Gestural communication in three species of macaques (*Macaca mulatta, M. nemestrina, M. arctoides*)

Use of signals in relation to dominance and social context*

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The present study compared the frequency and contextual usage of the most prominent gestural signals of dominance, submission, affiliation, and bonding in rhesus, pigtail, and stumptail macaques living in captivity. Most similarities among species were found in signals of dominance and submission and most differences in affiliative gestures and bonding patterns. Rhesus macaques have a relatively poor gestural repertoire, pigtail macaques possess conspicuous signals of affiliation and bonding, and stumptail macaques have the richest repertoire of assertive and submissive signals. The similarities and differences in the gestural repertoires of rhesus, pigtail, and stumptail macaques can be related to the intragroup social dynamics of these species as well as to their evolutionary history.

Keywords: Gestural communication, macaques, dominance, context, social organization, phylogeny

Comparisons of communication patterns across different animal species can provide evidence of the adaptive significance of signals and their phylogenetic history (e.g., Darwin, 1872; Wenzel, 1992). Since communication patterns are mainly adaptations to the social environment, in order to understand the adaptive significance and evolutionary history of the social signals observed in different species, information is needed on the social organization and behavior of these species as well as on their phylogenetic relationships (e.g. Preuschoft & van Hooff, 1996).

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The genus *Macaca* includes 19 different species, which are currently subdivided into 4 distinct phyletic groups on the basis of morphological and genetic characteristics (Brandon-Jones et al., 2004; Delson, 1980; Fa, 1989; Fooden, 1980). Previous qualitative descriptions of the repertoires of facial expressions and gestures of different macaque species reported that interspecific variation is generally less pronounced in the agonistic displays (e.g., threats) than in the displays of affiliation and bonding (Bernstein, 1970; Redican, 1975; Thierry et al., 1989; van Hooff, 1967). More quantitative data and direct comparisons between different species are needed, however, before any conclusions can be made about the evolution of gestural communication in macaques.

Rhesus (*Macaca mulatta*), pigtail (*Macaca nemestrina*) and stumptail macaques (*Macaca arctoides*) belong to three different phyletic groups within the genus *Macaca* (Delson, 1980; Fooden, 1980). Pigtail macaques and related species of the *Macaca silenus* group are believed to have undergone early differentiation and dispersal, while rhesus macaques and related species of the *Macaca fascicularis* group may have differentiated and dispersed more recently (Fa, 1989). Stumptail macaques are probably related to species in the *Macaca sinica* group but seem to have undergone the most recent differentiation (Fooden, 1980).

Rhesus, pigtail, and stumptail macaques have been the focus of a number of studies involving direct interspecific comparisons of aggressive, affiliative, and maternal behavior (e.g., Bernstein et al., 1983; Butovskaya, 1993a, b; de Waal & Ren, 1988; Maestripieri, 1994; Ruehlmann et al., 1988; Weigel, 1980) and these and other studies have highlighted both similarities and differences in their social organization. Rhesus macaques live in a relatively despotic and nepotistic society characterized by high rates of aggression and spatial avoidance, and in which grooming and agonistic support mainly occur within clusters of matrilineal kin (Bernstein & Ehardt, 1985; Kaplan, 1977). The social dynamics of pigtail macaques are quite similar to those of rhesus macaques, but the lower levels of spatial avoidance, the higher reconciliation frequency, and the higher rates of approaches and grooming between pigtail females relative to rhesus (Bernstein et al., 1983; Maestripieri, 1994) suggest that the pigtail macaque society is more cohesive and conciliatory than the rhesus society. Aggression rates have been reported as similar in pigtails and rhesus (Maestripieri, 1994) or lower in the pigtails (Bernstein et al., 1983). Aggression, however, more frequently involves the participation of third individuals in pigtails than in rhesus (Bernstein et al., 1983) and post-conflict reconciliation is also frequently extended to the opponent's kin and allies (Judge, 1991). The frequency of aggression in stumptails has been reported as higher than in rhesus and pigtails

