

GESTURAL COMMUNICATION AND ITS COGNITIVE IMPLICATIONS IN PIGTAIL MACAQUES (*MACACA NEMESTRINA*)

by

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Summary

The aims of this study were to identify the context of occurrence of some of the most prominent gestural signals in pigtail macaques and discuss the cognitive implications of some communicative interactions observed in this species. The occurrence of 15 selected visual and tactile behavior patterns in a multi-male multi-female captive group of pigtail macaques was recorded with the behavior sampling method in 100 h of observation. Bared-teeth, presentation, and lip-smack were primarily submissive signals displayed by both males and females, whereas nonthrusting mounts appeared to reflect dominance. Vento-ventral embracing and eyebrow displays were used as affiliative and bonding patterns between females and between males, respectively. The pucker was the most frequent signal observed in the group. Although the pucker occurred in several different contexts, in most cases this signal served a distance-reducing or summoning function. Gestural signals appeared to be used by pigtail macaques to communicate emotional states and intentions to other individuals as well as to request the participation of other individuals in specific social interactions.

Introduction

In recent years, there has been a growing interest in the study of social communication in nonhuman primates (Cheney & Seyfarth, 1990; King,

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1994). This interest has been stimulated by evidence that primates can communicate information about their social and physical environment in addition to emotional states or arousal (Gouzoules *et al.*, 1995). In recent years, there has also been a dramatic change in the approach to primate social communication. Until the late 1970s, the study of primate social communication, in particular in Old World monkeys and apes, was primarily concerned with visual displays, such as facial expressions and postures (Darwin, 1872; Andrew, 1963; Hall & DeVore, 1965; van Hooff, 1967; van Lawick-Goodall, 1972; Shirek-Ellefson, 1972; Redican, 1975). For example, Altmann (1967) estimated that only 5.1% of all signals by rhesus macaques (*Macaca mulatta*) included or consisted entirely of a vocalization. In the 1980s and 1990s, the emphasis of research has shifted to vocal communication, primarily because of the development of sophisticated technology for analysis of calls. For example, of the 21 research articles on primate social communication published by the journal *Animal Behaviour* from January 1990 to August 1995, 19 (90.47%) focus on vocalizations.

Although we possess an accurate description of the gestures displayed by several species of nonhuman primates (Darwin, 1872; Altmann, 1962; Hinde & Rowell, 1962; van Hooff, 1962, 1967; Andrew, 1963; Kaufman & Rosenblum, 1966; van Lawick-Goodall, 1972; Redican, 1975; Marriott & Salzen, 1978; Weigel, 1979), we know relatively little about the meaning of gestural signals. In fact, very few quantitative analyses of social communication in primates have been conducted, in which the most frequent signals in the gestural repertoire are analyzed and compared in terms of their context of occurrence and responses elicited (but see Kirkevold *et al.*, 1982; Preuschoft, 1992; Tomasello *et al.*, 1994).

The purpose of this study was to conduct a comprehensive analysis of some of the most common gestural (visual and tactile) signals in an Old World monkey, the pigtail macaque (*Macaca nemestrina*), whose rich gestural communicative repertoire has long been recognized (Cole, 1963; Bobbitt *et al.*, 1964; Kaufman & Rosenblum, 1966; Goosen & Kortmulder, 1979). For example, Goosen & Kortmulder (1979) recorded 19 different facial expressions in this species, to their knowledge the highest number ever published for any monkey species. Most of these expressions, however, were variations of some basic types.

Interest in pigtail macaque gestural communication has mostly concentrated on a single conspicuous facial expression, the *pucker* or *pucker face* (Bernstein, 1967; also referred to as *flehmen face*: van Hooff, 1962; *len*: Bobbitt *et al.*, 1964; *protruded lips face*: van Hooff, 1967; and *jaw thrust*: Kaufman & Rosenblum, 1966), which is frequently displayed in this species but only rarely observed in other primates (in rhesus macaques: van Hooff, 1967; in liontail macaques, *Macaca silenus*: van Hooff, 1967; in longtail macaques, *Macaca fascicularis*: Shirek-Ellefson, 1972).

Although the pucker has been the object of several investigations, the meaning of this signal is not clear. The best evidence available so far concerns the occurrence of the pucker in mother-infant interactions, where mothers use this signal to encourage their infants to follow (Jensen & Gordon, 1970; Castell & Wilson, 1971; Jensen *et al.*, 1973; Bolwig, 1980; Maestriperi, 1996). In interactions other than those between mothers and infants, however, the pucker was hypothesized to communicate different information according to age, sex, and social context (Caldecott, 1986).

Adult males have been observed to pucker to sexually receptive females while approaching them or during a genital inspection (van Hooff, 1962; 1967; Tokuda *et al.*, 1968; Christopher & Gelini, 1977; Goosen & Kortmulder, 1979; Caldecott, 1986), perhaps to induce them to present and facilitate copulation (van Hooff, 1967). After genital inspection of a female, the males may show the pucker while tilting their head upwards and gazing in the air suggesting to some observers a careful tasting of the smell (Schneider, cited by van Hooff, 1967, p. 57). The pucker has also been observed to precede affiliative interactions and thought to serve a distance-reducing function (Bobbitt *et al.*, 1969; see also Shirek-Ellefson, 1972, for longtail macaques). Caldecott (1986) noted that adult males puckered to juvenile males causing them to retreat, suggesting that the pucker may function as a threat. According to Christopher & Gelini (1977), a large number of puckers are apparently nonsocial, *i.e.* not directed toward another animal. These authors also suggested that male and female puckers are morphologically distinct and serve different functions: the male pucker serves to facilitate sexual receptivity in the female, whereas female puckers often precede aggression. However, Christopher & Gelini (1977) also suggested that the pucker may simply be an indicator of tension. The hy-

pothesis that the pucker may convey information to other individuals not involved in the interaction (*e.g.* an indication not to interfere) has also been put forward (Goosen & Kortmulder, 1979). Pigtail macaques frequently pucker to humans, and Bertrand (1976) reported that a hand-reared pigtail macaque used the pucker to request to be let out to urinate.

