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Facial Displays in Young Tufted Capuchin Monkeys *(Cebus apella)*: Appearance, Meaning, Context and Target

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Key Words
Facial displays · Communication · Ontogeny · Infancy · Capuchin monkey · *Cebus apella*

Abstract
Facial displays are important for communication, and their ontogeny has been studied primarily in chimpanzees and macaques. We investigated the ontogeny, communicative function and target of facial displays in *Cebus apella*. Our results show that facial displays are absent at birth and develop as infants grow older. Lip-smacking appears first (at about 1 month of age), followed by scalp-lifting, relaxed open-mouth, silent bared-teeth, open-mouth silent bared-teeth displays and finally the open-mouth threat face. Infants perform most facial displays in the same contexts as adults, with the exception of the silent bared-teeth display that young capuchins use primarily, or exclusively, in affiliative contexts. Interestingly, facial displays are exchanged very often with peers, less frequently with adults and almost never with the mother.

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Introduction

The communicative function of facial displays has been investigated primarily in Old World primate species, namely macaques and chimpanzees [Hinde and Rowell, 1962; van Hooff, 1967, 1972; Chevalier-Skolnikoff, 1973, 1982; Redican, 1975; Preuschoft, 1995; Preuschoft and van Hooff, 1995a, 1997; de Waal, 2003]. The very few studies focused on the ontogeny of facial displays (see Chevalier-Skolnikoff [1974] for *Macaca arctoides* and Plooij [1984] for *Pan troglodytes*) have shown that in macaques and chimpanzees facial displays develop gradually, changing in shape and

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often in function from the infant to the adult forms (see Maestripieri and Call [1996] for a review).

Recently, Visalberghi et al. [2006] have investigated the communicative function of facial displays in 20, mostly adult, *Cebus apella*. As in earlier reports on capuchin monkeys, the ontogeny of facial displays was not considered [Oppenheimer, 1973; Weigel, 1979]. In the present study we investigated at what age and in which context(s) infant capuchins exhibit facial displays and the role played by group members in eliciting them. In particular, we aimed at (1) establishing whether the chronological order in which the different facial displays appear in capuchins resembles that found in macaques and chimpanzees, (2) comparing the communicative function of each facial display in young capuchins with that already described for adults and (3) assessing whether certain individuals play a primary role in eliciting/receiving infants' facial displays and whether there is evidence that infants reciprocate facial displays. Let us examine what our expectations were.

Capuchins are relatively altricial primates [Elias, 1977; Antinucci, 1989; Fragaszy, 1989; Watts, 1990; Fragaszy and Adams-Curtis, 1998], their developmental milestones, such as weaning, physical and neurological maturity, occur later in life than in macaques and other monkey species, and earlier in life than in chimpanzees [Robinson and Janson, 1987; Fragaszy, 1990; Fragaszy et al., 1991, 2004; Schneider and Suomi, 1992; Fragaszy and Bard, 1997;]. In chimpanzees some facial displays are present very early in life whereas others develop during the first years of life [Bard, 2003]. Similarly, most communicative patterns of macaques develop gradually (see Chevalier-Skolnikoff [1974] for *M. arctoides*). Therefore, we expected that the appearance of the different facial displays would follow the same order in capuchins than in macaques and chimpanzees and that the timing would be intermediate between those of macaques and chimpanzees.

Although it has been argued that the communicative function of facial displays changes as infants grow older [Chevalier-Skolnikoff, 1974], quantitative information about such changes is lacking. In Old World primates, facial displays for social cohesion (lip-smacking and play face) appear earlier than fearful displays (grimace) and aggressive displays (threat) [Redican, 1975]. The silent bared-teeth display is very common and shows a certain degree of flexibility in its use across primate species and within species [Preuschoft, 1995, 2004; Preuschoft and van Hooff, 1995a, b, 1997; Preuschoft and van Schaik, 2000; Thierry, 2000a, b]. Tufted capuchins use the silent bared-teeth display in affiliative contexts as well as to signal submission to the dominant male [Visalberghi et al., 2006]. Therefore, we expected young capuchins to use this facial display mainly for affiliation.

Maestripieri and Call [1996] noted that in arboreal New World monkeys maternal facial displays seem to play a negligible role in the interactions with infants. Newborn capuchins spend most of their time on their mother's back, often in a cross-neck position [Fragaszy et al., 2004]; this dorsal position is likely to prevent face-to-face interactions between mother and infant. Therefore, we expected that individuals other than the mother will direct more facial displays to the infant than its mother and that these same individuals will in turn be more often the targets of the infant's facial displays than its mother.

Methods

Subjects

The study was carried out on two captive groups of tufted capuchins *(C. apella*[1]*)*. At the time of observations, group A consisted of 15 individuals, including 3 adult males, 3 adult females, 2 young adult males, 3 young adult females, 1 juvenile male, 2 juvenile females and 1 infant male, while group B contained 7 individuals, including 2 adult males, 1 adult female, 1 young adult female, 1 juvenile male, 1 infant male and 1 infant female (for age class, see Visalberghi [1988]). One infant female was born in each group 1 year after the main data collection (see Observational Methods section). Focal subjects were the 3 infants and the 4 juveniles. Group A was housed in the Primate Centre of the Istituto di Scienze e Tecnologie della Cognizione of the CNR (hosted by the Bioparco SpA of Rome) in 3 indoor cages (a total of 54 m^3) and 3 outdoor cages (a total of 40.5 m^3), all connected by means of sliding doors. Group B was housed in the Giardino faunistico di Piano dell'Abatino (Rieti) in 2 indoor-outdoor cages (indoor enclosure 31.5 m^3, outdoor enclosure 238 m^3) connected by a tunnel.