(Butovskaya 1993a, b; de Waal & Ren 1988; Weigel, 1980). Although some authors reported that stumptail aggression only rarely escalates to serious biting (de Waal & Ren, 1988), according to others biting is as frequent as in rhesus and more frequent than in pigtails (Bernstein, 1980; Ruehlmann et al., 1988). Stumptail macaques also exhibit higher rates of proximity, contact, huddling, and grooming than rhesus and pigtails (Bernstein, 1980; Butovskaya, 1993a; de Waal & Ren, 1988; Maestripieri, 1994). The co-existence of high intragroup aggression and high cohesion in stumptail macaques could be related to the retention of supernumerary adult males in the social group for competition with other groups or protection from predators (e.g. Bertrand, 1969; Estrada et al., 1977). Stumptail males have been reported as being twice as aggressive as rhesus males and four times as aggressive as pigtail males (Ruehlmann et al., 1988). Stumptail males are also significantly larger and more aggressive than females and easily overpower them also in sexual interactions, where forced copulations are not unusual (Bernstein et al., 1983; Bertrand, 1969; Ruehlmann et al., 1988). Moreover, post-copulatory tieing with females, prolonged mate guarding, and surreptitious copulations suggest intense mating and sperm competition between stumptail males (Brereton, 1993; Estep et al., 1988).

Variation in social organization between rhesus, pigtail, and stumptail macaques should be accompanied by differences in social communication. Previous studies investigating the use of nonvocal signals in each of these three species and comparing the size of their gestural repertoire suggested that this is indeed the case (Maestripieri, 1996a, b, 1999; Maestripieri & Wallen, 1997). The present study expands the previous comparative investigation of gestural communication in rhesus, pigtail, and stumptail macaques by investigating the frequency of occurrence of nonvocal signals and their use in relation to dominance rank and social context. The findings are discussed in light of information on social organization and phylogenetic relationships between rhesus, pigtail and stumptail macaques to elucidate the adaptive significance and evolution of gestural communication in these species.

Method

All study subjects lived in social groups housed in large outdoor compounds at the Field Station of the Yerkes National Primate Research Center in Lawrenceville, Georgia (U.S.A.). Group size and composition were similar to those in the wild. The rhesus group consisted of 2 adult males and 26 adult females

with their subadult, juvenile, and infant offspring. The pigtail group consisted of 5 adult males and 28 adult females with their offspring, and the stumptail group consisted of 8 adult males and 17 adult females with their offspring. The dominance hierarchy within each group was determined on the basis of data on aggression and spatial displacements recorded during previous studies.

Each group was observed for 100 hr during an 8-month period, between August 1994 and April 1995. Data were collected during 30-min observation sessions randomly distributed between 0800 and 1900 hr. Observations were made from a tower that provided an unrestricted view of the entire compound. All data were collected by the same observer using a tape-recorder and then transferred into a computer. Data were collected with the behavior sampling method, i.e., the observer watched the whole group and recorded each occurrence of a particular type of behavior, together with other related behaviors and details of the individuals involved.

Table 1. Behavioral definitions of gestures

Gesture	Definition
Lip-Smack (LS)	Rapid opening and closing of the mouth and lips, such that when the lips close they make an audible smacking sound.
Pucker (PC)	The lips are compressed and protruded, the eyebrows, forehead and ears are retracted.
Teeth-Chatter (TC)	The mouth is rapidly opened and closed and the lips are retracted, exposing the teeth.
Bared-Teeth (BT)	The mouth is closed and the lips and lip corners are retracted so that the teeth are exposed in a white band.
Eye-Brows (EB)	The scalp and brow are retracted and the mouth is open.
Touch-Face (TF)	One hand is extended to touch the face of another individual while standing or sitting in front of it.
Touch-Genitals (TG)	Manipulation of the genitals of another individual without olfactory inspection.
Present (PR)	The tail is raised to expose the genitals.
Hip-Touch (HT)	Brief touch of the hindquarters of another individual with one or both hands without putting arms around.
Hip-Clasp (HC)	The hindquarters of another individual are clasped with both arms, usually in the sitting position.
Mount (MT)	Mount with or without foot-clasp but with no intromission or thrusts.
Present-Arm (PA)	One arm or hand is extended across the face of another individual to be bitten.
Mock-Bite (MB)	Gripping another individual's skin with the teeth, slowly, without roughness, for several seconds.
Face-Inspection (FI)	Close inspection of the face of another individual, usually staring into its eyes for several seconds, while the other individual freezes (not recorded during feeding).
Embrace (EM)	Ventral embrace with both arms around the torso of another individual, in the sitting position and kneading the partner's fur or flesh.

