocalizations or elicited by infant vocalizations. Puckers were infrequent in the first 4 weeks of infant life, when infants spent most of their time in contact with their mothers, and increased thereafter (Fig. 1a). The rate at which mothers puckered to their infants when they were out of contact decreased with infant age (Fig. 1b).

Marked individual differences occurred in the frequency with which mothers puckered to their infants (Fig. 1a, b). Of socio-demographic characteristics of the mother–infant pairs, such as maternal age, parity, dominance rank and sex of the infant, the best predictor of inter-individual variability in the number of puckers was parity (step-wise multiple regression: $R=0.52$, $F_{1,13}=4.7$, $P<0.05$). The number of puckers was significantly higher for multiparous than for primiparous mothers as predicted (multiparous = 21.71 ± 5.86 , $N=7$; primiparous = 8.00 ± 2.99 , $U=12$, $N=8$, one-tailed $P<0.05$).

To assess whether the number of puckers was significantly associated with individual differences in the frequency with which mothers and infants increased or reduced distance from each other, I ran a step-wise regression analysis using the number of puckers as the dependent variable and

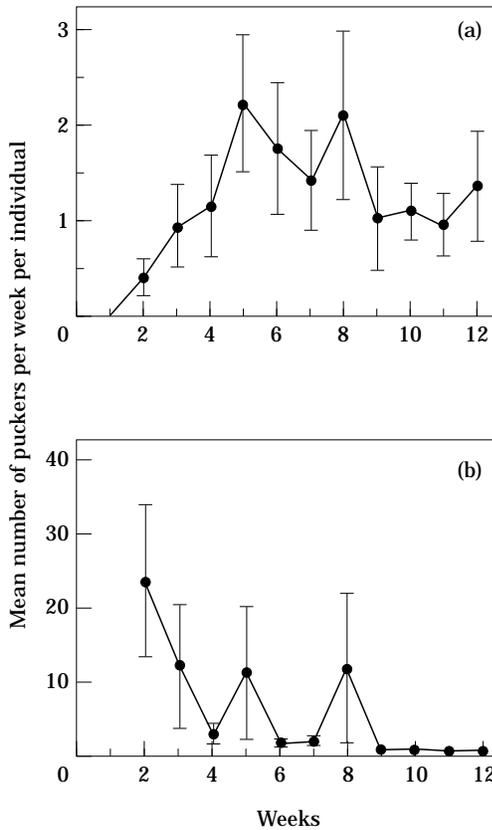


Figure 1. (a) Mean (\pm SE) number of puckers made by mothers in the first 12 weeks of infant life. (b) Mean (\pm SE) number of puckers made by mothers per 1000 s of time spent out of contact with their infants in the first 12 weeks of infant life.

the number of changes in mother–infant distance (approaches and leaves by mothers, approaches and leaves by infants) as independent variables. The best predictor of inter-individual variability in the number of puckers was the number of leaves by mothers ($R=0.76$, $F_{1,13}=17.62$, $P<0.01$). Thus, mothers that frequently left their infants also frequently puckered to them (Fig. 2a).

A significant association between maternal leaves and puckers was confirmed by two independent analyses. First, the mean duration of the time interval between when mother–infant distance increased and, when the pucker occurred, was shorter for puckers occurring after maternal leaves than after infant leaves (data pooled over the 12 weeks: after maternal leave = 14.20 ± 2.47 s; after infant leave = 37.08 ± 5.55 s; $z = -3.04$,

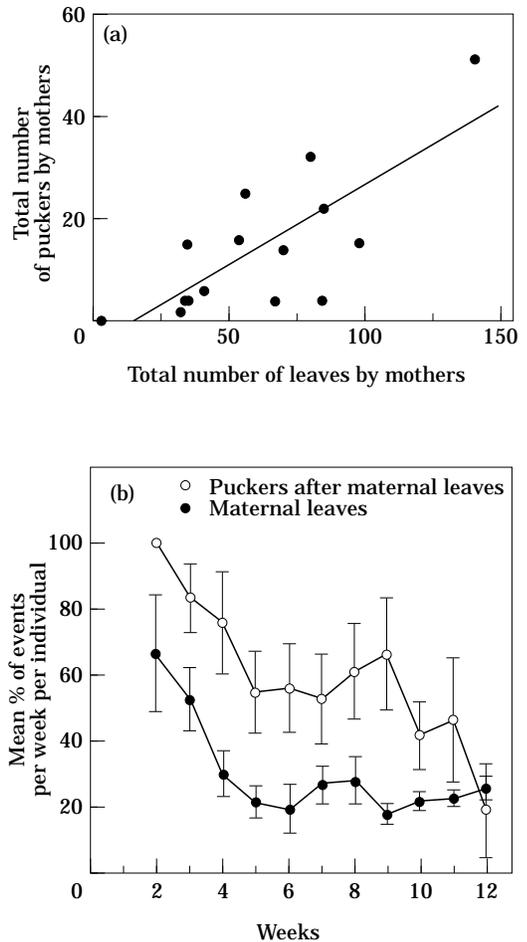


Figure 2. (a) Linear regression of number of puckers ($\bar{X} \pm$ SE) made by mothers and number of leaves by mothers. The regression is significant both with ($P<0.01$) and without ($P<0.05$) the data point with the highest number of puckers and leaves. (b) Mean (\pm SE) percentage of puckers occurring after maternal leaves and mean percentage of maternal leaves over the first 12 weeks of life (percentage of maternal leaves refers to all leaves not followed by a pucker).

