Gestural Communication in Macaques: Usage and Meaning of Nonvocal Signals*

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Abstract

Communication by facial expressions and body postures plays an important role in the social dynamics of macaques. Macaques use gestures to mediate both competitive and cooperative interactions with other group members. Gestures convey information on the emotional state of the sender and its impending behavior but can also be used to inhibit the behavior of another individual or to request its participation in specific activities such as grooming, agonistic support, mating or play. Although most gestures are used to mediate simple approach and avoidance interactions, the size of the gestural repertoire and the subtleties of gestural communication in macaques are unparalleled in other nonprimate animals.

1. Introduction

Most nonhuman primates live in groups and communication through vocal, gestural, tactile, and olfactory signals plays an important role in their social life. Gestural communication involving facial expressions and body postures drew considerable attention in the 1960s and 1970s, but in recent years most research efforts have concentrated on the study of vocalizations, due to the development of sophisticated technology for the recording and analysis of calls. The study of

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primate gestural communication currently lags far behind that of vocalizations and much of our knowledge of the usage and meaning of gestures is still speculative and based on purely descriptive studies. In particular, a reliable methodology for identifying and quantifying gestures has not yet been developed.

The study of gestural communication in monkeys has mostly concentrated on Old World monkeys such as macaques and baboons. Macaques are the only monkeys in which gestural communication has been studied quantitatively and, therefore, they are the best candidates for a comprehensive review of the literature on this phenomenon. Furthermore, macaques have been the subject of study for several decades and we possess a considerable amount of information on several aspects of their social, mating, and parental behavior, which is useful to understand their communication dynamics.

Macaque gestural communication, just like any other behavioral phenomenon, can be studied from different perspectives. Ethologists traditionally distinguish between approaches that focus on the ontogeny, causation, function, and evolution of behavior (Tinbergen 1963). An ontogenetic approach to macaque gestural communication would investigate the changes in the production, comprehension, and usage of gestures over the lifetime of individuals. Causation refers to the mechanisms and stimuli that control and regulate the use of gestures. A functional analysis would address both the immediate consequence or function of gestures and the adaptive value of gestural communication for the survival and reproductive success of the individual. Finally, an evolutionary approach would involve comparative analyses of gestural communication in closely related species to understand the origin and modification of gestures in relation to speciation and adaptive radiation. Although a full comprehension of macaque gestural communication would require an integration of analyses at all four levels, each approach can be pursued independently from all the others (see Maestripieri, in press).

In this article, I will briefly provide some basic information on the phylogeny and life history of macaques and then synthesize our current knowledge of the functional significance of macaque gestural communication. My primary interest here is to discuss how gestures are used and what social and communicative functions are accomplished through the use of gestures. Because, however, some information on the ontogeny, causation, and evolution of communication can be useful to understand the usage and meaning of macaque gestures, I will review and discuss some of this information as well.

2. MACAQUE PHYLOGENY AND LIFE HISTORY

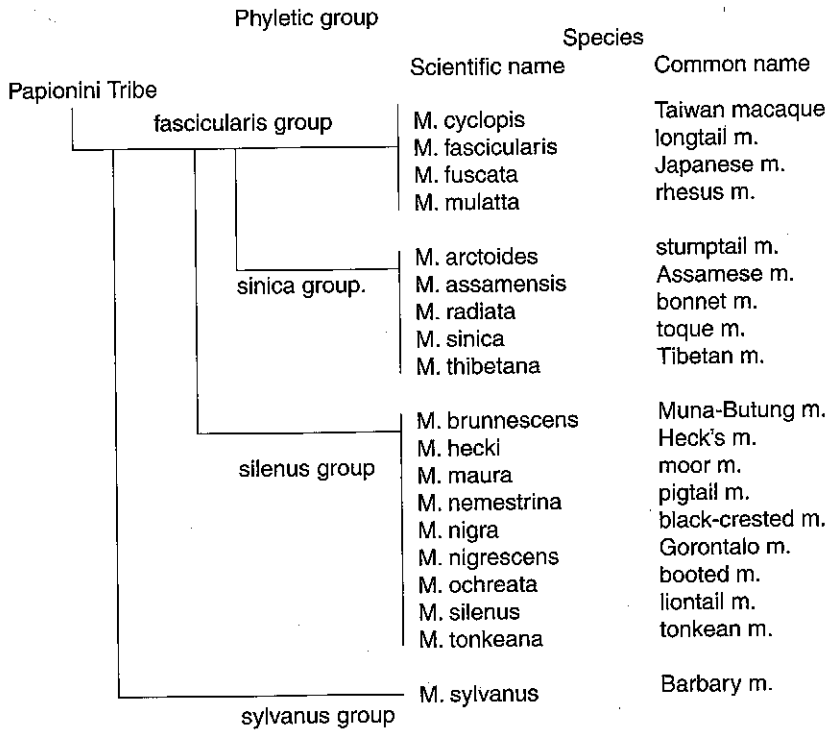

Figure 1. Cladogram of the genus *Macaca* showing the four phyletic groups and the 19 species with their scientific and common names.

Macaques are Old World monkeys belonging to the genus *Macaca*, in the family *Cercopithecidae*. The genus comprises 19 extant species, all of which with one exception (*Macaca sylvanus*) live in the Asian continent. Although there is some controversy among taxonomists and paleontologists, the genus *Macaca* is generally believed to have evolved in Africa from an ancestor resembling *Macaca sylvanus*, and subsequently spread into Asia where it differentiated into four distinct phyletic groups (Fig. 1; see Fa 1989 for a review). The species within each phyletic group are often anatomically, morphologically, and behaviorally similar to each other, though they are separated in their natural environment by geographic and ecological barriers (Fooden 1982).

Macaques live in multi-male multi-female groups ranging in size from 10 up to 100 individuals (Lindburg 1991). Females remain in their natal groups all of their life whereas males migrate to a new group at puberty, often after a period of solitary life. Macaque groups are therefore composed of clusters of related adult females with their offspring (matrilines) and unrelated adult males. All individuals within a group are ranked along a linear dominance hierarchy, with adult males usually outranking females. Related females occupy adjacent ranks and daughters rank below their mothers. Dominance ranks results from fights between individuals and are strongly affected by agonistic support provided by kin. Support among kin is accompanied by frequent affiliation consisting of contact, proximity, and grooming. Mating is generally promiscuous and males contribute little or nothing to parental care.