Unfortunately, none of the above-reported hypotheses concerning the meaning of the pucker was tested with or supported by convincing quantitative analyses. Moreover, the usage and meaning of the pucker were rarely investigated in relation to the occurrence of other signals in the pigtail macaques' repertoire. This analysis seems necessary also in light of recent studies of vervet monkey (*Cercopithecus aethiops*) vocal communication, indicating that the usage and meaning of vocalizations are best defined and understood in relation to the usage and meaning of other calls within the animals' repertoire (Cheney & Seyfarth, 1990).

Here I present a comparative analysis of the pucker and other gestural signals in pigtail macaques. The aims of this analysis are to characterize some of the most prominent signals in the pigtail macaque communicative repertoire, the most common social contexts, and the similarities and differences in usage of different signals. In particular, I discuss the meaning of pigtail macaque gestural signals and the cognitive implications of some communicative interactions observed in this species.

Methods

Subjects and housing

Subjects of this study were pigtail macaques living in a captive 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 (USA). The group consisted of 5 adult males, 9 juvenile males, 28 adult females, 23 juvenile females, and 13 yearlings and 7 infants of both sexes. All monkeys were fed early in the morning with monkey chow, and were fed for a second time in the afternoon with fresh fruit or vegetables. Water was freely available.

Data collection

The group was observed for 100 h from September 1994 to April 1995. Data were collected during 30-min observation sessions randomly distributed between 08:00 and 19:00 h. Observations were made from a platform which 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. Pilot observations showed a good consistency (more than 90%)

of the behaviors scored by the observer who collected the data and those scored by another observer.

Data were collected with the behavior sampling method (Martin & Bateson, 1986). Behavior sampling means that the observer watches the whole group of subjects and records each occurrence of a particular type of behavior, together with other related behaviors and details of the individuals involved. Behavioral sequences involving selected gestural 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 2 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. Observations included all individuals older than 1 year as actors or recipients ($N = 65$; 14 males; 51 females). Particular effort was made to avoid sampling specific individuals or classes of individuals preferentially because of their conspicuous physical appearance or activity patterns. Because data collected with the behavior sampling method would not be appropriate to estimate the rate at which specific individuals participated in specific communicative interactions, the analyses in this paper focus primarily on comparisons between sex-rank classes of individuals.

Behavioral definitions

The behavior sampling method was used to record the occurrence of 15 different gestural signals (see Table 1 for definitions). These behaviors were selected on the basis of a 3-year observational study of pigtail, rhesus, and stumptail macaques (*Macaca arctoides*) and represent behavior patterns that had been observed in at least one of the three species, although most were common to all three species. Other behaviors recorded included approaches and leaves within arm's reach, contact, grooming, aggression (threats, bites, chases), avoidance, vocalizations (screams and grunts), play, and infant handling. The dominance rank of all individuals in the group was assessed on the basis of data on aggression and spatial displacements that were collected prior to the beginning of this study.

Data analyses

The exchange of different gestures was first analyzed in relation to sex and dominance rank of the individuals involved to detect similarities and differences in the overall distribution of these behaviors in the social group. Then, the context of occurrence of signals with a similar sex and rank distribution was further compared to detect subtle differences in the usage and meaning of signals. In these analyses, the effect of rank concerns differences in dominance between individuals involved in dyadic interactions and not the individuals' position in the group's dominance hierarchy. The following main contexts of occurrence of gestures were considered: approach or withdrawal, contact, grooming, aggression, mating, play, infant handling, and other gestures.

The distributions of gestures among sex/rank classes of individuals were compared with the principal components analysis (Norusis, 1985). The principal components analysis is a statistical technique used to identify a relatively small number of factors, or principal components, that can be used to represent relationships amongs sets of many variables. The assumption of this analysis is that correlations between variables result from their

sharing these factors. In principal components analysis, linear combinations of the observed variables are formed. The first factor is the combination that accounts for the largest amount of variance in the sample. The second factor accounts for the next largest amount of variance and is uncorrelated with the first. Successive factors explain progressively smaller portions of the total variance, and are all uncorrelated with each other. Factor loadings are coefficients of correlation between the factors and the variables and, usually, only loadings greater than +0.50 or less than -0.50 are considered statistically significant. Eigenvalues are the sums of the squares of the factor loadings and reflect the total variance explained by each factor. To determine the number of factors considered in the analysis, only factors whose eigenvalue is greater than 1 are included. Since the factors are uncorrelated, the total proportion of variance explained is just the sum of the variance explained by each factor.

The distributions of different gestures across sex/age classes of individuals and in relation to their context of occurrence were analyzed with the analysis of variance (ANOVA) for repeated measures. Since the analysis was conducted at the level of the interaction and not of the individual, the same individuals contributed more than once to the dataset, thus violating one of the assumptions underlying chi-squared and related tests. ANOVA is usually recommended in these circumstances (Kramer & Schmidhammer, 1992). ANOVA's *F* and *p*-values refer to interaction effects only (behavior \times other variable, e.g. sex, rank, or context). This is because the goal of this analysis was not to assess differences in frequency of gestures regardless of context and individual characteristics or the main effects of sex, rank, or context on the total frequency of gestures. Rather, the interest was in assessing whether sex, rank and context of occurrence affected gestures in different ways. Bonferroni-Dunn tests were used as *post-hocs*. Correlations were calculated with the Pearson's coefficient of correlation (*r*). Student's *t*-tests were used for matched-pairs comparisons.