$N=14$, $P=0.001$). Therefore, puckers occurred in closer temporal association with maternal leaves than with infant leaves.

Second, if puckers occurred at random relative to whether the mother or the infant initiated the previous increase in distance, then the relative proportions of puckers occurring after maternal and infant leaves should simply mirror the relative proportions of maternal versus infant leaves. This

was not the case, however: the percentage of puckers occurring after maternal leaves [puckers after maternal leaves/(puckers after maternal leaves+puckers after infant leaves $\times 100$) = 54.65 ± 5.60] was significantly higher than the percentage of maternal leaves [maternal leaves/(maternal+infant leaves $\times 100$) = 23.13 ± 2.61 ; $z = -3.29$, $N=14$, $P=0.001$; only maternal and infant leaves not followed by a pucker were considered]. Therefore, puckers occurred after maternal leaves more than expected by chance. Figure 2b shows the changes with infant age in the percentage of puckers preceded by maternal leaves and in the percentage of maternal leaves. In weeks 11 and 12, the two percentages no longer differed significantly (week 11, $z = -0.94$, NS; week 12, $z=0.31$, NS). Therefore, the pucker was no longer significantly associated with maternal leaves in weeks 11 and 12.

After the occurrence of the pucker, distance between mother and infant was more likely to decrease than increase (mean number of approaches $\pm SE = 12.64 \pm 2.68$; mean number of leaves $\pm SE = 1.14 \pm 0.37$; $z = -3.29$, $P=0.001$). Overall, mothers and infants were equally likely to reduce distance after the pucker (mean number of maternal approaches $\pm SE = 5.43 \pm 1.06$; mean number of infant approaches $\pm SE = 7.21 \pm 1.92$; $z = -0.71$, NS). Puckers that were followed by another pucker (7%) and puckers that occurred when the infant was being kidnapped and restrained by another female (2.8%) were excluded from this analysis.

Mothers were primarily responsible for reduction of distance with their infants after the pucker in the first weeks of life (Fig. 3a), which usually occurred a few seconds after the display of the visual signal (Fig. 3b). The infant's role in reducing distance after the pucker increased with age (second-order polynomial regression: $R=0.93$, $F_{2,8}=25.68$, $N=11$, $P=0.0003$; Fig. 3a), which mirrored the general pattern of shift in responsibility for reducing mother-infant distance ($r_s=0.85$, $N=11$, $P<0.01$; Fig. 3a). The percentage of approaches made by infants after the pucker reached 95% in week 7, when it was significantly higher than the percentage of approaches made by the same infants without the pucker ($z = -2.20$, $N=7$, $P=0.01$). Therefore, in week 7, infants were significantly more likely to reduce distance from their mothers after a pucker than without a pucker.

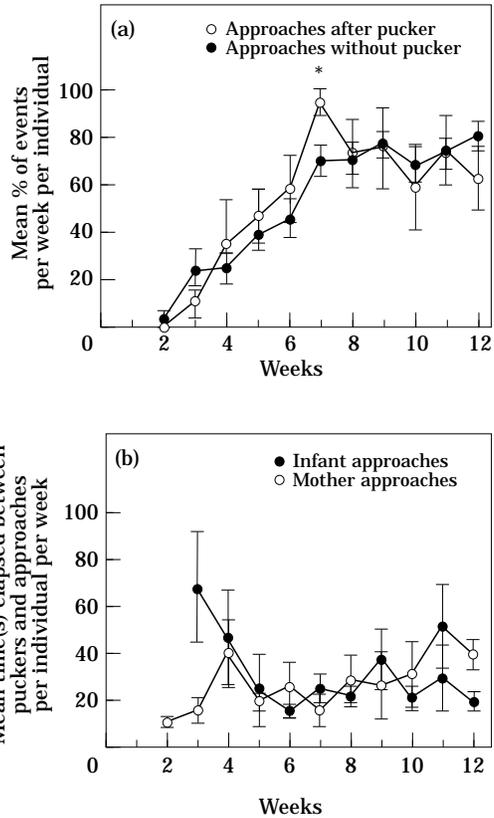


Figure 3. (a) Mean ($\pm SE$) percentage of puckers followed by infant approaches and mean percentage of infant approaches not preceded by a pucker over the first 12 weeks of life. The two percentages are significantly different in week 7. (b) Mean ($\pm SE$) latency of reduction in distance by mothers and infants after a pucker over the first 12 weeks of infant life.