Fifteen facial expressions, hand gestures, and body postures (collectively referred to as gestures) were selected for observation on the basis of previous studies and preliminary observations of the study subjects. The operational definitions of these signals are presented in Table 1. Since threat and play displays such as the "staring open-mouth face" and the "relaxed open-mouth face" (van Hooff, 1967) are remarkably similar in structure and contextual usage in these species, they were not included in this comparative study. Behavioral sequences involving the signals were recorded only when the behavior preceding the signal (e.g. approach or aggression) was actually observed, and were followed until the end (e.g., when two individuals were more than 5 m apart from one another and did not further interact for 10–20 s). The occurrence of any interaction between the sender and receiver of the signal as well as the behavior of any other individuals participating in the interaction were recorded. Other behavioral interactions recorded during the observation sessions included approaches and leaves within arm's reach, contact, grooming, aggression (threats, bites, chases), avoidance, vocalizations (screams and grunts), play, and infant handling.

The occurrence of signals was compared among the three species in relation to dominance rank and various social contexts including after receiving aggression, in response to an approach or another signal, unsolicited (i.e. in conjunction with a spontaneous approach), and before an affiliative interaction such as contact, grooming or play. These contexts were selected for analysis because previous studies showed that they are often associated with communicative interactions in all three species (Maestripieri, 1996a, b; Maestripieri & Wallen, 1997).

Interspecific comparisons in the frequency of gestures were conducted with a one-way analysis of variance (ANOVA). Comparisons of the contexts of occurrence of gestures were conducted with two-way ANOVAs for repeated measures. Bonferroni-Dunn tests were used as post-hocs. All statistical tests are two-tailed. Although statistical analyses of contextual usage of gestures used data points for all individuals, data are presented in terms of percentage scores.

Results

Figure 1 shows the frequency of occurrence of all gestures in the three species. A previous analysis showed that the frequency of gestures (all gestures combined) was significantly different in the three species, being lowest in rhesus macaques, highest in stumptails, and intermediate in pigtails (Maestripieri,

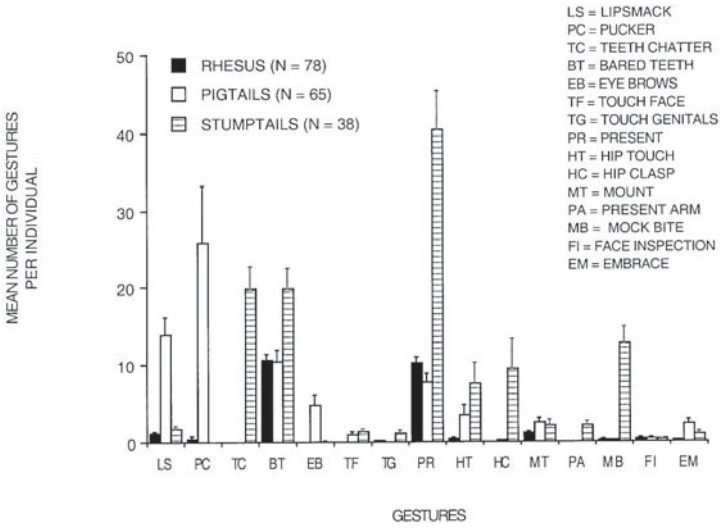

Figure 1. Mean (+ SEM) number of gestures per individual observed in the three species (Modified after Maestripieri 1999).

1999). In rhesus macaques, only 4 gestures were displayed with a frequency equal to or greater than 1 event per individual, compared to 8 gestures in pigtail macaques and 12 gestures in stumptail macaques.

Frequency of individual gestures

Lipsmack (LS), Bared-Teeth (BT), Present (PR), and Mount (MT) were frequent (≥ 1 event per individual) in all three species but their frequency of occurrence was significantly different (LS: $F_{2,178} = 28.05$, $p < 0.0001$; BT: $F_{2,178} = 10.51$, $p = 0.0001$; PR: $F_{2,178} = 57.15$, $p < 0.0001$; MT: $F_{2,178} = 3.11$, $p < 0.05$). Lip-Smack was more frequent in pigtails than in rhesus ($p < 0.0001$) and stumptails ($p < 0.0001$), whereas there was no significant difference between rhesus and stumptails. Bared-Teeth and Present were more frequent in stumptails than in rhesus ($p < 0.0001$) and pigtails ($p < 0.0001$), with no significant difference between rhesus and pigtails. Finally, Mount was more frequent in rhesus than in pigtails ($p = 0.02$), with no significant differences between rhesus and stumptails, or between pigtails and stumptails.