Macaque group-living probably results from the need to cooperate for protection from predators and/or defense of food resources from other conspecifics (Wrangham 1987). Limited resources such as food, shelter and mates, however, inevitably lead group members to compete with each other. Communication is an adaptation to social life and mediates both cooperative and competitive interactions with conspecifics. Two basic functions of communication are to bring individuals together when there is need for cooperation, and to keep them apart whenever competition arises. Many of the complexities of macaque social life and communication result from the elaboration of this simple system of approach and avoidance. For presentation purposes, the use of gestures in competition and cooperation will be reviewed by distinguishing four main types of social contexts: aggression, mating, affiliation, and parental care.

3. AGGRESSION

Competition over limited resources such as space, food, or mating partners has both benefits and costs. The benefits of competition include access to the contested resources whereas the costs may range from the time and energy invested in competition to the risk of injury or death in case of a fight. Communication in the context of competition allows individuals to negotiate access to resources while reducing the probability of costly fights. In macaques, competition occurs not only between individuals but also between families and groups. Therefore, gestures are used not only to communicate with competitors but also

with relatives, friends and allies who may provide their support in agonistic encounters.

3.1 *Threats*

Macaques use a variety of gestures to communicate their intention to engage in or to avoid a fight. Although an aggressive disposition can be communicated with piloerection or body movements, signals of threat mostly involve the face. Threats use all of most conspicuous elements of the face, forehead and eyebrows, eyes, nose, ears, and mouth. Facial expressions of threats are quite similar across macaque species and typically involve staring at the opponent with eyes wide open, mouth open without showing the teeth, eyebrows raised, and ears flattened (*M. arctoides:* Blurton-Jones & Trollope 1968; *cyclopis:* Poirier 1986; *fascicularis*: Shirek-Ellefson 1967; *fuscata*: Masataka & Fuji 1980; *mulatta*: Altmann 1962; *nemestrina*: Kaufman & Rosenblum 1966; *nigra*: Nickelson & Lockard 1978; *radiata*: Simonds 1965; *silenus*: Skinner & Lockard 1979; *sylvanus*: Zeller 1980; *thibetana*: Zhao 1994; *tonkeana:* Thierry et al. 1989). The number of facial elements present in the threat varies with its intensity: simple staring signals a threat of low intensity; as the intensity of the threat increases, the eyebrows, the ears, and the mouth are progressively recruited in the signal. The eyes seem to be the most constant component of the threat whereas the mouth is the most variable (Zeller 1980; 1996).

Threats occur in the contexts typical of competition and aggression such as feeding and mating. In addition, simple proximity to another individual can be sufficient to elicit a threat. In a dyadic interaction, the threat signals the individual's potential or intention to engage in a conflict. The relationship between threat and aggression, however, need not be necessary. Aggression may not be preceded by threats and in most cases, threats are not followed by aggression. A threat alone is often sufficient to resolve a contest between two individuals because the two individuals are likely to have met repeatedly in the past and have a good memory of the outcome of their agonistic encounters. Therefore it is in the interest of both opponents to settle their dispute with an exchange of signals rather than with another fight whose outcome is predictable.

In dyadic encounters, threats are usually displayed by higher-ranking to lower-ranking individuals. In some circumstances, however, subordinates may

threaten dominants. Such situations include when the object of competition is more valuable to the subordinate than to the dominant (e.g., the subordinate's offspring) or when subordinates have the opportunity to recruit other individuals as allies. Subordinate threats are often accompanied by recruitment screams and are sometimes referred to as defensive threats because they often occur in response to threat or aggression by dominants (e.g., *arctoides*: Blurton-Jones & Trollope 1968; *mulatta:* Gouzoules et al. 1984; *nemestrina*: Gouzoules & Gouzoules 1990; *silenus*: Skinner & Lockard 1979; *radiata*: Rahaman & Parthasarathy 1968).

Defensive threats are not the only signals with which macaques recruit agonistic support. While threatening another individual, support can be recruited by rapidly alternating the gaze between the target of the threat and the potential ally (e.g., in *fascicularis*: de Waal et al. 1976). In pigtail macaques, females attempt to recruit the aid of dominant males against their opponents with a combination of facial expressions and body postures (Maestripieri 1996a). The facial expression used in this context is the pucker, a gesture in which the lips are compressed and protruded and the eyebrows are raised. Females involved in a fight have been observed to walk towards a dominant male, then turn around and walk towards their opponent while puckering to the male over their shoulder. The pucker functions as a request to follow and its use here is similar to that observed in other contexts (see below).

In macaques, aggression and threats are used by dominant individuals to claim priority of access to resources. Dominants may also use other behaviors to maintain and reinforce their status, which are less strictly related to aggression than threats. Mounting is perhaps the most common assertive behavior in macaques and can be performed by dominants to subordinates of the same or the opposite sex (*arctoides*: Chevalier-Skolnikoff 1974b; *cyclopis:* Poirier 1986; *fascicularis*: Poirier & Smith 1974; *fuscata*: Hanby 1974; *mulatta*: Koford 1963; *nemestrina*: Maestripieri 1996a; *nigra*: Dixson 1977; *radiata*: Rahaman & Parthasarathy 1968; *silenus*: Skinner & Lockard 1979). Assertive mounting is morphologically similar to sexual mounting, but the mount may be incomplete and of shorter duration than a sexual mount. When performed by males, the mount may or may not involve foot-clasping and thrusting, but it usually does not involve intromission and ejaculation. When females mount males or other females, they sometimes climb on the back of the mountee, clasping its buttocks with their feet (e.g. Chevalier-Skolnikoff 1974b).

