

First steps in the macaque world: do rhesus mothers encourage their infants' independent locomotion?

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Abstract. This study investigated early interactions between 28 rhesus macaque, *Macaca mulatta*, mothers and their infants living in captive social groups to assess whether mothers actively encouraged their infants' independent locomotion and if such encouragement could be considered teaching. Mothers differed in their tendency to break contact with their infants in the first days of infant life, and this tendency increased significantly with previous reproductive experience. Mothers that left their infants early in life were also more likely to engage in backward walking and lip-smacking to their infants than mothers that did not leave their infants early in life. Infants that were left by their mothers in their first days of life broke and made contact with their mothers for the first time earlier than infants that were not left by their mothers. Interruption of contact with infants early in their life had no apparent immediate benefits to mothers but did have immediate risks because it increased the probability of infant kidnapping by other group members. Mothers whose infants gave a distress vocalization after the first interruption of contact broke contact with them less frequently in subsequent days than mothers whose infants did not vocalize. Although some of these findings are open to other interpretations, altogether they strongly suggest that some mothers actively encourage their infants' independent locomotion, that maternal encouragement is sensitive to infant competence, and that encouraged infants display some locomotor skills earlier in life than they would have without maternal encouragement.

It has long been known that animals in many gregarious species are capable of acquiring information concerning their environment or new manipulative skills through observation of or direct interaction with conspecifics. Classical examples are the waggle dance of honey bees, *Apis mellifera* (von Frisch 1950) and potato washing by Japanese macaques, *Macaca fuscata* (Kawai 1965). In recent years, efforts have been concentrated on distinguishing the mechanisms underlying different forms of social learning and the cognitive capabilities involved (e.g. Zentall & Galef 1988; Whiten 1989; Cheney & Seyfarth 1990; Visalberghi & Fragaszy 1990). Teaching is commonly distinguished from other forms of social information transfer such as local enhance-

ment or imitation because it requires the active participation of an individual in the role of 'instructor' (e.g. King 1991; Caro & Hauser 1992). A debate, however, has recently arisen over the conceptualization of this phenomenon and its existence in animals.

According to Cheney & Seyfarth (1990), teaching demands the ability to attribute mental states to others, in particular in terms of knowledge or ignorance. Cheney & Seyfarth (1990) briefly reviewed and discussed some anecdotal reports of teaching in animals and concluded that none of them qualified as teaching because instruction appeared to be stereotypic, passive, or resulting from an action that carried immediate benefits to the instructor. Furthermore, Cheney & Seyfarth (1990) interpreted the negative results of some of their own experiments on vocal communication in monkeys as evidence that 'monkeys do not teach each other' and 'this lack of pedagogy reflects the

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animals' inability to distinguish between their own states of mind and the states of mind of others' (page 253). Although Cheney & Seyfarth (1990) conceded that chimpanzees might differ from monkeys in their ability to teach, this possibility was denied by Tomasello et al. (1993) who, after reviewing some putative cases of teaching in wild chimpanzees (e.g. Nishida et al. 1983; Boesch 1991), concluded that 'it may be said quite simply that in their natural habitat chimpanzees do not actively instruct their young' (page 505). Both Cheney & Seyfarth (1990) and Tomasello et al. (1993) maintained that putative cases of animal teaching did not show any evidence of 'pedagogic intent' on the part of the instructor and should not therefore be considered as teaching.

In contrast, Caro & Hauser (1992) recently argued that the ability to attribute complex mental states to others is not a necessary condition for teaching in animals. They argued that some instances of social interactions between animals may be categorized as teaching even in the absence of complex cognitive abilities, provided that (1) the instructor modifies its behaviour only in the presence of a naive observer ('pupil'), (2) the instructor incurs a cost, or at least does not obtain an immediate benefit from modifying its behaviour, and (3) as a result of instruction, the pupil acquires knowledge or learns a skill earlier in life or more rapidly or efficiently than it might otherwise do, or that it would not learn at all (for more details, see Caro & Hauser 1992). Caro & Hauser (1992) did not include in their working definition of animal teaching other criteria, such as, that instruction must be sensitive to the pupil's changing skills or competence, in part because 'the data set on putative cases of teaching is of insufficient detail to warrant this yet' (Caro & Hauser 1992, page 154). Despite their use of a broader definition of teaching, Caro & Hauser (1992) found only little quantitative evidence of animal teaching in the literature and none of the examples cited fit their definition exactly. For example, there was no evidence that individuals that were not taught did not acquire the skill, nor that they acquired the skill later than those that were taught. Interestingly, the majority of putative cases of teaching were observed in parent-offspring interaction and involved parental encouragement or discouragement of some behaviour in the offspring.