Hip-Touch (HT), Mock-Bite (MB), Embrace (EM), Touch-Face (TF), and Touch-Genitals (TG) were observed in all three species, but only infrequently (< 1 event per individual) in one or two species. The frequency of occurrence of these gestures was significantly different in the three species (HT:

Table 2. Interspecific comparisons in the frequency of occurrence of gestures, the extent to which they are mostly directed up or down the hierarchy and their contextual use

Gesture	Frequency	Hierarchy		Aggression	Approach	Unsolicited	Pre-affiliation	Post-Present	Pre-Mount
Lip-Smack	P > R = S	(up)	P > R = S	P > S > R	P > S > R	R = S > P	R = S > P	——	——
Bared-Teeth	S > R = P	(up)	S > R = P	R = S > P	P > R = S	S > R = P	P > R = S	——	——
Present	S > R = P	(up)	S > R = P	R > P = S	R > P = S	S > P > R	P > S > R	——	——
Mount	R > P = S	(down)	R = P = S	——	——	R = P = S	R = P > S	R = S > P	——
Hip-Touch	P = S > R	(down)	R = P = S	——	——	R = P > S	R = P = S	S > R = P	R = P > S
Mock-Bite	S > R = P	(down)	R = P = S	——	——	——	——	——	——
Embrace	P > R = S	——	R = P = S	——	——	——	——	——	——
Touch-Face	P = S > R	(up)	P = S > R	——	——	——	——	——	——
Touch-Gen.	S > R = P	——	R = P = S	——	——	——	——	——	——
Pucker	P > R = S	——							
Teeth-Chatter	S > R = P	(up)							
Present-Arm	S > R = P	(up)							
Hip-Clasp	S > R = P	(down)							
Face-Inspect	——	(down)							

R = rhesus; P = pigtails; S = stumptails

F 2,178 = 6.17, $p < 0.01$; MB: F 2,178 = 68.51, $p < 0.0001$; EM: F 2,178 = 92.88, $p < 0.0001$; TF: F 2,178 = 8.04, $p < 0.001$; TG: F 2,178 = 12.28, $p < 0.0001$). Hip-Touch and Touch-Face were more frequent in pigtails and stumptails than in rhesus (all values $p < 0.01$; no significant differences between pigtails and stumptails), Mock-Bite and Touch-Genitals were more frequent in stumptails than in rhesus ($p < 0.0001$) and pigtails ($p < 0.001$; no significant differences between rhesus and pigtails), and Embrace was more frequent in pigtails than in rhesus ($p < 0.0001$) and stumptails ($p < 0.01$; no significant difference between rhesus and stumptails).

Pucker (PC) was common in pigtail macaques, but very rare in rhesus and nonexistent in stumptails. In contrast, Teeth-Chatter (TC), Present Arm (PA), and Hip-Clasp (HC) were common in the stumptails but virtually absent in the other two species. Finally, Face-Inspect (FI) was very infrequent (< 1 event per individual) in all three species. Table 2 summarizes the results of interspecific comparisons in the frequency of occurrence of all gestures. The gestures that were virtually unique to one species, or infrequent in all species, were not statistically compared among the species. The occurrence of these gestures will be discussed on basis of data analyses reported elsewhere (Maestripieri, 1996a, b; Maestripieri & Wallen, 1997).

Effects of dominance hierarchy

Lip-Smack, Bared-Teeth, and Present were displayed by subordinates to dominants more than vice versa in all three species (LS: F 1,180 = 40.70, $p < 0.0001$; BT: F 1,180 = 161.37, $p < 0.0001$; PR: F 1,180 = 112.11, $p < 0.0001$).