The cages were furnished with perches, slides, wooden structures, ropes and platforms. The monkeys were fed every afternoon with monkey chow, fresh fruit and vegetables. During the morning they received grains and other tiny food items. Water was present ad libitum.

Observational Methods

Data collection was carried out while the monkeys were kept outdoors. Data were collected between 9 a.m. and 6 p.m. for 1 year (June 2002 to June 2003), for a total of 250 h of observation. To increase our sample size concerning the assessment of the age of appearance of facial displays we observed 2 infants from July 2004 to January 2005 for a total of 80 h. For each group observations were made 2–3 days a week. A.D.M. made all the observations. Interreliability between A.D.M. and Dario Valenzano (who had previously studied capuchins' facial displays [Visalberghi et al., 2006]) calculated by comparing the 3 h of data collected independently from one another was higher than 90%.

Focal-animal sampling [Altmann, 1974] was used to score all the occurrences of 6 facial displays (see fig. 1 for an illustration of each facial display and Visalberghi et al. [2006] for a description) received or performed by the focal subject and of the other species-typical behaviours of the senders and receivers. The latter include social play, affiliation, submission, fear, aggression, sexual behaviours and mother-infant interactions (for a list of the behaviours and a brief description, see Visalberghi et al. [2006] and De Marco [2004]; for the sexual behaviours, see Carosi and Visalberghi [2002]). The behaviour of the focal subject was recorded on audio tape, and later the behavioural data were transcribed in protocols. Three infants (Ru, Py and Ra) were observed during 45- and 30-min sessions for a total of 45–46 h for each subject; each juvenile was observed during 15-min sessions for a total of 15–16 h for each subject. The last 2 infants (Po and Ry) were observed during 45- and 60-min sessions for a total of 40 h for each subject. Each of the sessions of observation was divided into 10-second intervals.

The set of data used to assess the appearance of facial display was based on 2 infants observed from birth, 1 infant observed from when she was 15 days old, 1 infant observed from when he was 1.5 months old and 1 infant observed from when he was 2.5 months old. Each subject contributed only to the facial display(s) for which she/he was young enough to make its contribution meaningful. The age range reported in the Results section refers to the age of the youngest and the oldest individuals receiving or performing for the first time a given facial display.

[1] The most recent classification of the genus *Cebus* [Rylands et al., 2000; Groves, 2001; Fragaszy et al., 2004] has split tufted capuchins (previously ascribed to the species *Cebus apella*) into 4 species *(Cebus apella, Cebus libidinosus, Cebus xanthosternos* and *Cebus nigritus).* The assignment of captive individuals to each of the latter 4 species is problematic because (a) the geographical origins of the colony founders are in most cases unknown, (b) some captive-bred capuchins descending from wild-caught founders are likely to be hybrids between the above species and finally (c) the morphological characters distinguishing the species are not yet clear cut.