Results

The total number of observed events for the 15 selected behaviors is reported in Table 1. Pucker, Lip-Smack and Bared-Teeth were the three most common behaviors observed in the group, accounting for 35.4%, 19.2%, and 14.2%, respectively, of all observed gestures. Teeth-Chatter and Present-Arm were never observed, and Touch-Genitals, Hip-Clasp, and Mock-Bite were each observed less than 15 times. Eighty-six PC, 11 LS, and 3 PR were displayed by mothers to their newborn babies. Because the occurrence of PC between mother and infant has been analyzed in detail elsewhere (Maestriperi, 1996), and because LS and PR were too infrequent to be analyzed, data analysis focused on all social interactions other than mother-infant interactions.

For analysis purposes, the 9 behavior patterns displayed more than 30 times to identifiable recipients (PC, LS, BT, PR, EB, HT, MT, EM, TF) were grouped into categories depending on the sex and dominance

TABLE 1. Behavioral definitions of gestural signals and total number of gestures observed in the study period

Behavior and Code	Definition	Events
Pucker (PC)	The lips are compressed and protruded, the eyebrows, forehead and ears retracted.	1679
Lip-Smack (LS)	Rapid opening and closing of the mouth and lips, such that when the lips close they make an audible smacking sound.	909
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.	675
Present (PR)	The tail is raised to expose the genitals.	496
Eye-Brows (EB)	The scalp and brow are retracted and the mouth is wide open.	309
Hip-Touch (HT)	Brief touch of the hindquarters of another individual with one or both hands without putting arms around.	224
Mount (MT)	Mount with or without foot-clasping but with no intromission or thrusts.	167
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. Unidirectional or mutual.	156
Touch-Face (TF)	One hand is extended to touch the face of another individual while standing or sitting in front of it.	64
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).	28
Hip-Clasp (HC)	The hindquarters of another individual are clasped with both arms, usually in the sitting position.	14
Mock-Bite (MB)	Gripping another individual's skin with the teeth, slowly, without roughness, for several seconds.	14
Touch-Genitals (TG)	Manipulation of the genitals of another individual without inspection.	1
Present-Arm (PA)	One arm or hand is extended across the face of another individual to be bitten.	0
Teeth-Chatter (TC)	The mouth is rapidly opened and closed as for LS, but the lips are retracted, exposing the teeth.	0

rank of the sender and the receiver (Table 2). Eighty-six BT were not included in Table 2 and in the analysis because they were not directed to any specific individual, being displayed by adult males during mounts with ejaculation (81) or by females after receiving aggression (5).

The distributions of PC, LS, BT, PR, EB, HT, MT, EM, and TF across sex/rank categories were analyzed with the principal components analysis. The analysis identified 4 factors which accounted for 91.5% of the total variance. Table 3 shows loadings and eigenvalues for these factors. In Factor 1, BT had the highest positive loading followed by PR and LS. MT, PC, HT, and EB were loaded negatively into this factor. LS, BT, and PR were all displayed by subordinates to dominants significantly more than *vice versa* (*t*-test for paired samples, BT: $t = 7.39$, $df = 62$, $p < 0.0001$; PR: $t = 5.21$, $df = 62$, $p < 0.0001$; LS: $t = 5.88$, $df = 62$, $p < 0.0001$; the alpha-male and the omega-female were excluded from this analysis because they had no individuals ranking higher and lower, respectively, than themselves). In contrast, MT (but not PC, HT, and EB) was displayed by dominants to subordinates significantly more than *vice versa* (*t*-test for paired samples, $t = -2.65$, $df = 62$, $p = 0.01$). Therefore, Factor 1 was labeled *Dominance/Submission*. In Factor 2, EM had the highest positive loading followed by LS, TF and PC. Because 97.4% of Embraces occurred between females and were initiated by both lower-ranking (53.5%) and higher-ranking (34.9%) females, Factor 2 was labeled *Female Affiliation*. In Factor 3, HT had the highest positive loading followed by PC. Because 62.5% of HT occurred between males and females and because 24.4% of male-female HT and 30% of male-female PC were followed by a mount (see below), the factor was labeled *Sexual Communication*. EB was the only behavior loaded positively in Factor 4, and EM was loaded negatively into this factor. Because EB frequently occurred between males irrespective of their dominance rank (see below) and because EM was mostly displayed by females, Factor 4 was labeled *Male Affiliation*.

Analysis of Factor 1, Dominance/Submission

The distributions of Lip-Smack, Bared-Teeth, and Presentation according to sex and rank of the individuals were compared to one another within each sex/rank category. ANOVA revealed significant differences between LS, BT, and PR only for female-female interactions in relation to rank

TABLE 2. Occurrence of the 9 most frequently displayed signals in relation to sex and dominance rank of sender and receiver

Sex of sender/receiver	Rank of sender/receiver	PC	LS	BT	PR	Behaviors					TF
						EB	HT	MT	EM	TF	
M-F	S-D	60	13	11	17	21	11	7	0	2	
	D-S	660	4	3	4	54	128	27	3	3	
M-M	S-D	27	264	74	90	53	30	13	1	29	
	D-S	6	6	0	14	53	9	25	0	2	
F-M	S-D	95	240	327	270	25	1	0	0	3	
	D-S	7	10	14	7	14	0	9	0	0	
F-F	S-D	400	325	157	72	17	14	21	92	14	
	D-S	338	36	3	19	72	31	62	60	9	
Total		1593	898	589	493	309	224	164	156	62	

M = male; F = female; D = dominant; S = subordinate.