The three species, however, differed significantly in the extent to which these gestures were directed up the hierarchy (LS: F 2,178 = 29.14, $p < 0.0001$; BT: F 2,178 = 8.50, $p < 0.001$; PR: F 2,178 = 47.90, $p < 0.0001$). Specifically, the proportion of Lip-Smack directed up the hierarchy was significantly higher in pigtails than in rhesus ($p < 0.0001$) and stumptails ($p < 0.0001$), with no significant difference between rhesus and stumptails. The proportion of Bared-Teeth and Present directed up the hierarchy was significantly higher in stumptails than in rhesus (BT: $p < 0.01$; PR: $p < 0.001$), and in pigtails (BT: $p < 0.01$; PR: $p < 0.001$), with no significant difference between rhesus and pigtails. Touch-Face was mostly displayed by subordinates in both pigtails and stumptails (F 1,35 = 5.97, $p < 0.05$), with no significant difference between these species. The two events observed among rhesus macaques were displayed by mothers to their newborn infants. Mount, Hip-Touch, and Mock-Bite were displayed by

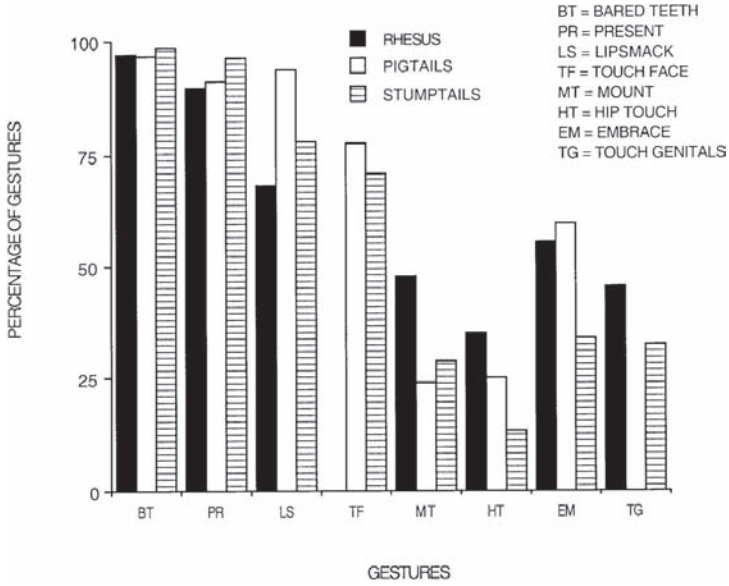

Figure 2. Percentage of gestures directed up the hierarchy in the three species. Only gestures occurring in at least two of the three species are shown.

dominants more than by subordinates in all three species (MT; F 1,134 = 9.67, $p < 0.01$; HT: F 1,108 = 6.96, $p < 0.01$; MB: F 1,50 = 16.09, $p < 0.001$) and there were no significant differences in the extent to which these behaviors were directed down the hierarchy. Embrace and Touch-Genitals occurred irrespective of dominance rank in all species. Figure 2 illustrates the percentage of gestures directed up the hierarchy (i.e. from subordinates to dominants) in the three species.

Contexts of occurrence

The occurrence of Lip-Smack, Bared-Teeth, and Present was compared in four social contexts: after receiving aggression, in response to an approach (in most cases, by a dominant individual), in conjunction with a spontaneous approach, and prior to affiliation. The first three contexts are mutually exclusive but the fourth can overlap with any of them (e.g., individuals can display a signal in response to aggression and then engage in affiliative behavior). There were significant interspecific differences in the occurrence of the three signals in the four contexts (aggression, LS: F 2,121 = 12.43, $p < 0.0001$, BT: F 2,169 = 46.46, $p < 0.0001$; PR: F 2,169 = 71.32, $p < 0.0001$; approach, LS: F 2,121 = 10.17,