Mounting can be used, like threats, to inhibit the behavior of subordinates but is perhaps best viewed as a display of strength or power, similar to branch shaking or other visual and acoustic displays (Modahl & Eaton 1977; Mehlman 1996). Although mounting may not be considered a gestural signal, assertive mounting and other displays can be regarded as communicative patterns that, similar to threats, allow individuals to settle a dispute without a fight. Mounts do not usually signal impending aggression but they can occur during or immediately after a conflict. Aggressor and victim can mount each other or they can mount or be mounted by a third individual not involved in the conflict. Mounts seem to have a different function depending on the identity and the rank of the individuals involved and their role in the conflict (e.g. Hanby 1974; Cordischi et al. 1991; Maestripieri 1996a, b; Maestripieri & Wallen 1997). The aggressor can mount the victim after the conflict to reassert the outcome of the conflict or mount a third individual to discourage the potential participation of this individual in the conflict or to gain its support. If aggression is followed by contact and grooming between aggressor and victim, the victim may be allowed to mount the aggressor prior to the occurrence of affiliation. The victim can also mount a third individual perhaps to reduce the risk of intervention or to gain support from this individual. Finally, a third individual, especially if dominant to both combatants, may mount the aggressor to put an end to the conflict, or the victim to reinforce their relative difference in rank.

Stumptail macaques use the mock-bite as an assertive behavior pattern (Bertrand 1969; de Waal & Luttrell 1989; Demaria & Thierry 1990; Maestripieri 1996b). During mock-bite interactions, one individual grips the other's skin with the teeth, slowly, for several seconds. The individual being bitten remains passive and does not attempt to flee. In most cases, one hand or arm is bitten, but the lips and the eyebrow ridges may also be bitten. Mockbites are displayed by dominants to subordinates in two main contexts: when a dominant approaches a subordinate who has recently been involved in a conflict with a third individual, or when two closely-ranking individuals threaten and attack each other, usually with slaps (Maestripieri 1996b). In this case, the mockbite may signal the end of the squabble, but sometimes both individuals attempt to mockbite each other (Maestripieri 1996b). Demaria & Thierry (1989) reported that the frequency of mock-bites was high immediately after group formation, and suggested that the mockbite perhaps functions as a regulator of social tension in the group. The mockbite is often preceded by an arm present, which

consists of extending an arm or hand across the face of the other individual to be bitten. The behavioral sequence involving arm present and mockbite has been interpreted as an interaction expressing the subordinate's acknowledgement of its lower dominance status (Demaria & Thierry 1990; but see Maestripieri 1996c). Similar to mounting, the mock-bite is not strictly a gestural signal. However, the mock-bite is a stereotyped form of aggression that has probably been ritualized over the course of evolution and has acquired a specific communicative function.

3.2 *Submissive signals: bared-teeth display and presentation*

In most cases, macaques respond to threats and other assertive signals from conspecifics with submissive gestures. Submissive gestures are a heterogeneous class of signals whose common function is to reduce the aggressive disposition of the individual to whom they are displayed. Submissive signals can be expressions of fear, postures that expose vulnerable regions of the body, or behavior patterns belonging to the mating or infantile repertoire. Although it is generally believed that the ability to display submissive signals is relatively independent from experience (Chevalier-Skolnikoff 1974a; Kirkevold et al. 1982; Mason 1985), the usage of submissive signals is probably learned during development, through direct experience and observation of interactions between other individuals (Mason 1985). In other words, individuals learn during development that expressions of fear or other behavior patterns are likely to reduce the aggressive disposition of an opponent and learn to display these signals in situations with risk of aggression. These situations include the aftermath of aggression, when the probability of further aggression is still high, threats, assertive signals, or simple proximity to a dominant individual.

The most common submissive signal in macaques is the bared-teeth display, also referred to as fear grin or grimace. In this expression, the mouth is closed and the lips and lip corners are retracted so that the teeth are exposed in a white band. The bared-teeth is present in all macaques, but some species have two or more variants of this signal (e.g. *nigra:* Bernstein 1970; Dixson 1977; Nickelson & Lockard 1978; *silenus:* Skinner & Lockard 1979; Johnson 1985; *sylvanus:* Preuschoft 1992). The bared-teeth display may or may not be accompanied by scream vocalizations. In the latter case, it is often referred to as "silent bared-teeth display" (e.g. de Waal & Luttrell 1985). The bared-teeth display

probably has a strong fear component because it is displayed by macaques in response to a variety of fearful and painful stimuli including anxiogenic drugs, electroshock, or simple hair-pulling during grooming (Miller et al. 1971; Lagarde et al. 1990; Maestripieri & Wallen 1997).

In most macaque species, the bared-teeth occurs primarily in response to threat or aggression, or in response to an approach by a dominant individual (e.g. *arctoides*: Blurton-Jones & Trollope 1968; Bertrand 1969; *fascicularis*: Poirier & Smith 1974; *fuscata*: Masataka & Fujii 1980; *mulatta*: Hinde & Rowell 1962; *nemestrina*: Kaufman & Rosenblum 1966; *nigra*: Dixson 1977; *radiata*: Kaufman & Rosenblum 1966; *silenus*: Skinner & Lockard 1979; *sinica*: van Hooff 1967; *sylvanus*: Preuschoft 1992). In this context, the most likely meaning of the bared-teeth is "I am afraid" or Do not attack me" or a combination of both (Maestripieri 1996c). The signal may or may not be effective in preventing aggression depending on the circumstances. In general, however, individuals are less likely to be attacked if they display the signal than if they do not (e.g. Preuschoft 1992). When the bared-teeth display is effective in preventing aggression, the signal may not be followed by any further interaction. The potential aggressor usually walks away from the sender of the signal and the latter does not attempt any social interaction with the former (e.g. Maestripieri 1996a, b).

Although this pattern of occurrence of the bared-teeth display is quite common in several species, there is some variability in both the interactions that precede the signal and those that follow it. The bared-teeth may occur without any prior interaction between individuals and may be followed by affiliation or mating (see below). Overall, it seems that in all macaque species, the bared-teeth display can occur both as a submissive and an affiliative signal. There is considerable variation, however, in the relative frequency with which the signal is used in the two contexts, ranging from a mostly submissive meaning in species of the *fascicularis* group (*cyclopis, fascicularis, fuscata,* and *mulatta*) to a mostly affiliative meaning in some species of the *silenus* group (e.g., *maurus, nigra,* and *tonkeana*).