TABLE 3. *Principal Components factor loadings of sex- and rank-related distributions of PC, LS, BT, PR, EB, HT, MT, EM and TF*

Factor 1 Dominance/Submission	Factor 2 Female Affiliation	Factor 3 Sexual Communication	Factor 4 Male Affiliation
BT = 0.84*	EM = 0.74*	HT = 0.60*	EB = 0.51*
PR = 0.82*	LS = 0.68*	PC = 0.59*	TF = 0.45
LS = 0.69*	TF = 0.65*	BT = 0.32	HT = 0.32
TF = 0.15	PC = 0.57*	PR = 0.27	PR = 0.22
EM = -0.09	MT = 0.43	LS = -0.07	LS = 0.05
PC = -0.53*	BT = 0.34	EB = -0.18	BT = -0.00
HT = -0.65*	EB = 0.32	EM = -0.19	MT = -0.14
EB = -0.66*	PR = 0.26	MT = -0.26	PC = -0.17
MT = -0.76*	HT = 0.25	TF = -0.46	EM = -0.63*
Eigenvalues (% variance)			
3.61 (40.10)	2.29 (25.50)	1.25 (13.90)	1.07 (12.00)

* Asterisks indicate behaviors with high loadings (absolute values > 0.5).

($F_{2,150} = 10.85$, $p < 0.0001$), with PR being more frequently directed down the hierarchy than BT ($p < 0.01$). The distributions of LS, BT, and PR did not differ significantly for male-female ($F_{2,39} = 0.36$, NS), male-male ($F_{2,39} = 2.62$, NS), and female-male ($F_{2,150} = 0.49$, NS) interactions in relation to rank.

LS, BT, and PR were further compared in relation to their most common contexts of occurrence. ANOVA revealed significant differences between LS, BT, and PR in most of the contexts considered (see Table 4 for F values). BT was more likely to occur in response to an approach and to aggression than PR and LS ($p < 0.001$); PR and LS did not differ significantly in these contexts. PR was most likely and BT least likely to be displayed in conjunction with a spontaneous approach to another individual, when this approach was unrelated to previous aggression ($p < 0.01$). However, LS was more likely to occur in conjunction with an approach following aggression than BT and PR ($p < 0.05$). In other words, while individuals displayed LS, BT, and PR soon after receiving aggression and usually while retreating or avoiding the aggressor, victims of aggression often subsequently re-approached the aggressor displaying LS but not BT or PR. BT was directed to the former aggressor in all but 5 cases, in which the victim did not address the display to any individual

TABLE 4. Contextual comparisons of LS, BT and PR in relation to behaviors that occur before, during, or after the signal

Context of occurrence	LS	BT	PR	F and p-values for comparisons*
Total N	898	594	493	
% Response to Approach	26.4	48.8	20.9	$F_{2,171} = 15.21$ $p < 0.0001$
% Response to Aggression	14.6	40.7	9.7	$F_{2,171} = 11.78$ $p < 0.0001$
% After Spontaneous Approach	19.6	2.8	48.7	$F_{2,171} = 21.72$ $p < 0.0001$
% Approach after Aggression	16.4	0.0	0.0	$F_{2,171} = 4.12$ $p < 0.05$
% Response to Pucker	0.8	0.0	16.4	$F_{2,171} = 6.54$ $p = 0.001$
% Followed by Contact/Grooming/Play	18.0	6.0	23.9	$F_{2,171} = 3.95$ $p < 0.05$
% Followed by Mount	1.0	24.9	0.4	$F_{2,171} = 9.71$ $p = 0.0001$
% Followed by other Gestures	1.1	4.2	21.7	$F_{2,171} = 6.54$ $p = 0.001$

* p-values for *post-hoc* tests are reported in Results.

in particular. Finally, PR was more likely to be displayed in response to PC by another individual than both BT and LS ($p < 0.01$).

LS and PR were more likely to be followed by affiliation (contact, grooming or play) than BT ($p < 0.05$). PR was more likely to be followed by a mount (with or without intromission and thrusts) than BT and LS ($p < 0.001$). LS was more likely to be followed by other gestures such as LS, PC, BT, EB, PR or HT, than BT and PR ($p < 0.01$). Therefore, while LS and PR were sometimes followed by affiliation, mounts or other communicative interactions, BT was rarely followed by any other social interaction.

LS, BT, and PR occurred relatively infrequently in contexts other than those considered in the above-reported analyses. 12% of BT occurred during male-female mount with ejaculation (often accompanied by squeak vocalizations), and 13.1% and 5.8% of LS were displayed by individuals while grooming or being mounted, respectively. 3.8% of BT and 1.6% of LS events occurred in response to aggression received by kin from a higher-ranking individual (usually a mother displayed BT or LS to an individual who had just attacked her offspring). About 2% of PR occurred during play and as 'protected-threat' (Wickler, 1967), that is were displayed by one individual to a second individual while simultaneously threatening a third individual.

The Mount without intromission or thrusts was negatively loaded in Factor 1 and was significantly directed down the hierarchy (see above). MT was displayed by both males and females in interactions with individuals of the same and different sex (see Table 2). MT occurred more frequently in male-female and male-male interactions than in female-male interactions ($F_{3,126} = 5.31$, $p = 0.001$; *post-hoc* tests, $p < 0.05$); the differences with female-female interactions were not statistically significant (*post-hoc* test, NS). MT occurred in various contexts such as after spontaneously approaching another individual, along with other gestures including PC, LS, BT, EB, HT, PR, and after aggression. In most cases, MT was either followed by no interaction (32.3%) or by grooming (31.7%).