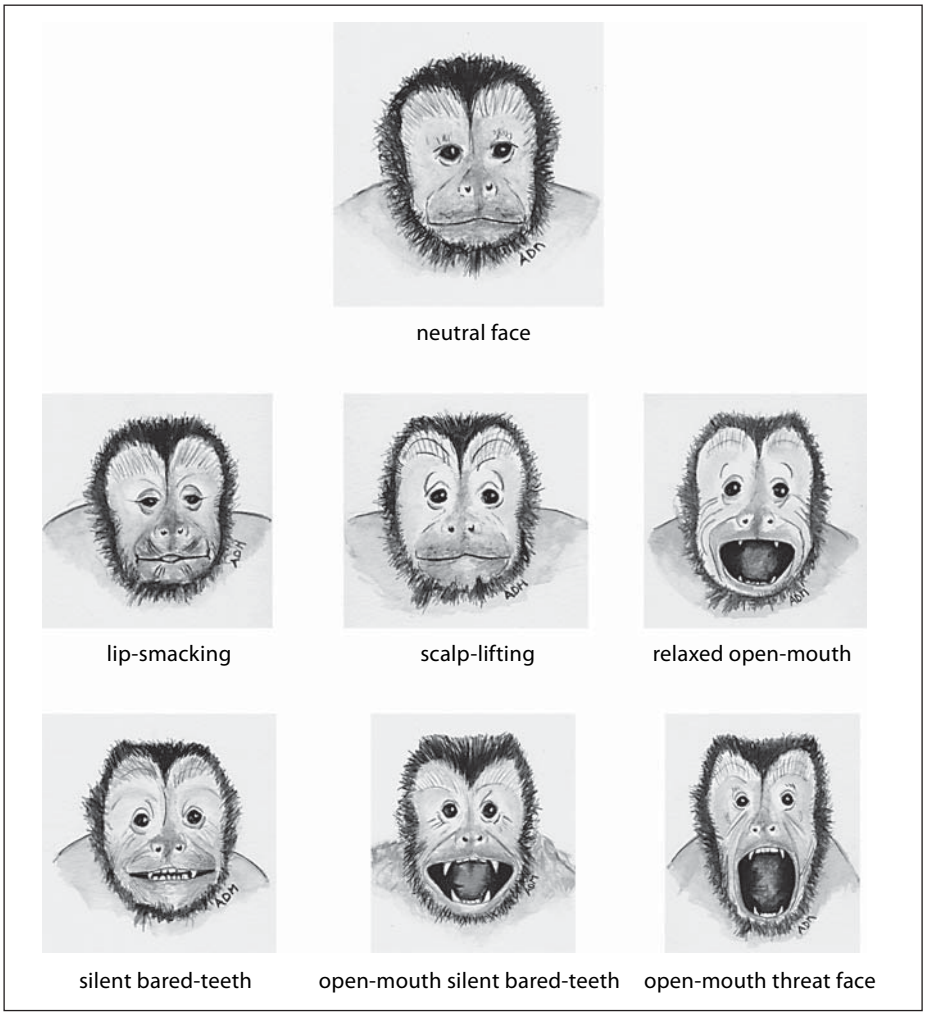

Fig. 1. Example of facial displays in young *C. apella*. Drawings by A.D.M.

Data Analysis

To understand the communicative function of a display we need to investigate its contextual embedding, its antecedents and its consequences [Bloomfield, 1933; Bühler, 1934; Smith, 1965]. We analysed the temporal relation between each facial display and another behaviour, or class of behaviours, performed by the sender or by the receiver, with the Pre-Post-Event Histograms program PPEH© [Preuschoft, 1995; Preuschoft and Singer, 1995]. For each facial display ('event') we analysed the behaviours occurring 3 min before ('pre') and 3 min after ('post') the occurrence of the facial display.

For each facial display there is (a) an intrasender sequence, in which the behaviours of the sender are analysed in relation to the facial display performed, and (b) an interaction sequence, in which the behaviours of the subject towards whom the sender performs the facial display are

analysed in relation to the facial display received. The analysis of the intrasender sequence is expected to yield an understanding of the *message* of the signal, while the analysis of the receiver's behaviour (interaction sequence) provides information about the *meaning* of the signal [Smith, 1965]. Moreover, the program PPEH allowed us also to provide a measurement of reciprocation of each facial display. For each sequence, the behaviour scored at a given 10-second interval was summed for all the sequences involving that facial display across all the subjects. The binomial test was then used to assess whether the total number of occurrences scored for each interval deviated significantly from the value expected on average over the 6-min time period. Due to the large number of tests carried out with the same sample of data, results were considered significant when $p < 0.005$ [Preuschoft, 1995].

Results

Age of Appearance of Facial Displays

The lip-smacking is the first facial display to be received (on the first day of life) and performed (23 days to 1 month and 10 days). Scalp-lifting was received and performed for the first time between about 1 month and 2.5 months of age (23 days to 2 months and 7 days received, 26 days to 2 months and 20 days performed).

The first received and performed relaxed open-mouth displays were observed between 1.5 months and 3 months and 10 days of age. However, we noticed that a few weeks earlier the infant repeatedly opens its mouth in the attempt to contact objects or other items. This mouthing behaviour gradually becomes not aimed at something, serving instead to initiate an affiliative and/or a social playful interaction (for similar observations in macaques and chimpanzees, see Hinde et al. [1964], Chevalier-Skolnikoff [1974] and Ploij [1984]).

We observed the first received and performed silent bared-teeth displays within a large time window (1 month and 20 days to 6 months and 15 days received; 2 months and 5 days to 5 months and 20 days performed). The received and performed open-mouth silent bared-teeth displays were observed between about 2 months and 5 days and 5.5 months. The open-mouth threat face display was the last display to be performed (4.5–10 months of age). This display was also the last to be received by infants; the youngest infant to receive an open-mouth threat face display performed by an adult male was 10 months old.

Communicative Function of Facial Displays

The relation between each facial display emitted, or received, by infants and juveniles and 4 behavioural categories of the sender (intrasender sequence) and 4 behavioural categories of the receiver (interaction sequence) inform us about its communicative function (table 1). The 4 behavioural categories considered are affiliative behaviours, play behaviours, submissive behaviours and agonistic behaviours.

Lip-Smacking Display. This display is significantly associated with affiliative behaviours both when performed (interval 0: intrasender, $n = 86$, $z = 18.02$, $p < 0.0001$; interaction, $n = 86$, $z = 9.38$, $p < 0.0001$) and when received by young capuchins (interval 0: intrasender, $n = 404$, $z = 43.93$, $p < 0.0001$; interaction, $n = 404$, $z = 18.81$, $p < 0.0001$; table 1). As illustrated in figure 2, the strong association between lip-smacking performed towards the infant and affiliative behaviours per-

Table 1. Facial displays performed and received by young capuchins (infants and juveniles, pooled data)