The second most common submissive signal in macaques is probably the hindquarter presentation. In this body posture, which is probably derived from the sexual repertoire (Darwin 1876), the hindquarters are oriented towards another individual and the tail is raised. Similar to the bared-teeth, subordinates present to dominants upon receiving aggression or in situations with high risk

of aggression (e.g., *arctoides*: Blurton-Jones & Trollope 1968; Rhine 1972; Rhine & Kronenwetter 1972; Maestripieri 1996b; *mulatta*: Chance 1956; Hinde & Rowell 1962; Lindburg 1971; Maestripieri & Wallen 1997; *nemestrina*: Maestripieri 1996a; *nigra*: Dixson 1977; *radiata*: Rahaman & Parthasarathy 1968; *silenus*: Skinner & Lockard 1979; Johnson 1985; *sylvanus*: Preuschoft 1992). For example, it is quite common for individuals to lift their tail while running away from an aggressor, or at the end of a chase, to stand with the tail raised and expose the genital areas to surrounding individuals (Maestripieri & Wallen 1997). Although it is conceivable to think that the presentation reduces the probability of aggression, firm evidence to support this hypothesis is not yet available.

Similar to the bared-teeth display, there is variability among species in the interactions that precede or follow the presentation. Whereas in species such as rhesus, the presentation is most commonly a response to aggression or approach from a dominant (Maestripieri & Wallen 1997), in species such as stumptails, subordinates approach and present to dominants without any solicitation and they usually walk away without any further interaction (Blurton-Jones & Trollope 1968; Bertrand 1969; Estrada et al. 1977; Maestripieri 1996b). Thus, the presentation appears to be used in an appeasing or preemptive manner. Similar to the bared-teeth, the presentation can be displayed to initiate affiliative interactions without any previous aggression (see below) and it is possible that different contextual usages of the presentation are associated with subtle differences in the structure of the posture (Kaufman & Rosenblum 1966; Blurton-Jones & Trollope 1968; Emory & Harris 1978).

The presentation is often associated with the mount, sexual or nonsexual. Some of the contexts of occurrence of the presentation are, therefore, similar to those described above for mounting. For example, macaques sometimes present to a higher-ranking individual while simultaneously threatening a third individual (Maestripieri 1996a; Maestripieri & Wallen 1997). In this case, the presentation's meaning may still be submission, but the context of occurrence suggests that it also functions as a request for support.

In rhesus macaques the most striking difference between the bared-teeth display and the presentation was in their occurrence in response to approaches (Maestripieri & Wallen 1997). The bared-teeth was primarily displayed when an individual approached from the front whereas the presentation occurred in response to an approach from the rear, or laterally. This finding provides an explanation for the existence and usage of two signals with similar function. An approach from a dominant animal always entails risk of aggression and abrupt movements or attempts to flee in these circumstances may actually increase the probability of an attack. It is probably for this reason that submissive behavior in a variety of mammalian species often has a strong immobility component ("freezing"). By presenting to a dominant animal approaching laterally or from the rear instead of turning and teeth-baring, macaques can maintain immobility while signaling submission. Similarly, by simultaneously presenting and teeth-baring after aggression or during a chase, rhesus macaques can reduce the risk of further aggression from different directions.

3.3 *Other submissive signals*

In addition to the bared-teeth and the presentation, macaques use a number of other submissive signals. Most of them are facial expressions in which the mouth is the most conspicuous element of the signal. Lip-smacking involves rapid opening and closing of the mouth and lips, so that when the lips close they make a smacking sound. Lip-smacking is present in virtually all macaque species and is used in variety of contexts (see below). Teeth-chattering involves rapid opening and closing of the mouth but, unlike lipsmacking, the lips are retracted exposing the teeth. Teeth-chattering is morphologically intermediate between bared-teeth and lipsmacking and is probably an evolutionary derivation of these two gestures (van Hooff 1967). Teeth-chattering is frequent in *M. sylvanus* (Preuschoft 1992) and in the species of the *sinica* group including *M. arctoides, assamensis, radiata, sinica* and *thibetana* (Bertrand 1969; Bernstein 1970; Rahaman & Parthasarathy 1968; Zhao 1994), but has only rarely been reported in the *silenus* and *fascicularis* groups (e.g. in *silenus*: Skinner & Lockard 1979).

In most macaque species, lipsmacking and teeth-chattering are displayed by subordinates to dominants more than vice versa, suggesting that these signals serve a submissive function (e.g., Altmann 1962; Hinde & Rowell 1962; Rahaman & Parthasarathy 1968; Dixson 1977; Hadidian 1979; Adams & Schoel 1982; Maxim 1982). Lip-smacking, however, is rarely the first signal displayed in response to threat or aggression. Lip-smacking may be displayed by the victim of aggression but usually only after another submissive signal such as the bared-teeth or presentation has occurred (e.g., Nickelson & Lockard 1978; Skinner & Lockard 1979; Maestripieri 1996a, b). For example, when pigtail macaques receive aggression, they first avoid aggressors and/or display the bared-teeth and

presentation, then they approach the aggressors and lip-smack to them (Maestripieri 1996a). Moreover, lip-smacking is more likely to be followed by affiliation than the bared-teeth or presentation (Maestripieri 1996a, b; Maestripieri & Wallen 1997). Therefore, even when displayed after aggression, lip-smacking communicates an intention to engage in affiliation instead of just an attempt to inhibit the aggressive disposition of the other individual.

Teeth-chattering often occurs in response to aggression or risk of aggression and can be temporally associated with the bared-teeth, being frequently displayed immediately before or after this signal (*arctoides*: Maestripieri 1996b; *radiata*: Rahaman & Parthasarathy 1968; *silenus*: Skinner & Lockard 1979; *sylvanus*: Preuschoft 1992). Teeth-chattering is also used during the course of affiliative interactions (see below) and seems to have a meaning similar to that of lipsmacking but appears to have a stronger emotional component, ranging from fear to excitement (Bertrand 1969; Chevalier-Skolnikoff 1974b; Maestripieri 1996b).