Analysis of Factor 2, Female Affiliation

Embrace was the behavior pattern with the highest loading value in Factor 2, and occurred mostly between females (see Table 2). 68% of female

EM was mutual. Embracing was mostly preceded by Pucker by one or both females (82%), and followed by grooming (71.8%; grooming was mutual in 33% of cases). Because EM was mostly a female behavioral characteristic, the analysis of this affiliative behavior in relation to the other gestures loaded into Factor 2, namely TF, PC, and LS, focused on female-female interactions. ANOVA revealed significant differences between EM, TF, PC, and LS for female-female interactions in relation to rank ($F_{3,199} = 5.09$, $p = 0.002$), with LS being more frequently directed up the hierarchy than EM, TF, and PC ($p < 0.01$).

Most TF (about 90%) between females occurred immediately before or simultaneously with Lip-Smack and Pucker to other females. Therefore, the analysis of female gestures associated with EM focused on a comparison of LS and PC. LS was more likely to occur in response to aggression (LS = 32.9%, PC = 0.3%; $F_{1,90} = 31.99$, $p < 0.0001$) and to an approach than PC (LS = 22.7%, PC = 6.7%; $F_{1,90} = 18.48$, $p < 0.001$). The proportion of LS and PC occurred in conjunction with a spontaneous approach to another individual was not significantly different (LS = 17.2%, PC = 33%; $F_{1,90} = 0.05$, NS). PC was more likely to occur in response to another PC than LS (LS = 1.9%, PC = 19.1%; $F_{1,90} = 5.01$, $p < 0.05$). PC was also more likely to be displayed when a female was sitting at a distance (from 1-2 m up to 20-25 m) from another female (LS = 1.7%, PC = 12%; $F_{1,90} = 4.98$, $p < 0.05$) or when a female turned around and moved away from another female than LS (LS = 0%, PC = 12.1%; $F_{1,90} = 4.49$, $p < 0.05$). In 83% of cases of PC being displayed by a female sitting at a distance or turning around and moving away ($N = 178$), the receiver of the signal immediately approached or followed the sender, in 34.4% of cases after having displayed the PC herself. These sequences were accompanied by one of these 3 events: 1) the receiver of the first PC initiated grooming with the sender; 2) the two females negotiated the initiation of grooming with grooming solicitations, *i.e.*, by lying down or exposing the part of the body to be groomed; 3) the two females embraced and engaged in mutual grooming.

Overall, PC was more likely to be followed by affiliation (contact and grooming, with or without EM) than LS (LS = 17.1%, PC = 69.6%; $F_{1,90} = 79.31$, $p < 0.0001$). When a female displayed PC while approaching another female, in 50% of cases she proceeded to make contact

and initiate grooming with her immediately after the display of the signal, whereas in 33% of cases she initiated affiliation after the second female responded with PC. LS was more likely than PC to be followed by other facial expressions and gestures including BT, PR, HT, and MT (LS = 24.6%, PC = 12.1%; $F_{1,90} = 12.08$, $p < 0.001$). Finally, PC was more likely to precede an episode of infant handling than LS (LS = 2.7%, PC = 19.1%; $F_{1,90} = 4.12$, $p < 0.05$). In other words, females often approached a new mother displaying PC and subsequently briefly touched or groomed the infant. The alpha female, however, often attempted to pull infants away from their mothers after having approached and displayed PC. When the mother resisted the kidnapping attempt, the alpha female displayed PC again to the mother and embraced and groomed her.

Analysis of Factor 3, Sexual Communication, and of sex differences in the usage of the pucker

The two behavior patterns loaded positively into Factor 3 were HT and PC and they were displayed by both males and females. Males displayed most PC (95.6%) and HT (78.1%) towards females. PC between males was mostly displayed by juveniles during chase play (90.9%). Females displayed most PC (87.8%) and HT (97.8%) towards other females. Male-female PC and HT were highly correlated ($r = 0.96$, $N = 14$, $p < 0.0001$), but that was not the case for female-female PC and HT ($r = 0.16$, $N = 51$, NS). These analyses suggest that the significant association between the distributions of PC and HT highlighted by the principal components analysis probably reflected the occurrence of PC and HT in male-female interactions, hence the label Sexual Communication for Factor 3.

Because males often used PC for mating-related interactions whereas females used PC for affiliative purposes (see analysis of Factor 2), a question arises as to whether this signal is used with a different meaning by males and females. To address this question, the occurrence of PC in male-female (MF) and female-female (FF) interactions was compared. PC was never displayed in response to aggression in MF interactions and only twice in FF interactions. PC was more likely to be displayed in response to an approach in FF than in MF interactions (MF = 0.5%, FF = 6.7%; $F_{1,57} = 4.80$, $p < 0.05$). The proportion of PC occurred in conjunction with a spontaneous approach was not significantly different in FF and MF