$p < 0.0001$; BT: F 2,169 = 58.03, $p < 0.0001$; PR: F 2,169 = 49.05, $p < 0.0001$; unsolicited, LS: F 2,121 = 20.86, $p < 0.0001$; BT: F 2,169 = 11.50, $p < 0.0001$; PR: F 2,169 = 71.24, $p < 0.0001$; pre-affiliation, LS: F 2,121 = 14.68, $p < 0.0001$; BT: F 2,169 = 13.09, $p < 0.0001$; PR: F 2,169 = 50.29, $p < 0.0001$). Pigtails displayed Lip-Smack more frequently after receiving aggression and in response to an approach than rhesus (aggression, pigtails: 14.58%, rhesus: 1.96%, $p < 0.0001$; approach, pigtails: 26.39%, rhesus: 1.96%, $p < 0.0001$) and stumptails (aggression: 8.82%, $p < 0.01$; approach: 20.58%, $p < 0.05$). Stumptails displayed Lip-Smack in response to aggression and approach more than rhesus ($p < 0.01$). In contrast, rhesus and stumptails displayed Lip-Smack with a spontaneous approach more than pigtails (rhesus: 52.94%; pigtails: 19.59%; stumptails: 41.17%; rhesus-pigtails: $p < 0.001$, stumptails-pigtails: $p < 0.001$, rhesus-stumptails, NS). Lip-Smack was more likely to be followed by affiliation in rhesus (60.78%) and stumptails (57.35%) than in pigtails (18.04%; rhesus-pigtails: $p < 0.001$, stumptails-pigtails: $p < 0.001$, rhesus-stumptails, NS). In the pigtails, Bared-Teeth was less likely to occur after receiving aggression (41.08%), more likely to occur in response to an approach (49.23%), and more likely to be followed by affiliation (6.11%) than in rhesus (aggression: 64.76%; approach: 26.73%; affiliation: 2.18%; all p values < 0.001) and stumptails (aggression: 67.99%; approach: 20.58%; affiliation: 2.39%; all p values < 0.001). Rhesus and stumptails did not differ significantly in any of these contexts. Bared-Teeth, however, was displayed unsolicited by stumptails (3.45%) more than by rhesus (2.18%; $p < 0.05$) and pigtails (2.88%; $p < 0.05$; rhesus-pigtails, NS). Rhesus displayed Present in response to aggression (35.64%) and approach (39.16%) more than pigtails (aggression: 9.74%; approach: 20.89%; $p < 0.001$) and stumptails (aggression: 6.58%; approach: 22.96; %; $p < 0.01$; pigtails-stumptails, NS). Stumptails displayed unsolicited Present (69.73%) more than rhesus (22.32%; $p < 0.0001$) and pigtails (48.68%; $p < 0.01$). Pigtails displayed unsolicited Present more than rhesus ($p < 0.05$). In pigtails, Present was more likely to be followed by affiliation (23.93%) than in rhesus (3.13%; $p < 0.0001$) and stumptails (10.57%; $p < 0.01$). Present was more likely to be followed by affiliation in stumptails than in rhesus ($p < 0.01$).

Mount was compared in the following contexts: unsolicited (i.e, one individual approached another one and mounted him/her without any prior interactions between them), in response to Present, and before affiliation. There were no significant differences among species in the occurrence of unsolicited Mount (rhesus: 17.86%; pigtails: 18.18%; stumptails: 20.51%), but species differed significantly in the proportion of Mount that occurred in response to

Present (F 2,83 = 8.46, $p < 0.001$) and prior to affiliation (F 2,83 = 6.02, $p < 0.01$). Specifically, rhesus and stumptails were more likely to display Mount in response to Present (rhesus: 58.33%; stumptails: 51.28%) than pigtails (33.33%; $p < 0.01$; rhesus-stumptails, NS), and in rhesus and pigtails Mount was more likely to be followed by affiliation (rhesus: 30.95%; pigtails: 33.33%) than in stumptails (5.13%; $p < 0.01$; rhesus-pigtails, NS).

Hip-Touch differed among species in the extent to which it was displayed unsolicited (F 2,74 = 7.69, $p < 0.001$) or in response to Present (F 2,74 = 4.86, $p = 0.01$). Hip-Touch also differed in the extent to which it was followed by Mount (F 2,74 = 3.98, $p < 0.05$) but not by affiliation. Hip-Touch was more frequently unsolicited in rhesus (64.86%) and pigtails (88.39%) than in stumptails (19.50%; $p < 0.001$), and occurred more frequently in response to Present in stumptails (64.18%) than in rhesus (27.02%; $p < 0.05$) and pigtails (8.48%; $p < 0.01$). In rhesus and pigtails, Hip-Touch was also followed by Mount (rhesus: 16.21%; pigtails: 19.19%) more frequently than in stumptails (4.96%; $p < 0.05$).