The aim of this study was to investigate whether rhesus monkey mothers living in captive social

groups actively encourage early independent locomotion of their infants and if such encouragement can be interpreted as teaching. Rhesus monkey infants spend most of their first days of life on their mothers' nipple, and a large part of the first 2-3 months in body contact or close proximity to them (e.g. Simpson et al. 1986). Mothers play a larger role in regulating contact initially, but responsibility for breaking and making contact shifts to infants usually in the second or third month of life, as infants gradually increase the frequency and duration of their 'radial trips' from their mothers (e.g. Hinde & White 1974; Simpson et al. 1986). In several species of monkeys and apes, mothers have been observed to leave their young infants and encourage them to walk independently and to follow by walking backwards and lowering the head while lip-smacking or 'puckering' (see Maestriperi & Call, *in press*, for a review). Lip-smacking and pucker are facial gestures that may precede a reduction in inter-individual distance for friendly purposes in primates (Shirek-Ellefson 1972; Redican 1975). Although maternal encouragement of early infant locomotion has rarely been investigated quantitatively, Hinde & Simpson (1975) noted that some rhesus monkey mothers left their infants and engaged in these 'games' frequently in the first days of infant life while others did not show these interactions. Hinde & Simpson (1975) suggested that 'through this game, the mother could discover when her infant first becomes quick to follow her when she leaves, and when he first follows her after a delay' (page 53). These authors also noted that mothers that engaged in these early interactions with their infants subsequently had well-meshed relationships with their young, in the sense of having coordinated activity and little conflict over the initiation and termination of the partner's contacts (Hinde & Simpson 1975).

The quantitative observations of the present study confirm and extend some of Hinde & Simpson's (1975) intuitions and, altogether, they strongly suggest that maternal encouragement of early independent locomotion of infants in rhesus macaques can be considered a form of instruction.

METHODS

Subjects and Housing

Subjects of this study were 28 rhesus macaque mother-infant pairs living in captive social

groups. Seventeen of these pairs belonged to five groups housed in small outdoor pens ($5.4 \times 2.4 \times 2.4$ m) at the Sub-department of Animal Behaviour of the University of Cambridge in Madingley (Cambridge, U.K.). Each group in the colony consisted of a single adult male with three to eight adult females and their subadult, juvenile, and infant offspring. Eleven pairs belonged to a social group housed in a large outdoor compound (25×25 m) at the Field Station of the Yerkes Regional Primate Research Center in Lawrenceville, Georgia (U.S.A.). The group consisted of three adult males and 35 adult females with their subadult, juvenile, and infant offspring. Detailed information concerning characteristics of all mothers and their infants is given elsewhere (Maestriperi 1993b, 1994). All monkeys were fed early in the morning with monkey chow, and for a second time in the afternoon with fresh fruit or vegetables. Water was freely available.

Procedure

The data at Madingley were collected from April to October 1991, those at Yerkes from April to September 1993. In all cases, behavioural observations of the mother–infant dyad started the day after the birth of the infant (day 1 of infant age). Each mother–infant dyad was focally observed in 4 weekly 30-min observation sessions for the first 12 weeks of lactation (see Martin & Bateson 1986, for a description of the focal sampling technique). A total of 24 h of observation for each mother–infant pair were collected. Observation sessions were randomly distributed between 0800 and 1900 hours. All data were collected by the same observer using a portable computer programmed to allow the collection of true frequencies, durations and sequences of behaviour. The following behavioural measures were used.

Time in contact

The percentage of observation time the mother–infant pair spent in body contact.

Contacts made and broken

The number of contacts made and broken by mother and infant. Contacts were defined as movements that resulted in any body contact

between mother and infant except brief hits. For analysis purposes, infant attempts to break contact that were prevented by the mother by restraining her infant (see below) were lumped together with successful attempts, unless otherwise specified.

Mean duration of non-contact time bouts

The mean time elapsed since contact between mother and infant was broken and subsequently restored.

Backward walking and lip-smacking to the infant

We recorded the identity of the mothers that were observed to engage in backward walking and lip-smacking to their infants after interruption of contact (see Introduction for description of the interaction) and the first occurrence of these interactions between mothers and infants. No data concerning the frequency and duration of these interactions are available.

Maternal restraining

The number of attempts by the infant to break contact that were prevented by the mother, for example, by pulling the infant by its tail or leg.