interactions (MF = 48.7%, FF = 33%; $F_{1,57} = 3.00$, NS). PC was more likely to be displayed in response to another PC in FF than in MF interactions (MF = 0%, FF = 19.1%; $F_{1,57} = 5.89$, $p = 0.01$). The proportion of PC displayed while sitting at a distance from another individual or while moving away from her did not differ significantly in FF and MF interactions (sitting, MF = 21.9%, FF = 12%; $F_{1,57} = 1.30$, NS; moving away, MF = 29.3%, FF = 12%; $F_{1,57} = 3.03$, NS). When males puckered to females while sitting at a distance or approaching and then moving away from them ($N = 369$), in 36.8% of cases females approached or followed the males (often while themselves displaying PC) and either presented their hindquarters or groomed them. When females did not approach or follow the males, females either puckered to males without approaching (8.1%) or did not respond at all. Females were more likely to approach and groom a male than present if the male puckered while sitting at a distance (sitting, groom = 86.1%; present = 21%), and more likely to approach and present than groom if the male puckered while walking away from them (walking away, groom = 13.9%; present = 79%; $F_{1,51} = 38.07$, $p < 0.0001$). In 5 cases, a male interrupted a female grooming bout and relocated himself from a sunny to a shaded area, then puckered to the female; the female re-approached the male and resumed grooming. On 9 occasions, the alpha or the beta-male puckered at a distance to a female who was presenting and/or being genitally inspected by a lower ranking male. In 8 out of 9 occasions, the female immediately walked away from the low ranking male. Overall, PC was more likely to be followed by affiliation (contact and grooming, with or without EM) and infant handling in FF than in MF interactions (affiliation, MF = 7.9%, FF = 69.6%; $F_{1,57} = 9.55$, $p < 0.01$; infant handling, MF = 0%, FF = 19.1%; $F_{1,57} = 5.95$, $p = 0.01$). PC was more likely to be followed by mount in MF than in FF interactions (MF = 30%, FF = 0%; $F_{1,57} = 4.42$, $p < 0.05$).

The most common contexts in which females puckered to males (6.4% of total PC) included: in response to male PC (36.3%), while spontaneously approaching a male (24.5%), and sitting at a distance or approaching/moving away from a male (23.5%). The latter category included what appeared to be some attempts to recruit agonistic support from high ranking males. In other words, after having received aggression, usually from a low ranking male, and having uttered scream vocalizations, some females

approached a higher ranking male, then turned around and puckered to the male over their shoulder while walking toward the former aggressor. This sequence was repeated 2-3 times if the high ranking male did not follow the female after the first solicitation.

Analysis of Factor 4, Male Affiliation

Eye-Brows was the only behavior pattern positively loaded into Factor 4, while Embrace was loaded negatively into this Factor. EB was more frequent in male-male interactions than in female-male and female-female interactions (see Table 2; $F_{3,126} = 6.52$, $p = 0.0004$; p -values for both *post-hoc* comparisons < 0.05 ; p -values for all the other individual comparisons were nonsignificant). Therefore, EB was displayed by males more frequently than by females, and was frequently exchanged between males. The frequency of EB directed up and down the hierarchy across all individuals was not significantly different (t -test for paired samples, $t = -1.35$, $df = 62$, NS). Therefore EB occurred between two individuals irrespective of their differences in dominance rank.

The two most common interactions in which EB occurred were: while spontaneously approaching another individual (58.9%), and in response to another EB (10%). EB was also frequently accompanied by other gestures including HT, LS, PC, TF, EM, PR, and MT. Among adult males, the exchange of EB was frequently accompanied by approach-retreat interactions, Hip-Touch, and occasionally brief bouts of play. EB was frequently exchanged between individuals, and often accompanied by grunts, in some specific contexts such as immediately before or after agonistic support (17.1%; the signal was exchanged between supporter and beneficiary), the reintroduction of individuals to the group after a brief removal (particularly the reintroduction of the alpha-male; 6.8%), the aftermath of episodes of female mobbing of high ranking males (4.5%; the signal was displayed by the victim of mobbing towards high ranking males and females, notably the alpha-female, after aggression had ended), and the group's reaction to an external threat or disturbance (3.5%). The exchange of EB between two individuals was never followed by aggression or avoidance between these individuals, and overall, 27.2% of EB were followed by contact, grooming or play.

Analysis of infrequent behaviors

All of the Face-Inspection ($N = 28$) and Mock-Bite events ($N = 14$) were displayed by dominants to subordinates. All of the Hip-Clasp events ($N = 14$) occurred between individuals of the same sex (5 between two males, 9 between two females), and were often accompanied by grooming and/or affiliative gestures such as PC, EB, PR, HT and MT. The only observed Touch-Genitals event occurred between two adult males during a brief play interaction.

Discussion

Dominance and submission

The pucker was the most frequent gestural signal in pigtail macaques, followed by the lipsmack, the bared-teeth, and the presentation. The distributions of the 9 most frequent gestures in relation to sex and rank of individuals were grouped into 4 factors by the principal components analysis. The first factor, which accounted for about 40.1% of the variability, consisted primarily of dominance/submission behaviors. Mounts without intromission and thrusts were significantly directed down the hierarchy whereas bared-teeth, presentation, and lip-smack were significantly directed up the hierarchy.

The nonthrusting mount appears to be an assertive behavior in pigtail macaques and probably reflects dominance relationships between individuals. Bernstein (1972), however, did not find a correlation between the direction of mounting and the dominance hierarchy in this species. Bared-teeth, presentation, and lip-smack frequently occurred in response to aggression and to approaches by other individuals (see also Goosen & Kortmulder, 1979). BT occurred more frequently than PR and LS in these contexts and was not generally followed by any further social interaction. In contrast, PR and LS were more likely to be followed by affiliation, other gestures, or mounting than BT. Presentation was more frequently directed down the hierarchy than BT and LS in interactions between females. PR was most likely and BT least likely to be displayed while spontaneously approaching another individuals but LS was most likely to occur when a victim of aggression re-approached its former aggressor after fleeing. Bernstein

(1972) also observed that the distribution of lip-smack in pigtail macaques is similar to that seen for submissive responses. Lipsmack was frequently displayed by individuals while grooming or being mounted.