	Affiliative behaviours		Play behaviours		Submissive behaviours		Agonistic behaviours		Reciprocation
	intrasender sequence	interaction sequence	intrasender sequence	interaction sequence	intrasender sequence	interaction sequence	intrasender sequence	interaction sequence	
Displays performed									
Lip-smacking (n = 86; N = 137)	$p < 0.0001$	$p < 0.0001$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	$p < 0.0001$
Silent bared-teeth (n =313; N = 454)	$p < 0.0001$	$p < 0.0001$	n.s.	n.s.	n.s.	n.s.	n.s.		$p < 0.0001$
Relaxed open-mouth (n = 97; N = 181)	$p < 0.005$	$p < 0.0001$[a]	$p < 0.0001$	$p < 0.0001$	n.s.	n.s.	n.s.	n.s.	$p < 0.0001$
Open-mouth silent bared-teeth (n = 277; N = 386)	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	n.s.	n.s.	n.s.	n.s.	$p < 0.0001$
Scalp-lifting (n = 177; N = 213)	$p < 0.0001$	$p < 0.0001$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	$p < 0.0001$
Open-mouth threat face (n = 13; N = 16)	n.s.	n.s.	n.s.	n.s.	$p < 0.005$[a]	n.s.	$p < 0.0001$	n.s.	n.s.
Displays received									
Lip-smacking (n = 404; N = 678)	$p < 0.0001$	$p < 0.0001$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	$p < 0.0001$
Silent bared-teeth (n = 203; N = 280)	$p < 0.0001$	$p < 0.0001$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	$p < 0.0001$
Relaxed open-mouth (n = 110; N = 188)	$p < 0.005$	n.s.	$p < 0.0001$	$p < 0.0001$	n.s.	n.s.	n.s.	n.s.	$p < 0.0001$
Open-mouth silent bared-teeth (n = 213; N = 290)	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	n.s.	n.s.	n.s.	n.s.	$p < 0.0001$
Scalp-lifting (n = 110; N = 129)	$p < 0.0001$	$p < 0.0001$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	$p < 0.0001$
Open-mouth threat face (N = 2)	–	–	–	–	–	–	–	–	–

For each facial display, we assessed whether there was a significant relation between the facial display and the behaviour of the sender (intrasender sequence) and between the facial display and the behaviour of the receiver (interaction sequence) scored within the 10-second interval of the display (see the PPEH analysis in the Methods section). When no significant relation was found within the 10-second interval in which the display was performed, we analysed the intervals immediately preceding and following the display. The last column indicates whether the receiver has reciprocated the display by performing the same display within the same 10-second interval. For a list of the behaviours characterizing each context and a brief description, see Visalberghi et al. [2006] and De Marco [2004]. n = Total number of sequences analysed; N = total number of facial displays observed. The discrepancy between these two values is due to the fact that (1) the PPEH program for each interval analyses the same facial display performed only once (even if the display is repeatedly performed) and (2) the number provided by the program refers only to the number of complete sequences.

[a] Significant statistical analyses referring to the intervals preceding and following the display, respectively.

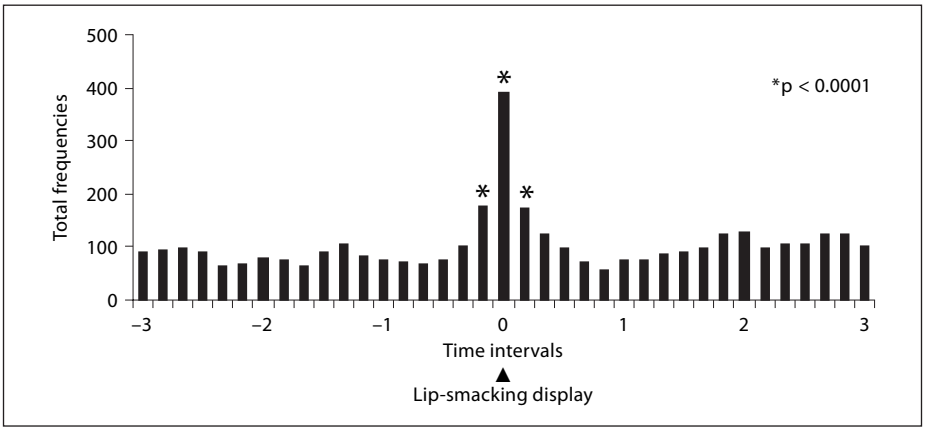

Fig. 2. Intrasender sequences (n = 106) representing the frequency distribution of affiliative behaviours (hand contact, muzzling, grooming, embracing, licking, sniffing, touching genitals) performed by the sender of a lip-smacking display towards the infant during its first month of life. The lip-smacking display occurs at interval 0 (on the abscissa), time intervals of 10 s extend from 3 min before the lip-smacking display until 3 min after it.

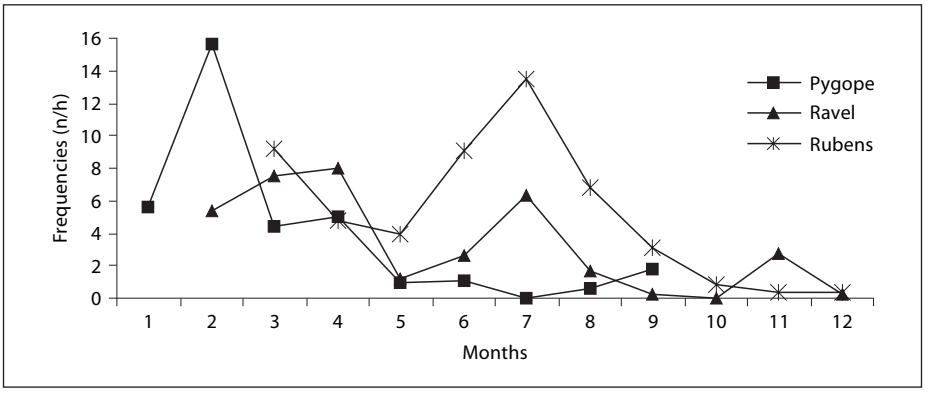

Fig. 3. Frequency distribution of lip-smacking performed towards the 3 infants from birth to 12 months.

formed by the sender is already well established during the infant's first month of life (interval 0: n = 106, z = 28.57, $p < 0.0001$). In the first weeks, the infant does not yet respond to this display; later, at about 1 month, he starts responding with affiliative behaviours and sometimes by reciprocating the lip-smacking. Lip-smacking displays performed towards infants by group members are significantly associated with the infants' behaviour of nursing, or being on the nipple (interval 0: n = 396, z = 31.02, $p < 0.0001$) and not with play behaviours.