Infant screaming

The number of infant scream vocalizations after interruption of contact with their mothers or during interactions with other group members.

Infant kidnapping

A kidnapping episode was scored when any individual prevented the infant from returning to its mother for more than 1 min and the infant showed clear signs of distress (screaming or jerking). During kidnapping, mothers appeared motivated to retrieve their infants, by following the kidnapper and sitting next to her (see Maestriperi 1993c).

Maternal dominance rank relative to other group members was assessed on the basis of the direction of bared-teeth displays (de Waal & Luttrell 1985). Rhesus females can generally be ranked in a linear dominance hierarchy with daughters ranking below their mothers. The

mothers' rank was divided into high, middle, or low according to whether they fell into the upper, medium or lower third of the social hierarchy in their own groups.

Statistical Analyses

Non-parametric statistics were used. Tests were two-tailed unless a specific prediction was tested, and therefore a one-tailed test was used. Probability ≤ 0.05 was considered statistically significant while $0.05 < P \leq 0.1$ was considered a tendency.

RESULTS

Do Some Mothers Leave Their Infants Earlier than Others?

Contact between mothers and infants was first seen to be broken by mothers in 13 pairs ('Mother' or 'M' pairs) and by infants in 15 pairs ('Infant' or 'I' pairs). At the time when contact was first broken, infants in M pairs were younger than infants in I pairs (infant age in days, $\bar{X} \pm \text{SE}$: M pairs: 5.61 ± 1.22 ; I pairs: 12.27 ± 1.19 ; Mann-Whitney U -test: $U=29.5$, $P=0.001$). In 11 out of 13 M pairs, mothers broke contact with their infants for the first time in the first week of infant life, and in four of such pairs on the first day of infant life. In six of the I pairs, the mother prevented the infant's first attempt to break contact by physically restraining it, whereas none of the M mothers opposed resistance to their infants' first attempt to break contact (Fisher's test: $P < 0.01$). Thus, whereas M mothers were responsible for early contact interruption, I mothers waited for their infants to break contact (or attempt to do so) for the first time, or actively delayed the timing of first infant departure.

Although no data concerning the frequency or the duration of these interactions were available, eight out of 13 M mothers were observed to engage in backward walking and lip-smacking to their infants at least once prior to the infant's first attempt to re-establish contact (see below), whereas only one of the I mothers displayed this behaviour in the same period (Fisher's test: $P=0.01$).

Twelve out of 13 mothers in M pairs were multiparous as opposed to only eight out of 15 mothers in I pairs (Fisher's test: $P=0.05$). M

mothers did not differ from I mothers in terms of their age (years, $\bar{X} \pm \text{SE}$: M mothers: 7.54 ± 0.91 ; I mothers: 6.67 ± 2.74 ; $U=79.5$, NS), dominance rank (M mothers: high: 3; middle: 6; low: 4; I mothers: high: 3; middle: 7; low: 5; NS), or sex of their infants (M infants: 9 males, 4 females; I infants: 10 males; 5 females; NS). Rhesus mothers at Madingley did not differ significantly from mothers at Yerkes in terms of responsibility for breaking contact for the first time (Madingley mothers: M=8; I=9; Yerkes mothers: M=5; I=6; Fisher's test: NS).

Do Some Infants Depart from and Return to Their Mothers Earlier than Others?

M infants broke contact with their mothers for the first time at an earlier age than I infants (age in days, $\bar{X} \pm \text{SE}$: M infants: 8.07 ± 1.00 ; I infants: 12.27 ± 1.19 ; $U=47$, $P=0.01$). Thus, infants that were left by their mothers earlier in life broke contact with them for the first time earlier than infants that were not left by their mothers. In both M and I pairs, mothers always made contact with their infants after contact was broken for the first time, and most mothers continued to be solely responsible for making contact in subsequent days. M infants made contact with their mothers for the first time at an earlier age than I infants (M infants: 9.46 ± 1.20 ; I infants: 21.86 ± 2.19 ; $U=12$, $P=0.0001$). This result is perhaps not surprising because M infants made contact for the first time at an age when some of the I infants had not yet left their mothers for the first time. The time interval, however, between when contact was successfully broken for the first time and when infants made contact for the first time was shorter for M infants than for I infants (days, $\bar{X} \pm \text{SE}$: M infants: 3.85 ± 0.87 ; I infants: 7.80 ± 1.55 ; $U=54$, $P=0.05$). Thus, after all infants had the opportunity to spend some time away from their mothers, M infants returned to their mothers more rapidly than I infants.