Altogether, these results suggest that bared-teeth, presentation, and lip-smack primarily communicate submission, *i.e.* are displayed to reduce risk of aggression. The hypothesis that these behaviors actually reduce risk of aggression must be further tested, however, by comparing the probability of occurrence of aggression when these behaviors are or are not displayed. The bared-teeth appears to be the purest submissive signal in the pigtail repertoire, and is primarily a reactive signal, namely elicited by the behavior of another individual. This expression could simply reflect fear ("I am afraid of aggression") or intention to modify the behavior of another individual ("Do not attack me"), or both (Maestriperi, in press). In contrast, PR and LS appear to have both a submissive and an affiliative component. In other words, in addition to being displayed to reduce the aggressive disposition of another individual, they might also communicate the intention to engage in affiliative interactions. If this explanation is correct, the typical sequence with which pigtail macaques re-approach former aggressors after fleeing, and lip-smack to them (see also Goosen & Kortmulder, 1979) probably signals an attempt at reconciliation, a behavioral phenomenon that is conspicuous in this species (Judge, 1991).

Affiliative behavior and female bonding

The affiliative component of lip-smack was also indicated by the association of this behavior with the distribution of Embrace among individuals. Most embracing occurred between females irrespective of their dominance rank, was mutual, and was followed by grooming. Embracing between female pigtail macaques was previously described by Kaufman & Rosenblum (1966), who subjectively interpreted this behavior as a "temporary state of dominance equivalence" (p. 216). Vento-ventral embracing is not uncommon in other primate species (see Thierry, 1984), and in particular in pygmy chimpanzees (*Pan paniscus*) where it is considered a bonding pattern between females (Kano, 1992).

The distributions of Pucker and Touch-Face across sex-rank classes of individuals were also significantly associated with those of Embrace and Lip-Smack. Most Touch-Face between females occurred immediately be-

fore or simultaneously with Lip-Smack and Pucker, suggesting that this behavior is either added to LS or PC to form a composite signal or that it serves an attention-getting function. In other words, females may touch the face of another female while displaying a facial expression to get this individual's attention. In rhesus macaques, mothers were observed to touch the face of their infants when lip-smacking to them at a short distance (Maestriperi & Wallen, *subm.*). If Touch-Face actually serves an attention-getting function and is not a ritualized component of a composite gestural signal, the cognitive implications of this behavior are noteworthy because they may suggest the ability to take another individual's perspective. However, it could also be that monkeys have learned that their visual signals are more likely to be responded to if other individuals are facing them or if they touch their face without understanding why that is the case.

Lip-Smack between females was more frequently directed up the hierarchy than the pucker, and was more likely to occur in response to aggression or approaches than PC. LS and PC were equally likely to be displayed while spontaneously approaching another individual, but PC was more likely to be followed by affiliation than LS. The pucker was rarely, if ever, displayed in response to aggression, so this signal seems to lack the submissive component of lip-smack. Van Hooff (1967) observed that the pucker "often alternates with lipsmacking and seems to have much the same motivation, expressing mainly the tendency to approach and the tendency to flee, the first probably dominating" (p. 58).

The meaning of the pucker

To better understand the meaning of the pucker, some specific contexts of occurrence of this behavior when displayed by both females and males must be discussed. Females puckered to other females (and less frequently to males) while sitting at a short (1-2 m) or long (20-25 m) distance from them, or puckered over their shoulder while moving away from them. Similar interactions were observed when males puckered to females. Females occasionally puckered to males in what appeared to be attempts to recruit their support in a conflict, while males puckered to females to lure them away from other males. Females often puckered in response to female pucker, and approached the sender of the signal to engage in friendly interactions such as Embrace, contact, grooming, or infant handling. When

displayed by males to females, the pucker was often associated with Hip-Touch and mounting (see also Tokuda *et al.*, 1968; Christopher & Gelini, 1977; Goosen & Kortmulder, 1979). Juvenile males puckered to one another during chase play.

Two conclusions concerning the meaning of the pucker can be initially drawn. First, this behavior is generally displayed in an affiliative context, and in particular, more so than lip-smack. Second, the pucker is a true social signal, that is, it is always directed to another individual. The fact that pigtail macaques pucker over the shoulder, while moving away from another individual, and sometimes at a long distance from another individual, may have produced the impression in the human observer that the pucker is not directed to any individual or is displayed while 'gazing in the air' (see Introduction for references). Caldecott (1986) suggested that the pucker may result in avoidance, but his subjective interpretation was based on a few observed interactions in wild pigtail macaques, in poor visibility conditions and with only an approximate recognition of individuals. Christopher & Gelini (1977) reported that female puckers were often part of a sequence that ended in aggression. However, they were unable to assess whether the signal was a threat or an appeasement gesture. Moreover, they noted that the pucker was directed up the hierarchy as often as down, which argues against the hypothesis that this signal communicates threat or submission. In fact, in pigtail macaques, aggression and submission are mostly unidirectional and dependent on the dominance hierarchy (*e.g.* Bernstein, 1969).

The results reported here support the hypothesis that the pucker serves a general distance-reducing or summoning function (Bobbit *et al.*, 1969; Shirek-Ellefson, 1972). The pucker seems to have this function when used by both females and males, contrary to what was suggested by Christopher & Gelini (1977). Although male-female puckers are often followed by sexual behavior whereas female-female puckers precede embracing, grooming or infant handling, these interactions have in common the feature that the pucker allows individuals to reduce distance and engage in nonaggressive interactions. The summoning function of the pucker between adults is consistent with the function of this behavior in mother-infant interactions (Jensen & Gordon, 1970; Castell & Wilson, 1971; Jensen *et al.*, 1973; Bolwig, 1980; Maestriperieri, 1996).