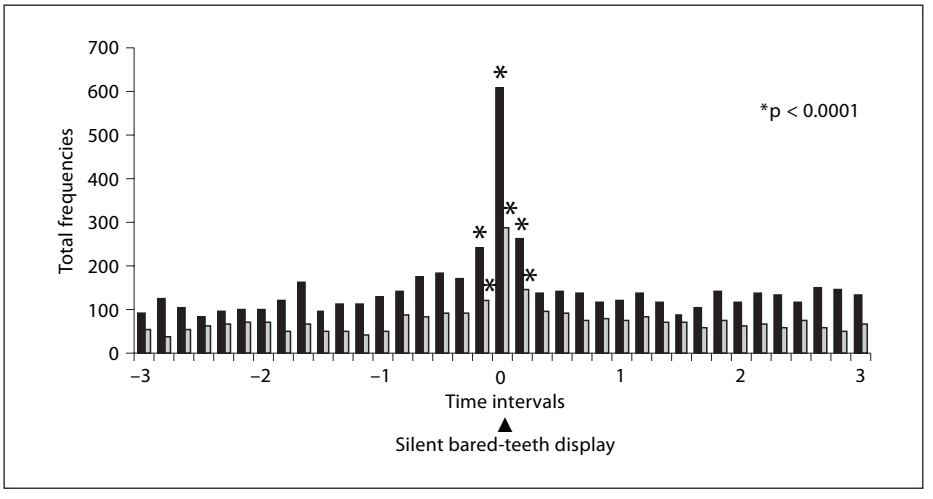

Fig. 4. Frequency distribution of affiliative behaviours (hand contact, muzzling, grooming, embracing, licking, sniffing, touching genitals) performed by infants and juveniles in the context of silent bared-teeth displays. Intrasender sequences (black bars, n = 313) are contrasted with interaction sequences (grey bars, n = 203). The silent bared-teeth display occurs at interval 0 (on the abscissa), time intervals of 10 s extend from 3 min before the silent bared-teeth display until 3 min after it.

As shown in figure 3, the frequency of lip-smacking performed towards infants is especially high early in life and decreases as infants grow older. In general, lip-smacking elicits the same facial display (interval 0: performed, n = 86, z = 11.07, $p < 0.0001$; received, n = 404, z = 11.54, $p < 0.0001$; table 1). Data collected during 7 months for the 3 infant capuchins when they were 3–9 months of age show that they performed lip-smacking less frequently than they received it (median, lower and upper quartile: performed, 0.42, 0.2–1.31; received, 4.28, 2.02–6.61; Wilcoxon matched-pairs signed-ranks test: T = 0, n = 7, $p < 0.02$).

Silent Bared-Teeth Display. The silent bared-teeth displays performed and received by young capuchins are significantly associated with affiliative behaviours both in the intrasender sequences (interval 0: performed, n = 313, z = 38.92, $p < 0.0001$; received, n = 203, z = 33.70, $p < 0.0001$) and in the interaction sequences (interval 0: performed, n = 313, z = 24.10, $p < 0.0001$; received, n = 203, z = 30.73, $p < 0.0001$; table 1 and fig. 4). As figure 5 and table 1 demonstrate, this display is very often reciprocated (interval 0: performed, n = 313, z = 40.99, $p < 0.0001$; received, n = 203, z = 41.47, $p < 0.0001$). In most cases reciprocation is almost immediate; however, it could also be slightly delayed, as illustrated in figure 5 by the significant values for the intervals adjacent to the 0 interval. Especially peers and adults, other than the dominant male, perform this display to the infant. The first use of this display as a signal for subordination was observed when an infant was about 1 year old [De Marco, pers. observation].

Play Face Displays. Both the relaxed open-mouth and the open-mouth silent bared-teeth displays are significantly associated with playful behaviours both in the