Is Maternal Contact-breaking Sensitive to the Infant's Responses?

In five out of 13 M pairs, infants screamed when their mothers first broke contact, whereas none of the I infants screamed when contact was first successfully broken (Fisher's exact probability test: $P=0.01$). Infant screaming can be

conceivably interpreted as a sign of distress caused by interruption of contact with the maternal body and therefore a potential indicator of infant maturation. Among M pairs, infants that screamed when their mothers first broke contact with them ('Screamers', $N=5$) tended to be younger than those that did not scream ('Non-screamers', $N=8$; age in days, $\bar{X} \pm \text{SE}$: Screamers = 3.4 ± 1.50 ; Non-screamers = 7.0 ± 1.63 ; $U=11$, $P=0.1$). The age at which Screamers and Non-screamers broke contact for the first time was not significantly different (Screamers: 7.2 ± 1.31 ; Non-screamers: 8.62 ± 1.44 ; $U=15.5$, NS). If mothers were sensitive to their infants' responses after the first interruption of contact, one should expect mothers of Screamers to be less encouraging of their independent locomotion than mothers of Non-screamers. This prediction was confirmed by the data. The rate at which Screamers' mothers continued to break contact in the time interval between the first interruption of contact and the first time their infants broke contact themselves was significantly lower than the rate at which Non-screamers' mothers broke contact in the same time interval (number of contacts broken by mothers per 1000 s; $\bar{X} \pm \text{SE}$: Screamers: 0.50 ± 0.42 ; Non-screamers: 2.57 ± 1.12 ; $U=9$, one-tailed $P<0.05$). Because Screamers tended to be younger than Non-screamers when contact was first broken by their mothers, it is possible that the difference between the rate of subsequent contact breaking by mothers simply resulted from infant age and not from the infant's vocal response after contact was broken. This possibility, however, can be dismissed because, among all 13 M pairs, the rate at which mothers continued to break contact after the first interruption of contact and before the first time their infants broke contact was not correlated with infant age when contact was first broken (Spearman's correlation, $r=0.16$, NS).

Does Early Interruption of Contact with Infants have Immediate Costs to Mothers?

Despite the fact that in the first week M mothers and infants were separated for short time bouts (mean duration of non-contact time $\pm \text{SE}$ = 29.68 ± 5.65 s; kidnapping time excluded), six of 13 M infants were kidnapped by other individuals at least once during this period, whereas none of the 15 I infants was (Fisher's test: $P<0.01$).

DISCUSSION

Contact between rhesus mothers and infants was first seen to be broken by mothers in 13 pairs and by infants in 15 pairs. Because observation of mother-infant pairs was not continuous since birth, it is possible that the first observed interruption of contact was not the first time contact between mothers and infants had been broken. It is reasonable to assume, however, that the observed differences in responsibilities for breaking contact reflected true probabilities of breaking contact for the first time. If responsibility for first breaking contact simply resulted from chance, one would not have expected a difference in infant age between M and I pairs when contact was first broken. In contrast, M infants were significantly younger than I infants when contact was first broken. Therefore, differences between M and I pairs in responsibility for breaking contact for the first time did not arise by chance but reflected significant behavioural differences between M and I pairs.

Infants that were left by their mothers in their first days of life broke and made contact with them for the first time earlier than infants that were not left by their mothers in their first days of life. There are at least two possible interpretations of these findings and of the above-reported difference in responsibility for first breaking contact in M and I pairs. On the one hand, it may be argued that maternal behaviour caused changes in infant behaviour and, specifically, allowed infants to exhibit patterns of behaviour (breaking and making contact with their mothers) earlier in life or more rapidly than they would have done otherwise (the 'cause-effect' hypothesis). According to this hypothesis, M and I mothers differed in their propensity, and perhaps ability, to stimulate their infants' independent locomotion. Thus, unlike I mothers, M mothers encouraged their infants to depart from them by breaking contact with them early in life, and to return to them after separation by lip-smacking to them. On the other hand, it may be argued that maternal behaviour did not cause changes in infant behaviour but that infants differed in the degree of maturation for their age and maternal behaviour was simply tuned to infant maturation (the 'tuning' hypothesis). Thus, it is possible that M infants broke contact with their mothers earlier and returned to them for the first time more rapidly in life than I

infants because they were better developed for their age (e.g. I infants may have been born premature). If this hypothesis is correct, however, it implies that mothers were able to make an accurate assessment of their infants' degree of maturation and potential locomotor skills before contact was broken for the first time (perhaps by assessing their infants' size, weight and mobility on their own body) and adjusted their behaviour accordingly. In other words, it is possible that differences in responsibility for breaking contact for the first time in M and I pairs merely reflected differences in infant maturation and not different propensities on the part of the mothers to encourage infant independence.