The latency of infant response to the pucker decreased with infant age (second-order polynomial regression: $R=0.78$, $F_{2,7}=5.50$, $N=10$, $P<0.05$; Fig. 3b) whereas the time taken by mothers to reduce distance after the pucker did not vary significantly with infant age ($r=0.42$, $F_{2,8}=0.88$, $N=11$, NS; Fig. 3b). To test whether the decrease in the latency of infant response was due to repeated exposure to the signal or to younger infants being slower in responding than older infants, I investigated whether the variability in the time taken by infants the first time they reduced distance after a pucker was predicted by the number of puckers previously received or by infant age. A multiple regression analysis indicated that neither infant age (6.00 ± 0.70 weeks)

nor the number of previous puckers (2.79 ± 0.60) predicted variability in the time taken by infants the first time they reduced distance after the pucker (21.64 ± 6.56 s).

The number of puckers received by infants was negatively correlated with the percentage of time spent in contact with their mothers ($r_s = -0.53$, $N=15$, one-tailed $P < 0.05$) and positively correlated with the number of approaches and leaves made by infants (approaches, $r_s = 0.44$, $N=15$, one-tailed $P < 0.05$; leaves, $r = 0.41$, $N=15$, one-tailed $P < 0.05$). Therefore, infants that received more puckers spent less time in contact with their mothers and approached and left them more than infants that received fewer puckers.

DISCUSSION

Pigtail macaque mothers puckered to their infants when out of contact with them, and the pucker was more likely to be followed by a decrease rather than an increase in distance by the infant or its mother, as previously demonstrated by Jensen & Gordon (1970). Several lines of evidence indicated that the display of the pucker was significantly associated with the mothers' tendency to leave their infants. Mothers that frequently left their infants also frequently puckered to them, puckers were more likely to occur after maternal leaves than after infant leaves, and puckers occurred more rapidly after maternal leaves than after infant leaves. These findings, along with the observation that multiparous mothers puckered to their infants more frequently than primiparous mothers, suggest that some mothers use the pucker in conjunction with contact-breaking and leaving to encourage their infants to walk independently and to follow or make contact. Similar interactions between mothers and infants have been documented for other species of cercopithecine monkeys and apes (Maestriperi 1995a, b; Maestriperi & Call, in press).

One difficulty in demonstrating the occurrence of instruction in animals is determining whether the instructor's behaviour is aimed at facilitating learning in the 'pupil' and not at achieving other, self-related goals. Primate mothers and infants use behavioural signals to coordinate their activity in a variety of contexts (Maestriperi & Call, in press). The unique characteristic of the mother-infant communicative interactions described in

this study is that the mother creates the opportunity for the occurrence of the signal and its response in the infant. Infants usually emit distress signals when hungry, in pain or unable to regain contact with their mothers; similarly, mothers use vocal or non-vocal signals to retrieve their infants at times of danger or when ready for travel (Maestriperi & Call, in press). In these cases, mothers and infants appear to emit a signal in response to a problem that requires the coordination of their behaviour for its solution. When cercopithecine and ape mothers increase the distance from their infants while emitting retrieval signals such as facial expressions, gestures and postures, the problem (i.e. the momentary separation) seems to be created by the mother for no apparent goal other than learning or practising its solution. In other words, in these circumstances, the mother's behaviour is suggestive of 'pedagogic intent' (but see Maestriperi 1995a, for a discussion of levels of intentionality).

For an interaction to qualify as instruction or teaching, the occurrence of learning in an individual as a result of exposure to the instructor's behaviour must also be demonstrated. In the present study, the infant's initiative in reducing distance after the pucker increased with its age and the latency of response gradually decreased in the first 6–7 weeks of life. Although the developmental changes in the infant's response to the pucker suggest that some social learning may take place, the evidence is insufficient to discard the alternative hypothesis, that these changes reflect maturation of motor skills or broader changes in the mother-infant relationship. In fact, the developmental changes in the infant's role in reducing distance after the pucker were very similar to those concerning its initiative in maintaining contact and proximity with its mother regardless of the pucker. Also, the latency to the first reduction of distance by the infant after the pucker was not significantly affected by previous exposure to maternal puckers, as predicted by the learning hypothesis. The developmental changes in the infant's response to the pucker were particularly evident in the first 6–7 weeks of life, suggesting that this period may be crucial for the development of infant skills that are important for the regulation of the mother-infant relationship in pigtail macaques.

Infants that received more puckers from their mothers during their first 12 weeks of life spent

less time in contact with their mothers, and approached and left them more frequently than infants that received fewer pucks. These results suggest that infants that were more encouraged by their mothers were also more active and independent. Alternative explanations are also plausible, however. For example, the percentage of time mothers and infants spent in contact was determined by both maternal and infant behaviour, and mothers that frequently puckered to their infants were also those that frequently left them. Similarly, some infants may have made a high number of contacts with their mothers because their mothers frequently left them, regardless of the number of pucks received. Therefore, the differences in infant activity and time spent with mothers may have resulted from general differences in maternal activity, and not specifically from differences in mothers' tendency to encourage infant independence.

The results of the present study are suggestive of but offer no conclusive evidence that macaque mothers engage in teaching. Further quantitative data on the short- and long-term consequences of early maternal behaviour for infant development are needed to assess unequivocally whether the role played by primate mothers in the acquisition of infant skills is mediated by active transfer of information.

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