The frequency of Mock-Bite, Embrace, Touch-Face and Touch-Genitals was too low in some species for a quantitative contextual analysis. Mock-Bite was often displayed after attacking another individual (rhesus: 40%; pigtails: 35.71%; stumptails: 57.20%) and often followed by Bared-Teeth. Embrace was mostly displayed by females (rhesus: 66.67%; pigtails: 97.43%; stumptails: 84.21%) and was often followed by huddling or grooming (rhesus: 77.78%; pigtails: 71.79%: stumptails: 42.10%). Touch-Face was often displayed in conjunction with facial expressions such as Bared-Teeth, Lip-Smack, Pucker, or Teeth-Chatter (rhesus: 100%; pigtails: 79.68%: stumptails: 82.69%). Touch-Genitals was mostly exchanged between males (rhesus: 100%; pigtails: 100%: stumptails: 74.42%).

Species-specific or infrequent gestures

Pucker was the most frequent gesture observed in pigtail macaques. Pucker was never observed among stumptails and only on a few occasions among rhesus. In pigtails, Pucker was displayed by both males and females independent of their dominance rank and in a variety of social contexts, including mating, grooming, and interactions with infants. Eye-Brows was also unique to pigtail macaques, where it was frequently exchanged between males, irrespective of their dominance rank, in conjunction with approach-retreat interactions, Hip-Touch, grunts, and occasionally brief bouts of play. Eye-Brows occurred in conjunction with agonistic support and was often followed by affiliation.

Teeth-Chatter, Present Arm, and Hip-Clasp were virtually unique to stumptail macaques. Teeth-Chatter was mostly directed up the hierarchy and often associated with Hip-Touch, Hip-Clasp, Mount and Embrace between females. Present-Arm was mostly displayed by subordinates and followed by Mock-Bite by dominants. Hip-Clasp was mostly displayed by the alpha male, and occurred in contexts similar to those of Hip-Touch, and primarily in response to Present. Unlike Hip-Touch, most Hip-Clasp was directed to juveniles and infants who solicited this behavior in the presence of an external threat to the group or during disputes with other juveniles. Face-Inspect occurred with a frequency lower than 1 event per in individual in all three species and was typically displayed by dominants after they approached subordinates. It elicited freezing in the subordinate or a submissive signal such as Bared-Teeth.

Discussion

Several main findings emerge from this comparative study of gestural communication in macaques. First, the gestural repertoire of rhesus macaques is generally poor in comparison to that of pigtail macaques, and especially that of stumptail macaques. Rhesus macaques exhibit fewer signals and use some of them with a lower frequency than the other species (Maestripieri, 1999). Second, most communication in these three species appears to revolve around issues of dominance and submission (Maestripieri, 1996a, b; Maestripieri & Wallen, 1997). Third, most similarities in the gestural repertoires of rhesus, pigtail and stumptail macaques were found in submissive and assertive signals and the greatest variability in communicative patterns related to affiliation and bonding. Even among the submissive and assertive signals, however, there are quantitative differences among the species, as submissive and assertive signals were more numerous and more frequent among stumptails than among rhesus and pigtails.

Bared-Teeth, Present, and Lip-Smack were among the most frequent signals occurring in the three species and, in all species, they were strictly directed up the hierarchy. In contrast, Hip-Touch and Mount (and in the stumptails also Mock-Bite) were generally directed down the hierarchy. Other gestures, which were limited to one or two species and did not have a clear relationship with dominance, were Pucker, Embrace, and Touch-Genitals.

In rhesus macaques Bared-Teeth and Present were mainly displayed in response to aggression or an approach by a dominant individual and rarely

followed by affiliation. Although rhesus macaques have few affiliative signals relative to the other species, Lip-Smack appears to have a stronger affiliative component in rhesus than in the other species, as this signal was often unsolicited and followed by affiliation. In pigtail macaques, Bared-Teeth and Present occurred in contexts similar to those of rhesus and stumptails, but they were more frequently followed by affiliation. In pigtails, however, the contextual use of Lip-Smack was more similar to that of Bared-Teeth and Present than in the other species. Pucker was the most frequent gesture observed in pigtail macaques. Previous studies showed that Pucker is used to coordinate and facilitate the occurrence of mating, grooming, and interactions with infants (Maestripieri, 1996a; see also Jensen & Gordon, 1970). Pigtail macaques also exhibit frequent bonding patterns such as Embrace and Eye-Brows. In stumptail macaques, Bared-Teeth and Present were very frequent, mostly unsolicited, and strongly directed up the hierarchy, suggesting that they serve an appeasing function. Stumptail macaques possess further submissive gestures such as Present-Arm, Teeth-Chatter, and Touch-Face. Furthermore, in this species, Mount was more likely to occur in response to Present and less likely to be followed by affiliation than in the other species, suggesting that this behavior, along with Hip-Touch, has a strong assertive component. Stumptail macaques also have bonding patterns such as Embrace, Hip-Clasp, and Touch-Genitals, some of which may serve a reassurance or protection function.