In some species lip-smacking and teeth-chattering involve tongue protrusion and are referred to as lip-grin, grin-lipsmack, or clonic-jaw-movement (*arctoides:* Blurton-Jones & Trollope 1968; *assamensis*: Bernstein 1970; *maurus*: Watanabe & Brotoisworo 1982; *nigra*: Bernstein 1970; Dixson 1977; Hadidian 1979; Bernstein & Baker 1988; *radiata*: Kaufman & Rosenblum 1966). Some authors reported that lip-smack with tongue protrusion is associated with aggressive (e.g. staring and chasing) rather than submissive or affiliative behavior (e.g. Bernstein 1970; Dixson 1977; Bernstein & Baker 1988) but there is no unequivocal evidence to support this claim.

As already mentioned, stumptail macaques present a hand or an arm to be gently bitten by dominants. This invitation to mockbite can occur in response to aggression, notably slapping, in response to an approach, or even without any prior interaction (Maestriperi 1996b). Present-arm seems to communicate submission in a conflict but without necessarily reflecting fear; its occurrence during squabbling may mean "I give up, do not attack me anymore."

4. MATING

Mating poses a number of behavioral and social problems to macaques that must be solved with communication. There are several important restrictions

imposed on mating activity, including the receptive state of the female, the preference for particular type of mates, and the presence of other individuals. The most important pre-conditions for mating include a female in her receptive phase of the cycle and mutual attraction between mating partners. Forced copulation is present only in a few species of macaques (e.g. *arctoides*), and more commonly, mating requires the cooperation of male and female to take place. Males and female must communicate to one another their intention to mate and coordinate their behavior so that a sexual interaction can physically take place.

Because of the difference in body size between males and females and the fact that they normally compete for resources, aggression between potential mates is always latent. Moreover, the social organization and mating system of most macaque species are such that members of a mating pair often barely know each other. During the mating season, solitary males approach groups of unfamiliar individuals and attempt to lure females away from their group to engage in mating (*fascicularis*: van Noordwijk 1985; *fuscata*: Sugiyama 1976; *mulatta*: Lindburg 1971; *nemestrina*: Caldecott 1987; *thibetana*: Zhao 1993; 1994). Females in estrous are strongly attracted to strange males and may temporarily leave their group to solicit sexual activity from peripheral males. Mating can be completed in a few seconds behind a bush or may require hours or days of close proximity, e.g. when multiple mounts are necessary to achieve ejaculation. In either case, the risk of aggression between potential mates is high.

Females in estrous signal their readiness to mate by approaching males and presenting their hindquarters to them. The presentation functions to both reduce the probability of male aggression and invite the male to mount. In species in which males are multiple-mount ejaculators and male and female form long-lasting consortships, females sit by the males and follow them around repeating the presentation and sometimes also slapping the male's hips or feet with their hands (Caldecott 1986). Estrous females may occasionally climb on the male's back and engage in a series of pelvic thrusts to encourage their partner. During consorts, females will also frequently threaten any other individuals within visual distance from themselves and the males. During threats, females may stand up and present to the male, thereby increasing the probability of a mount.

Male communication in the context of mating serves two main purposes: first, the male must communicate his nonaggressive intention while approach-

ing the female and inhibit her fleeing or aggressive reaction; second, the male must position himself and the female so that a mount can physically take place. In addition, because males may be prevented from approaching a female from the presence of other individuals, they use gestures to lure females away from their companions and encourage them to follow (e.g., Caldecott 1987; Zhao 1993).

Macaque males communicate with estrous females with a combination of facial expressions, tactile signals, and body postures. Facial expressions such as the pucker, bared-teeth, lip-smack, and teeth-chatter are displayed while approaching an estrous female or while turning and moving away from her, to encourage her to follow. There is considerable variability among species in the extent to which each gesture occurs in this context, and in some species two or more gestures can be used interchangeably. The use of the pucker is particularly prominent in species such as pigtail (Tokuda et al., 1968; Christopher & Gelini, 1977; Goosen & Kortmulder, 1979; Caldecott, 1987; Maestripieri, 1996a; Oi 1996) and liontail macaques (Johnson 1985; Lindburg et al. 1985), where this signal is virtually the only one used by males to begin mating interactions. The same expression is also used, though less frequently, by male longtail (Shirek-Ellefson 1967; Poirier & Smith 1974) and rhesus macaques (Lindburg 1971; Maestripieri & Wallen 1997). In *M. mulatta* and in other species such as *fuscata, nigra, maurus,* and *tonkeana,* males also use the bared-teeth and lip-smack while approaching estrous females (Dixson 1977; Mohdal & Eaton 1977; Thierry et al. 1989; Petit & Thierry 1992; Maestripieri & Wallen 1997), while in *M. sylvanus, arctoides* and other species of the *sinica* group, the teeth-chatter is more common (Blurton-Jones & Trollope 1968; Bertrand 1969; Chevalier-Skolnikoff 1974b; Rahaman & Parthasarathy 1968; Preuschoft 1992; Zhao 1993).

Facial expressions that in an agonistic context would have a clear submissive meaning such as bared-teeth, lip-smack, or teeth-chatter, are now displayed by dominant males to subordinate females with a different meaning. The function of male pucker, bared-teeth, lip-smack, or teeth-chatter in this context seems to be to communicate a reduction in distance for friendly purposes (Maestripieri 1996a). Depending on whether the male is approaching or moving away from the female, the signal serves as an encouragement not to run away or to follow, respectively. In pigtail and liontail macaques, females respond to the male pucker by puckering themselves while approaching (Johnson 1985; Maestripieri 1996a).

Once distance between male and female has been reduced, males use tactile signals such as hip-touches to induce the female to present her hindquarters. When the hip-touch is followed by a genital inspection, either by sniffing the female genital area or by inserting a finger in her vagina (*arctoides*: Bertrand 1969; *radiata*: Rahaman & Parthasarathy 1968), the male usually continues to pucker, grin, lip-smack, or teeth-chatter during the inspection, perhaps to reassure the female and prevent her from leaving (e.g. Rahaman & Parthasarathy 1968; Dixson 1977; Maestripieri 1996a, b). Then, the male will mount the female or turn away and leave.