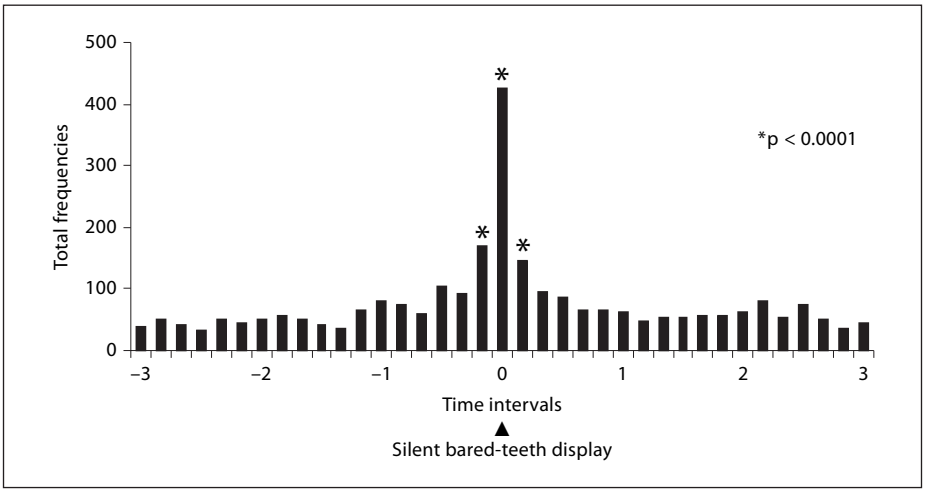

Fig. 5. Interaction sequences (n = 313) representing the frequency distribution of silent bared-teeth displays performed by group members in relation to silent bared-teeth displays by the sender (infants and juveniles). The silent bared-teeth display occurs at interval 0 (on the abscissa), time intervals of 10 s extend from 3 min before the silent bared-teeth display until 3 min after it.

intrasender sequences (relaxed open-mouth, interval 0: performed, n = 97, z = 12.03, $p < 0.0001$; received, n = 110, z = 14.80, $p < 0.0001$; open-mouth silent bared-teeth, interval 0: performed, n = 277, z = 13.67, $p < 0.0001$; received, n = 213, z = 9.77, $p < 0.0001$) and in the interaction sequences (relaxed open-mouth, interval 0: performed, n = 97, z = 15.80, $p < 0.0001$; received, n = 110, z = 12.49, $p < 0.0001$; open-mouth silent bared-teeth, interval 0: performed, n = 277, z = 16.31, $p < 0.0001$; received, n = 213, z = 6.44, $p < 0.0001$). Figure 6 illustrates the relation between the relaxed open-mouth display and play.

These two displays are also significantly associated with affiliative behaviours both when performed (relaxed open-mouth, interval 0: intrasender, n = 97, z = 3.01, $p < 0.005$; open-mouth silent bared-teeth, interval 0: intrasender, n = 277, z = 27.24, $p < 0.0001$; interaction, n = 277, z = 27.24, $p < 0.0001$) and when received (relaxed open-mouth, interval 0: intrasender, n = 110, z = 3.37, $p < 0.005$; open-mouth silent bared-teeth, interval 0: intrasender, n = 213, z = 27.47, $p < 0.0001$; interaction, n = 277, z = 16.09, $p < 0.0001$). Both these displays are reciprocated (relaxed open-mouth, interval 0: performed, n = 97, z = 40.15, $p < 0.0001$; received, n = 110, z = 39.48, $p < 0.0001$; fig. 7; open-mouth silent bared-teeth, interval 0: performed, n = 277, z = 33.69, $p < 0.0001$; received, n = 213, z = 33.63, $p < 0.0001$; table 1).

Scalp-Lifting Display. This display, both when performed and received, is significantly associated with affiliative behaviours in the intrasender sequences (interval 0: performed, n = 177, z = 22,66, $p < 0.0001$; received, n = 110, z = 21.04, $p < 0.0001$) and in the interaction sequences (interval 0: performed, n = 177, z = 20.91, $p < 0.0001$; received, n = 110, z = 12.46, $p < 0.0001$; table 1). This display is very often

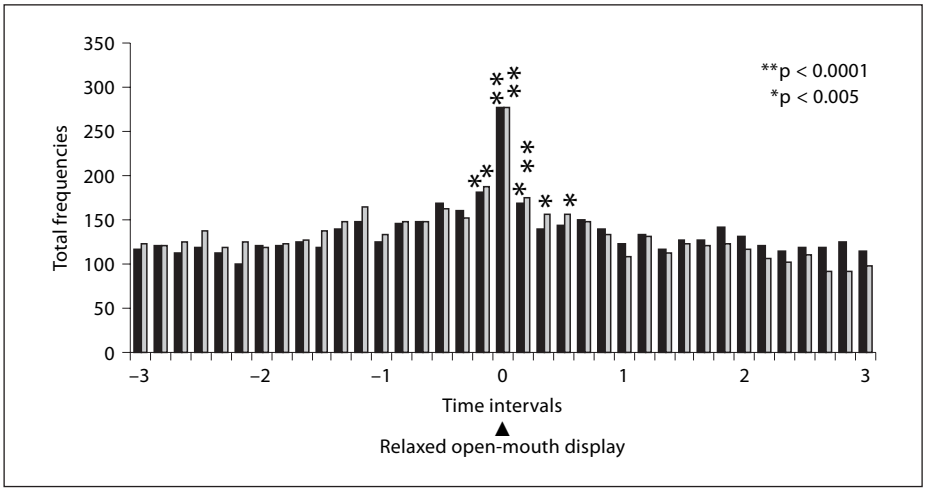

Fig. 6. Frequency distribution of play behaviours (play chase, rough and tumble, acrobatics, object play, touch and run, play mount, play bite) performed by infants and juveniles in the context of relaxed open-mouth displays. Intrasender sequences (black bars, n = 97) are contrasted with interaction sequences (grey bars, n = 110). The relaxed open-mouth display occurs at interval 0 (on the abscissa), time intervals of 10 s extend from 3 min before the relaxed open-mouth display until 3 min after it.