It may be argued that whereas the richness of the dominance/ submission communicative repertoire reflects the potential for competition and conflict within groups, affiliative signals and bonding patterns probably reflect the need for intragroup cohesion and cooperation for defense against predators or competition with other groups. In a despotic and nepotistic society like that of rhesus macaques there may be little pressure to develop a sophisticated system of affiliative signals and bonding patterns. Maintenance of group structure and coordination of behavior between individuals can be effectively achieved if a few unequivocal indicators of differences in dominance are recognized and if unrelated or distantly-ranked individuals simply avoid each other (Maestripieri, 1999). In pigtail macaques, instead, complex dynamics of intragroup cooperation and high levels of social tolerance appear to have led to the evolution of intense affiliative communication and bonding patterns. The variety of assertive and submissive signals observed in stumptail macaques suggests a great potential for intraspecific conflict. Communication of dominance and submission, however, is also frequently accompanied by expressions of reassurance and bonding, suggesting the need for intragroup cohesion and cooperation.

Submissive signals such as Bared-Teeth and Present are remarkably similar in rhesus, pigtail, and stumptail macaques suggesting that these signals (probably along with threat displays, the play-face, Lip-Smack, and Mount) were present in the ancestor of these species. In fact, these signals also appear in most, if not all, of the other African *Cercopithecidae* (Andrew, 1963; van Hooff, 1967; Redican, 1975). Pucker is a common gesture in pigtail and liontail macaques (*Macaca silenus*; Lindburg et al., 1985; Johnson, 1985) but rare in rhesus and longtail macaques (*Macaca fascicularis*; Shirek-Ellefson, 1972) and absent in the stumptails, suggesting that it may be a relatively ancestral signal that has been conserved in the *silenus* group but partially lost in other species. Ventro-ventral Embrace has been reported in species of all four phyletic groups of macaques (Thierry, 1984), and especially in the *silenus* group (Dixson, 1977; Skinner & Lockard, 1979; Thierry, 1984) and in *Macaca fascicularis* (Shirek-Ellefson, 1972), which is closely related to rhesus macaques. It seems likely, therefore, that Embrace is a relatively ancestral pattern that has become very infrequent in rhesus macaques. Finally, Teeth-Chatter has been reported in Barbary macaques (*Macaca sylvanus*; van Hooff, 1967), which are believed to be the most ancestral macaque species, and in macaque species of the *sinica* group (e.g. bonnet, Tibetan, and assamese macaques), which are probably closely related to stumptail macaques (Fooden, 1980). This suggests that Teeth-Chatter evolved relatively early in macaques, was retained in Barbary macaques and species of the *sinica* group including stumptail macaques, and was lost in other species such as pigtail and rhesus. Different macaque species, however, may have independently evolved Teeth-Chatter from other signals such Bared-Teeth and Lip-Smack (see van Hooff, 1967).

Signals such as Eye-Brows, Teeth-Chatter, Hip-Clasp, Present-Arm, and Mock-Bite may have evolved independently in some macaque species. Eye-Brows has also been reported in *Macaca silenus* (Johnson, 1985; Skinner & Lockard, 1979), suggesting that it may have evolved independently species of the *silenus* group. Hip-Clasp and especially Present-Arm and Mock-Bite are behavior patterns virtually unique to stumptail macaques. Hip-Clasp and perhaps also Touch-Genitals between stumptail adults probably develop from ritualized interactions between adults and infants in which adults lift the infant's hindquarters and hold them briefly while manipulating the infant's genitals and teeth-chattering (this interaction has been referred to as "bridging"; Bertrand, 1969; see Ogawa, 1995, for *Macaca thibetana*).

In conclusion, this study suggests that the similarities and differences in the gestural repertoires of rhesus, pigtail, and stumptail macaques can be related to

the intragroup social dynamics of these species as well as to their evolutionary history. Future studies should extend the comparison of communication patterns to other species of macaques and discuss their findings in relation to the phylogeny and social evolution of this primate genus.

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