Although the data are insufficient to discard unequivocally one hypothesis in favour of the other, several different sets of observations make the 'tuning' hypothesis improbable. First, in 11 out of 13 M pairs, mothers broke contact with their infants for the first time in the first week of infant life, and in four of such pairs as early as the first day of infant life. The shortness of this time interval would require an extreme ability on the part of the mother to make an accurate assessment of the degree of maturation and potential locomotor skills of her infant without testing them directly. Second, five out of 13 M infants screamed when their mothers first broke contact, whereas none of the I infants screamed when contact was first successfully broken. Because infant screaming upon interruption of contact with the maternal body is probably an indicator of infant maturation (see below), this result argues against the hypothesis that M infants were better developed than I infants when contact was first broken. Third, in six of the I pairs, mothers prevented their infants' first attempts to break contact, whereas none of the M mothers opposed resistance to their infants' first attempts to break contact. This suggests that, unlike M mothers, I mothers did not encourage early independent locomotion of their infants and in some cases, actively delayed the timing of their infants' first departure from them. Fourth, if the speed with which infants made contact for the first time only reflected age-dependent maturation of locomotor skills, the result that M infants made contact for the first time more rapidly than I infants is counter-intuitive because this difference occurred despite the fact that M infants were younger than I infants. In contrast, this finding could be

explained by hypothesizing that M mothers encouraged their infants to return to them after contact was broken more than I mothers did. In support of this hypothesis, eight out of 13 M mothers were observed to engage in backward walking and lip-smacking to their infants at least once prior to their infants' first attempts to re-establish contact, whereas only one of the I mothers displayed this behaviour in the same period. Finally, the finding that M mothers were, on average, more reproductively experienced than I mothers fits well with the hypothesis that the behavioural differences between M and I pairs were due to maternal rather than infant characteristics. Therefore, altogether, these observations strongly suggest that differences in infant behaviour are more likely to have resulted from differences in maternal behaviour than in the infants' maturation in relation to their age.

M infants that screamed when contact with their mothers was first broken tended to be younger than M infants that did not scream. This finding supports the hypothesis that infant screaming after interruption of contact was a good indicator of the degree of infant maturation and suggests that M infants were 'honest' in signalling to their mothers their developmental condition (see Godfray 1991, for a discussion of honest communication between parents and offspring). The hypothesis that maternal contact-breaking was sensitive to infant developmental condition was supported by the finding that M mothers of screaming infants broke contact with their infants less frequently in subsequent days than M mothers of Non-screamers.

Early interruption of contact between M mothers and infants was associated with a higher probability of infant kidnapping, when compared with I pairs. Infant kidnapping by non-lactating females in monkeys may last from a few minutes to many hours and may occasionally cause infant death from starvation and dehydration (Maestripiéri 1993c). The risk of death from starvation and dehydration is presumably higher for younger than for older infants. Younger infants also are more vulnerable to harassment from other individuals than older infants and risk of harassment is higher when infants are away from their mothers than when they are in contact with them (Maestripiéri 1993a). In fact, interruption of contact with their infants causes anxiety in their mothers, and maternal anxiety decreases with

infant age (Maestriperi 1993a, 1994). Therefore, by breaking contact earlier in life, M mothers exposed their infants to a higher risk of kidnapping and increased the probability of reproductive costs to themselves.

When kidnapping time is excluded, M mothers and infants were separated, on average, for less than 30 s during the first week of infant life. It is unlikely that mothers gained any immediate benefits from being separated from their infants for such a short time (for example, time to devote to other activities such as feeding or grooming) or that these benefits outweighed the risks of separation. In fact, when contact with infants is broken in the first weeks, rhesus mothers are highly vigilant of their infants and other group members (Maestriperi 1993a) and engaging in feeding or grooming would undermine their potential for protective intervention (for grooming, see Maestriperi 1993d). Early encouragement of infant independence, however, may have benefits to mothers in subsequent months because it might reduce the costs of infant carrying (Altmann & Samuels 1992) and anticipate the time of weaning, thus increasing the mother's probability to ovulate and conceive again in the next mating season (Simpson et al. 1981; Gomendio 1989). In addition, infants that start to return to their mothers earlier in life may be safer from predators and other dangers in the environment than infants that do so later in life. The data were insufficient to test all of these hypotheses adequately because the study was conducted in captivity and observations were limited to the first 12 weeks of infant life. Other studies of rhesus macaques, however, have shown that mothers that give birth in the next year leave their infants more often in their first 5 months than mothers that skip at least 1 reproductive year (Simpson et al. 1981; Gomendio 1991).