During copulation, both male and female display facial expressions. The female reaches back grasping the male's flank or leg with her hand and lip-smacks; the male displays a bared-teeth associated with a high-pitched vocalization, or teeth-chatters (e.g., Rahaman & Parthasarathy 1968; Nickelson & Lockard 1978; Maestripieri 1996a, b). The function of these facial expressions is not clear and they could simply reflect an underlying orgasm-related emotion (Goldfoot et al. 1980). Since males sometimes bite females on their neck during copulation, female lipsmacking may be an appeasing response aimed at reducing the probability of aggression. The function of the male bared-teeth or teeth-chatter is not clear because the signal does not appear to be directed to the female, who is usually holding her face down when the signal occurs. The signal, however, could be directed to other individuals.

In some species of macaques, adult males are harassed during copulation by other individuals, notably adult females and juveniles of both sexes (Niemeyer & Anderson 1983). This is particularly dramatic in stumptail macaques in which the male remains temporarily immobilized during copulation. The mating pair is surrounded by other individuals who alternately threaten and slap the male and teeth-bare and teeth-chatter in response to the male's threats (Gouzoules 1974). Although stumptail males usually threaten the surrounding individuals who harass them, the bared-teeth showed during copulation may have originated from this phenomenon of harassment.

The facial expressions displayed by males and females before and during copulation, including pucker, bared-teeth, lipsmack, teeth-chatter may also be displayed before and after male-male and female-female mounting (e.g., Blurton-Jones & Trollope 1968; Rahaman & Parthasarathy 1968; Chevalier-Skolnikoff 1974b). The function of the gestures may be the same as for sexual mounting, though mounting may have a more assertive or affiliative connotation.

5. AFFILIATION

Macaques do not interact with all members of their social group with the same frequency. Moreover, the quality of the interaction varies dramatically with the identity of the participating individuals. Macaques maintain close proximity to their relatives and friends when sitting, feeding, or walking, and ignore or avoid some of the individuals in their group. The most common forms of affiliation in macaques involve physical contact between individuals. Huddling and grooming are observed in virtually all macaque species. Affiliative interactions that are conspicuous in some species but not in others include mounting, ventro-ventral embracing, and various forms of clasping (e.g., hip-clasping or genital manipulation; Thierry 1984).

Although, in most cases, individuals who engage in affiliative interactions are more familiar with each other than two potential mating partners, relatedness or familiarity in no way guarantees immunity from aggression. In fact, in some cases aggression between closely-related individuals is more frequent than between unrelated individuals, though this effect is a likely result of the fact that the former have more opportunities for aggression (e.g. Bernstein et al. 1993). In any case, reduction of distance and establishment of contact for affiliative purposes is always associated with some risk of aggression and, therefore, similar to mating, reduction of distance is often preceded by an exchange of signals.

Prior to an affiliative interaction, an individual may use a gesture to communicate the intention to reduce distance or to induce another individual to come closer. Depending on the relative dominance rank of the individuals, the signal could also inhibit the aggressive behavior of a dominant individual or the fleeing response of a subordinate. The facial expressions that occur prior to affiliation are the same as those used to reduce distance prior to mating and include the pucker, lip-smack, teeth-chatter or the bared-teeth. For example, an individual may pucker or lip-smack while approaching another individual and then begin a grooming bout. Alternatively, an individual may pucker or lip-smack to another one without moving and request that the other approach.

Although pucker, lip-smack, teeth-chatter or the bared-teeth have all been observed to precede affiliative interactions in virtually every macaque species, their relative frequency of usage in this context shows dramatic interspecific differences: pucker and lipsmack are the most common affiliative signals in

pigtail (Maestripieri 1996a) and liontail macaques (Johnson 1985; Lindburg et al. 1985), the lip-smack is probably most common in rhesus, Japanese, and longtail macaques (Shirek-Ellefson 1967; Masataka & Fujii 1980; Maestripieri & Wallen 1997), both lip-smack and teeth-chatter occur in the Barbary macaques (Preuschoft 1992), bonnets (Rahaman & Parthasarathy 1968) and stumptail macaques (Blurton-Jones & Trollope 1968; Bertrand 1969; Maestripieri 1996b), and the bared-teeth is quite common in Barbary macaques (Preuschoft 1992) and among the Sulawesi macaques (*maurus*: Petit & Thierry 1992; *nigra*: Darwin 1872; Bernstein 1970; Dixson 1977; Thierry et al. 1989; *tonkeana*: Preuschoft & van Hooff 1996). As previously mentioned, the presentation is also used to encourage individuals to approach.

Once distance is reduced, individuals may use other signals or their concomitant behavior to indicate the type of affiliative interaction they intend to engage in. Grooming is usually requested by lying on the ground and exposing the part of the body to be groomed (Boccia 1986). Interactions involving mounting, hip-clasping, or genital manipulation are usually preceded by a hindquarter presentation (e.g., Altmann 1962; Blurton-Jones & Trollope 1968; Thierry 1984; Cordischi et al. 1991). Hip-clasping involves an individual holding the hindquarters of another individual with both hands, while sitting or standing. In stumptail macaques, hip-clasping tends to be mostly displayed by dominants to subordinates thus suggesting that this interaction has an assertive meaning similar to mounting (de Waal & Luttrell 1989; Maestripieri 1996b). Like mounting, the combination of presentation and hip-clasping can occur after a conflict between two individuals and signals their reconciliation (de Waal & Luttrell 1989). Hip-clasping, however, is frequently solicited and received by juveniles during situations of tension such as the presence of an external threat, suggesting that it serves a reassurance function (Maestripieri 1996b).

Genital manipulation usually occurs between two males and involves one individual reaching out and fondling the other's genitalia. The recipient of the interaction can stand in front of the actor, sometimes lifting a leg to facilitate manipulation. Alternatively, genital manipulation may occur during a mount between two males, when the mountee reaches back between his legs and fondles the mounter's genitalia. The meaning of this interaction is not clear, but it may serve an appeasement function or generally strengthen bonding between the males (Bertrand 1969; Maestripieri 1996b).