The pucker, however, is a complex communicative pattern that probably has more than one meaning. Interactive behavioral sequences initiated with the pucker often follow different courses (see also Goosen & Kortmulder, 1979), suggesting that the pucker's meaning may depend on the context in which it occurs, including the actor's concomitant behavior (Leger, 1993), or perhaps on subtle morphological differences in the structure of the facial expression. For example, when the pucker is displayed while approaching another individual, its meaning could be "Do not run away from me" or "Do not attack me" (in this, the signal could overlap with lip-smack). When displayed from a distance or while moving away from another individual, the meaning of the pucker seems to be "Approach me and groom me" or "Follow me". The finding that when males puckered to females while sitting at a distance, females were more likely to approach and groom than present, whereas the reverse was true when males puckered over their shoulder while moving away, indicates that concomitant behavior may be important to characterize the meaning of the pucker (see also Goosen & Kortmulder, 1979).

Another characteristic of the pucker is its occurrence in 'conversational' exchanges (see Snowdon & Cleveland, 1984), namely the pucker is often responded to by another pucker (sequences of puckers were also noted by Christopher & Gelini, 1977). For example, when females approached other females while puckering and then initiated contact or grooming, females sometimes initiated affiliation after the receiver of the signal responded with another pucker. Interestingly, Mori (1975) suggested that Japanese macaques (*Macaca fuscata*) exchange vocalizations before grooming interactions, which have the meaning of offering an invitation to groom, accepting an invitation to groom, or requesting grooming from another individual. Likewise, Bolwig (1978) argued that a lower ranking baboon (*Papio cynocephalus*) is unlikely to approach one of higher rank "without first having obtained permission" (p. 92).

Hinde (1985) has suggested that it may be profitable to think of animal signals as expressions involving negotiation, which are necessarily made in interaction with a recipient and are partly determined by the recipient's response. From this perspective, the pucker in pigtail macaques could often be interpreted as a bid, as the sender communicates its intention to initiate a friendly interaction, and the responder contributes to determine

the subsequent course of the interaction with another pucker or with other behavior.

The pucker seems to serve an important function in coordinating the social interactions of pigtail macaques and, in particular, facilitating the occurrence of affiliative or sexual interactions. It can be safely excluded that the pucker primarily reflects an underlying emotional state, unless we characterize the desire to be approached and groomed as an emotional state. The pucker sometimes provides information concerning the actor's subsequent behavior or intentions (*e.g.* when displayed during an approach) or reflects an attempt to influence the behavior of another individual (*e.g.* when displayed as an invitation to approach and groom, or to follow and present). The pucker does not appear to be strongly ritualized and strictly limited to specific individuals or circumstances. Louboungou & Anderson (1987) failed to condition the pucker with operant procedures in one pigtail macaque, but the reasons for the failure were not clear. Although the pucker sometimes functions as an invitation to another individual to approach and groom, the signal is not iconic, that is, its structure does not contain any elements of the activities to which it refers. For example, whereas the typical primate grooming invitation posture is a signal that in itself contains the elements of the grooming activity, the pucker is not in any way intrinsically related to grooming (*e.g.* it is not displayed during grooming). Therefore, the use of the pucker in some circumstances by pigtail macaques is consistent with the hypothesis that primates can use relatively arbitrary signals to coordinate their social activities or transmit information about features of their environment (Gouzoules *et al.*, 1995).

Male bonding

The distribution of Eye-Brows was not positively correlated with that of any other behavior pattern, but was negatively correlated with that of Embrace. EB was displayed by males more frequently than by females, and was frequently exchanged between males, irrespective of their dominance rank. EB was highly variable in terms of behaviors that preceded or followed it, but it was frequently displayed while approaching another individual and in response to another EB. Among adult males, the exchange of EB was frequently accompanied by approach-retreat interactions, Hip-Touch, grunts, and occasionally brief bouts of play. EB occurred in situations

of tension, external threat, or when the dominance status of males was challenged. EB also occurred in conjunction with agonistic support and was often followed by affiliation.

The Eye-Brows display, which resembles the play-face but differs for the mouth not being as wide open as in the play-face, has been described but not systematically investigated in previous studies of pigtail macaque social communication (Christopher & Gelini, 1977; Goosen & Kortmulder, 1979). Bernstein (1972) observed that the alpha male presented to other males during periods of high tension and sometimes after an active agonistic episode. Subordinate males approached the alpha male and hip-touched him or, if more confident, mounted him. Bernstein (1972), however, did not describe the occurrence of EB between males.

Interactions between males similar to those associated with EB in pigtail macaques have been described in baboons, where they have been referred to as 'greetings' (Pelaez, 1982; Colmenares, 1990, 1991; Smuts & Watanabe, 1990). In baboons, greetings have been hypothesized to allow males to negotiate important aspects of their relationships including cooperation and alliance formation (Colmenares, 1990, 1991; Smuts & Watanabe, 1990). This interpretation appears generally consistent with the observations reported here. EB could be interpreted as a bonding pattern between males and could serve a function similar to that of embracing between females. However, Eye-Brows is probably related to maintenance of dominance and perhaps, coalition formation, whereas Embrace seems to lack this agonistic component. The fact that the distributions of these behavior patterns across individuals are negatively correlated, and that females show both patterns, suggest that Eye-Brow and Embrace play different roles in the dynamics of communication and bonding in pigtail macaques. Further studies should address the variability of contexts in which EB occurs and the information content, if any, of this gesture.

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