Although some of the results of this study are open to other interpretations, when combined, these results strongly suggest that some mothers actively encouraged their infants' independent locomotion and their infants displayed some locomotor skills earlier in life than they would have without maternal encouragement. Maternal encouragement of independent locomotion of infants appeared sensitive to the infants' tolerance of interruption of contact with the maternal body, and therefore possibly to the infants' degree of maturation. Finally, leaving their infants early in

their life carried no apparent immediate benefits to mothers but it entailed some risk because it increased the probability of infant kidnapping by other group members. Backward walking or lip-smacking to the infant after interruption of contact are two aspects of the mother's behaviour that are a more direct expression of encouragement of infant independent locomotion than simple contact-breaking. The finding, however, that mothers that left their infants earlier in life were also more likely to engage in these interactions suggests that the two measures are related to each other and reflect a maternal tendency to encourage infant independent locomotion.

If we assume that teaching requires the ability to attribute mental states to others (e.g. Cheney & Seyfarth 1990), the early interactions between rhesus mothers and infants reported in this study do not qualify as teaching because they offer no evidence that monkey mothers attribute mental states to their infants or vice versa. In line with Caro & Hauser's (1992) position, however, I argue that attribution of mental states is not a necessary condition for teaching. It is generally accepted that teaching is differentiated from other forms of social information transfer by the active participation of an individual in the role of instructor (e.g. King 1991; Caro & Hauser 1992). According to this definition, for a social interaction to qualify as teaching there must be evidence that the instructor's behaviour is aimed at modifying the pupil's behaviour and not at some other goal. In other words, the possibility that the pupil's instruction occurs only through casual exposure to the instructor's behaviour must be excluded. From an operational standpoint, the hypothesis that the instructor has a 'pedagogic intent' and its behaviour qualifies as instruction is supported if instruction has immediate costs or at least no immediate benefits to the instructor and if it is sensitive to the pupil's competence (Caro & Hauser 1992). Both criteria are met by the observations reported here.

Although the attribution of mental states to others may be necessary or helpful in some complex forms of teaching, for example, those involving verbal or abstract knowledge, I argue that this ability is not necessarily required for encouraging motor or manipulative skills, such as walking or nut-cracking (Boesch 1991). In this case, for instruction to occur or to be efficient, it is simply required that the instructor's behaviour be elicited

and/or modified in relation to the pupil's performance or lack of performance. Animals modify and adjust their behaviour in relation to the behaviour of others in a variety of contexts: this ability may be favoured by natural selection and may evolve independently from the ability to attribute mental states to others. In this view, the encouragement of infant motor or manipulative skills is probably very similar in animals and humans (see Hay 1977) and only requires a modification in the instructor's behaviour after an assessment of the pupil's performance. Whether the instructor has the ability to attribute mental states to its pupil, e.g. knowledge or ignorance (Cheney & Seyfarth 1990), or the pupil internalizes anything subjective from the interaction (Tomasello et al. 1993) is irrelevant.

The results of this study indicate that maternal encouragement of infant independent locomotion in rhesus macaques can begin as early as the first day of infant life. Independent locomotion can be viewed as the first phase of a process of infant independence that culminates with the achievement of nutritional independence. Regulation of mother-infant contact plays an important role throughout this process because it is through contact with its mother's body that the infant obtains both transportation and nourishment. This study suggests that mothers play an active role in the process of infant independence by encouraging contact interruption and independent locomotion of their infant in the first days of infant life and by discouraging contact and suckling later on through rejection behaviour (e.g. Gomendio 1991). These results also show that behavioural variability among rhesus mothers may arise as early as the first day of infant life, and that part of this early variability is associated with differences in previous reproductive experience. The individual differences in maternal behaviour observed in the first days of infant life may not necessarily be consistent throughout the entire period of infant dependence because much of the subsequent maternal behaviour can be influenced by the social environment and in particular by interactions between infants and other group members (e.g. Nicolson 1987). The study of mother-infant interactions in the first days of infant life, however, could contribute much to our understanding of individual differences in maternal behaviour and the processes of social learning involved in primate infant development.

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