Sometimes several signals and affiliative interactions can occur in a rapid sequence. For example, individual A may approach and lipsmack to individual B, then present to B. B may then mount A (or clasp his/her hips or genitals) and either of them or both can initiate a grooming bout (Cordischi et al. 1991). Alternatively, individual A may approach and pucker to individual B, B can return the pucker to A, and then both embrace and groom each other (Maestripieri 1996a). Behavioral sequences involving presentation, mounting or clasping are frequent between male adults or juveniles while ventro-ventral embracing is more common among females (*arctoides*: Bertrand 1969; Maestripieri 1996b; *fuscata*: Hanby 1974; Hanby & Brown 1974; Cordischi et al. 1991; *mulatta*: Kaufmann 1967; Lindburg 1971; Reinhardt et al. 1986; Maestripieri & Wallen 1997; *nemestrina*: Maestripieri 1996a; *nigra*: Dixson 1977; *radiata*: Simonds 1965; but see Sugiyama 1971; *silenus*: Skinner & Lockard 1979; *tonkeana*: Thierry 1984).

Similar to mating, an exchange of signals can also occur during the affiliative interaction. The signal may be the same or different as that used to reduce distance. For example, pigtail macaques mostly use the pucker to reduce distance prior to grooming but then lip-smack during grooming (Maestripieri 1996a). Lip-smacking during grooming is observed in most, if not all, macaque species. During grooming, the groomee may direct the action of the groomer toward specific areas of the body or signal its intention to terminate the interaction with postural changes (Boccia 1986). In pigtail macaques, groomees have been observed to interrupt the interaction, move a few steps away from the groomer, and then solicit an approach and resumption of the activity with the pucker (Maestripieri 1996a).

Mounting, embracing, and various forms of clasping may be accompanied by lipsmacking or teeth-chattering by one or both partners (*arctoides*: Bertrand 1969; Rhine & Kronenwetter 1972; Chevalier-Skolnikoff 1974b; *nemestrina*: Maestripieri 1996a; *nigra*: Dixson 1977; *radiata*: Simonds 1965; Rosenblum & Kaufman 1966; Rahaman & Parthasarathy 1968; Sugiyama 1971; *silenus*: Johnson 1985). The function of these signals displayed during the interaction may be multiple: they minimize risk of aggression and promote bonding. They may also reflect excitement: the teeth-chatter and screams accompanying female-female mounting in stumptail macaques are associated with marked physiological signs of arousal (Goldfoot et al. 1980).

Two categories of signals occurring in affiliative interactions deserve a special discussion: greetings and play. Greetings is rather vague term used to

describe what appear to be complex communicative interactions characterized by facial expressions, stereotyped body movements, grunt vocalizations, and tactile interactions such as hip-touch and genital manipulation. In macaques and other monkeys, notably baboons, greetings are especially common between adult males. Some components of the greeting ceremony, such as the use of facial expressions to reduce distance have already been described because they also occur prior to other affiliative interactions. The context of occurrence of greetings, however, is mostly limited to situations of tension or upheaval and the communicative exchange is usually not followed by grooming.

During greetings, pigtail macaques use a specific facial expression, termed eye-brows (Maestripieri 1996a). The eye-brow display consists of raising the eyebrows to show the white eyelids and opening the mouth halfway. The individual displaying the signal often walks or runs parallel to the individual to which the signal is directed, and the signal is often accompanied by grunting. This interaction is not limited to adult males. Adult females, especially if high-ranking, can display the signals to adult males or other females. The contexts of occurrence of this signal include the aftermath of a conflict in the group in which many individuals were involved, the mobbing of a high-ranking male by a group of lower ranking females, or the reintroduction of a high-ranking individual into the group after a period of absence. What all these situations have in common is that they pose a challenge to the social status of high ranking individuals or to the stability of their alliances. In baboons, it has been argued that greetings are linked to negotiation of dominance relationships between individuals, alliance formation, and decision-making processes relative to the direction of travel (Smuts & Watanabe 1990; Colmenares 1991).

Play is characterized by the occurrence of the typical relaxed-open-mouth expression know as the "play face" (van Hooff 1962; 1967). The play face consists of a wide opening of the mouth, as if to attempt to bite, but without clenching the teeth. The play face is displayed almost exclusively by juvenile and subadult macaques, namely the class of individuals that most engage in play, and occasionally by adult males (Symons 1978; Kirkevold et al. 1982; Preuschoft 1992). Play faces are usually displayed simultaneously by two play partners and may be associated with soft vocalizations (Symons 1978; Preuschoft 1992). Although the play face is remarkably similar among individuals and macaque species, it does not occur in contexts other than play. Moreover, the play face only occurs during contact play involving struggle. It is never used to initiate

play from a distance or in forms of play other than struggle, such as chase (Preuschoft 1992). In contrast, chase play is initiated by typical summoning signals such as presentation, pucker, lip-smacking, or other specific patterns such as the bouncing gait or tail pulling (e.g. Bertrand 1969; Skinner & Lockard 1979; Preuschoft 1992; Maestripieri 1996a).

Traditional explanations of play signals in monkeys and other animals maintain that they are a form of "metacommunication", namely a form of communication about communication (Bateson 1953; Altmann 1962; Bekoff 1972). In this view, an individual displaying a play signal is communicating that from that moment on, patterns of behavior such as biting and slapping cease to have their normal aggressive significance and acquire a new, playful meaning. In other words, play signals would mean "this is not meant seriously". This explanation, though certainly applicable to humans, may not be correct for animals including primates because it implies quite sophisticated cognitive processes, for which there is no evidence in primates. Specifically, the metacommunication hypothesis implies that individuals attribute knowledge to others and use signals to modify their knowledge, rather than just their behavior (see also Maestripieri 1996c). Although the play face is traditionally considered a signal, the possibility that the play face is simply one form of play cannot be ruled out.

6. PARENTAL CARE

Parental care represents another specific context of occurrence of gestures. Macaque infants communicate their basic needs (food, transport, and protection) to their mothers mainly with vocalizations such as coos, screams, and geckers (Maestripieri & Call 1996). In contrast, mothers communicate with their infants primarily with facial expressions and body postures. As in other contexts, the main function of gestures is to allow reduction of distance between mother and infant. Unlike other contexts, however, the use of gestures does not result from the need to minimize risk of aggression. Rather, gestures are used by mothers to control their infants' activity and to regulate the maintenance of proximity.