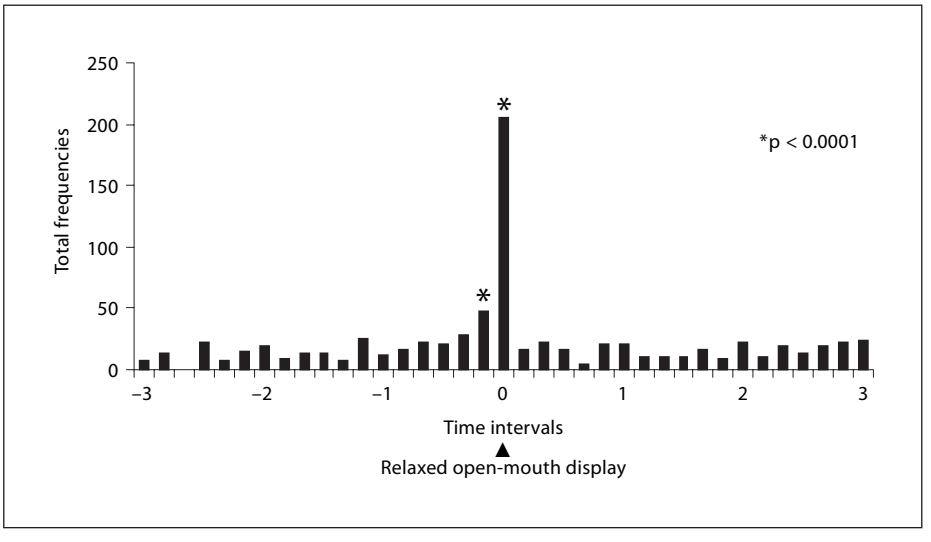

Fig. 7. Interaction sequences (n = 97) representing the frequency distribution of relaxed open-mouth displays performed by group members in relation to relaxed open-mouth displays by the sender (infants and juveniles). The relaxed open-mouth display occurs at interval 0 (on the abscissa), time intervals of 10 s extend from 3 min before the relaxed open-mouth display until 3 min after it.

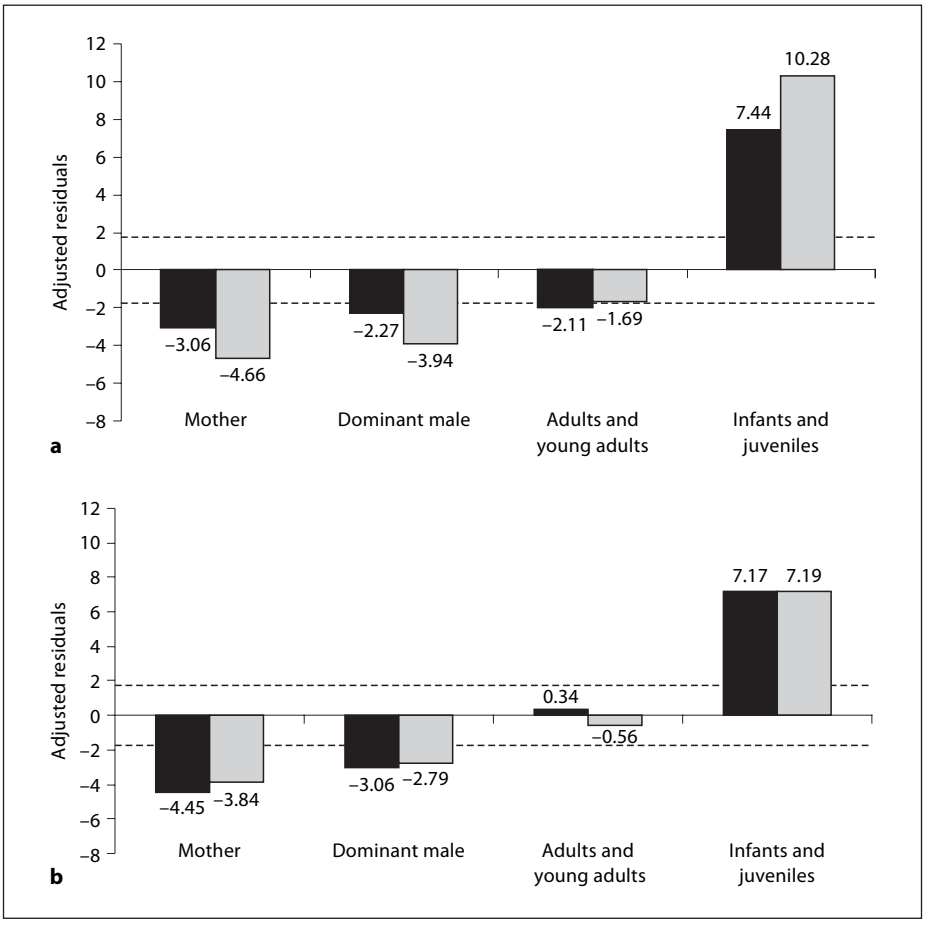

Fig. 8. Adjusted residuals of the frequencies with which infants (black bars) and juveniles (grey bars) performed facial expressions to (**a**) or received facial displays from (**b**) different individuals or age class. The dashed lines indicate the p = 0.05 level.

reciprocated (interval 0: performed, n = 177, z = 34.96, $p < 0.0001$; received, n = 110, z = 33.66, $p < 0.0001$; table 1).