Macaque mothers retrieve their infants from a distance by using the pucker, the bared-teeth, the lip-smack, or the presentation, depending on the species or the circumstance (*arctoides*: Burton 1972; *mulatta*: Harlow et al. 1963; Seay 1966; Hinde & Simpson 1975; Maestripieri & Wallen 1997; *nemestrina*: Jensen & Gordon 1970; Maestripieri 1996d). Some of these signals are used interchangeably and they often occur in rapid succession, e.g., a mother will first lip-smack or teeth-bare to her infant and then turn around and raise her tail (Hinde & Simpson 1975). These interactions are particularly frequent in the first weeks of infant life, when mothers display these expressions to their infants while walking backwards as a way to encourage their infants' independent locomotion (Maestripieri 1995; 1996d).

The same signals used by mothers with their infants can also be displayed by other adult females and males to unrelated infants. In virtually all macaque species, adult females lip-smack, teeth-chatter, or teeth-bare to young infants prior to approaching and touching them or as a way of luring them away from their mothers (e.g., Skinner & Lockard 1979; Maestripieri & Wallen 1997). Adult and juvenile females may also encourage infants to follow by turning their back to the them, presenting the hindquarters, and looking at the infant with the head between their legs. In species in which males frequently interact with infants such as Barbary macaques, the same facial expressions and body postures are used by males (Burton 1972). When infants become more independent from their mothers, usually after their first 6 months of life, and they are no longer attractive to other individuals, they display and receive gestures with a frequency and in contexts similar to those of adult individuals.

7. THE INFORMATION CONTENT OF MACAQUE GESTURES

A coarse-grained analysis of macaque gestural communication suggests that macaques have several gestures that serve a similar function and that each gesture can be used in different contexts with different meanings. To a human observer, macaque gestures also appear to be graded signals rather than discrete (Marler 1965). For example, threats vary in their constitutive elements in relation to the intensity of the threat. Macaque facial expressions also seem to merge into one another in both their morphology and their meaning (Shirek-Ellefson 1972). For example, the defensive threat merges with the bared-teeth, the bared-teeth merges with teeth chattering, teeth-chattering merges with lip-smacking, and lipsmacking merges with the pucker.

Based on our current understanding of macaque gestures, the relation between the structure of gestures and their meaning seems to be probabilistic rather than fixed. In this view, the social context provides crucial information to reduce ambiguity in the meaning of the gesture. It cannot be ruled out, however, that what appear as graded signals to humans are in fact discrete and distinct signals to macaques. Macaques may not only be better at discriminating their gestures from one another but also at identifying subtle differences in the gesture structure associated with different contexts of usage or the identities of individuals (Zeller 1980). To fully understand the nature of macaque gestures we need both better techniques for recording and analyzing gestures and a better understanding of macaque perceptual abilities relative to our own.

The view of macaque gestures as graded signals merging into one another is mainly the result of the notion that gestures only reflect emotional and motivational states. In this view, the flexibility in the combination of elements in each gesture would be an adaptation to reflect the intensity of the emotion or motivation underlying the gesture. Similarly, the structural similarities among gestures would allow the expression of rapid transitions in emotional or motivational states (Shirek-Ellefson 1972).

The view that primate signals only reflect emotional or motivational states has now been abandoned by many scientists. Although macaque gestures do not appear to be used to communicate about aspects of the external environment such as the presence of food or predators, they convey information about a range of social activities occurring in the group, which involve the sender of the signal, its recipient, and in some cases also a third individual. Their information content may range from the expression of an emotional state (fear or excitement) to the request for participation in a specific activity (grooming, agonistic support, play, and perhaps also direction of travel), and they often also contain an indication of the location where the activity will take place.

Most macaque gestures are undoubtedly under volitional control and are used intentionally, namely with the goal of obtaining a specific behavioral response from another individual. While in most cases the gesture is aimed at eliciting or inhibiting an immediate response, in some interactions the exchange of gestures seems to be aimed at obtaining more general and long-term changes in behavior. For example, gestures exchanged during greetings seem to be aimed at promoting future tolerance and cooperation among individuals and gestures used during mother-infant interactions function to encourage developmental processes of infant independence whose benefits to mothers will only be apparent in subsequent months.

The fact that macaque gestures are not used to transmit information about the presence and location of food or predators is not surprising. Communication about food and predators often occurs over a long distance and between individuals that are out of each other's sight, thus in situations in which vocalizations are more effective than gestures. In fact, the basic repertoire of alarm and food calls possessed by macaques is quite similar to those of other mammals and birds living in similar environments and facing similar ecological problems. In contrast, it appears that selective pressures responsible for the evolution of macaque gestural communication have mainly operated at the level of intragroup social dynamics, favoring the use of gestures to control and coordinate the behavior of individuals within the social group.

Unlike communication over food or predators, the exchange of signals in the contexts of aggression, affiliation, mating, and parental care occurs between individuals that are in close visual, and often also physical contact. Gestures convey information about external events in addition to the emotion and motivation of individuals, but the external events that are often most relevant to macaques are those occurring in their social group and involve the activity of other individuals. Although most contexts of usage of gestures consist of variations on a basic theme of approach and avoidance, nevertheless the size of the gestural repertoire and the subtleties of gestural communication in macaques are unparalleled in other animals, with the exception of other Old World monkeys and the apes.

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THE ONTOGENY OF CHIMPANZEE GESTURAL SIGNALS: A COMPARISON ACROSS GROUPS AND GENERATIONS*

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ABSTRACT

Observations of the gestural communication of two groups of captive chimpanzees are reported. For one group the observations represent a fourth longitudinal time point over a 12 year period; the other group was observed for the first time. There were two main questions. The first concerned how young chimpanzees use their gestures, with special foci on the flexibility displayed in signal use and on the sensitivity to audience displayed in signal choice. It was found that chimpanzees are very flexible in their signal use (different signals for same goal, same signal for different goals) and somewhat sensitive to audience (signal choice based on attentional state of recipient). The second question was how chimpanzees acquire their gestural signals. Comparisons between the two groups showed much individual variability both within and between groups. In addition, when each of the two contemporary groups was compared with the previous longitudinal time points for one of the groups, no differences in concordance were found. It was

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