Open-Mouth Threat Face Display. This display is rarely performed by young capuchins towards a partner (n = 16). In the intrasender sequences, the open-mouth threat face display is significantly associated with agonistic behaviours (interval 0: n = 13, $p < 0.0001$; table 1). Young capuchins were the target of this display only twice, one of which occurred when an adult male performed it toward a 10-month-old infant. This low frequency does not allow the PPEH analysis. However, in both the cases in which young capuchins received the open-mouth threat face, the sender performed agonistic behaviours.

Table 2. Developmental milestones and age of appearance of facial displays performed towards a group member in 3 primate species

Parameter	*Cebus apella*	*Macaca arctoides*[1]	*Pan troglodytes*
Percent weight of brain/weight of mother's brain[2]	49 [1]	61 [2]	36–46 [3]
First off mother	9 weeks [4]	2 weeks [5]	16–24 weeks [6]
>50% of daytime off carrier	19 weeks [4]	10 weeks [5]	48 weeks [7]
Appearance of LPS	3–6 weeks	2–12 days [8]	9 weeks[3]
Appearance of ROM	6–12 weeks	3–5 weeks [8]	12–24 weeks [7, 9]
Appearance of SBT	8–22 weeks	13 days to 6 weeks [8]	not available
Appearance of OMTF	18–40 weeks	3–24 weeks [8]	not available

LPS = Lip-smacking; ROM = relaxed open-mouth display; SBT = silent bared-teeth display; OMTF = open-mouth threat-face. 1 = Elias [1977]; 2 = Holt et al. [1975]; 3 = Sacher and Staffeldt [1974]; 4 = Fragaszy, Scollay and Baer, unpublished data; 5 = Hinde et al. [1964]; 6 = Goodall [1967]; 7 = Plooij [1984]; 8 = Chevalier-Skolnikoff [1974]; 9 = Goodall [1986].

[1] The first 3 values refer to other species of *Macaca*.

[2] Brain weight was measured at birth and given as percent of the adult female's brain weight.

[3] Plooij [1984] described a movement of the mouth resembling the first lip-smacking displays.

Typically young capuchins direct this display towards stimuli outside their cage (n = 28), while performing agonistic behaviours ($p < 0.0001$).

Target of Facial Displays

The facial displays performed by infants and juveniles were not distributed among group members as expected by chance ($\chi^2 = 74.29$, d.f. = 3, $p < 0.01$; $\chi^2 = 145.89$, d.f. = 3, $p < 0.01$, respectively). For each age class the expected value was based on the number of individuals belonging to it. Similarly, the facial displays received by infants and juveniles were not performed by group members as expected by chance ($\chi^2 = 80.79$, d.f. = 3, $p < 0.01$; $\chi^2 = 74.77$, d.f. = 3, $p < 0.01$, respectively).

In particular, infant and juvenile capuchins exchanged facial displays especially with peers, less often with non-peers and very rarely with their mother and with the dominant male. In fact, the adjusted residuals show that the frequencies with which facial displays were performed (fig. 8a) and received (fig. 8b) are below chance for the mother and the dominant male, significantly above chance for peers, whereas no significant trend was found for non-peers. Adjusted residuals exceeding 1.96 are significant at the 5% level [Everitt, 1977].

Discussion

Appearance of Facial Displays

Our results indicate that capuchins' facial displays appear at different times during the first months of life. Table 2 reports the timing of physical (percent brain weight at birth/maternal brain weight) and behavioural milestones (the age at which the infant is for the first time off the mother and the age at which the infant spends more than 50% of the time off the carrier) as well as the timing appearance of 4 facial

displays (lip-smacking, silent bared-teeth, relaxed open-mouth, open-mouth threat face) in *Cebus*, *Macaca* and *Pan*. As expected, capuchin infants have intermediate values between macaque and chimpanzee infants for the appearance of facial displays.

No facial display was observed during the infants' first weeks of life, when sleeping is the predominant state [Byrne and Suomi, 1995]. As in many other species [Redican, 1975], lip-smacking is the first display performed by capuchin infants since it is adaptive to perform affiliative displays and not aggressive ones [Chevalier-Skolnikoff, 1974]. At about 2 months of age, capuchins begin to explore their environment and to actively engage in social interactions [Byrne and Suomi, 1995], and at about 3 months they are motorically skilled enough to embark on social play [Fragaszy, 1990]. At 1.5–3 months of age, after a period during which infants mouth objects by opening their mouth in a somehow exaggerated manner, the play face display appears. So, the play face does not have a communicative function when it first appears and seems to derive from mouthing behaviour. Infant capuchins, like macaques [Hinde et al., 1964; Chevalier-Skolnikoff, 1974] and chimpanzees [Ploij, 1984], begin very early in their life to mouth everything that happens to be in front of them and, before mouthing it, they perform an open-mouth display. Gradually, mouthing loses the aim of achieving contact and the open-mouthed approaches become more and more frequently used by infants to initiate their affiliative and playful interactions, becoming ritualized.

Only later do facial displays with teeth exposed (the silent bared-teeth and the open-mouth silent bared-teeth) emerge. In *Macaca tonkeana* an open-mouth display, observed during the first months of age, is followed by a final form with teeth exposed and jaws closed, or opened [Thierry et al., 1989].

The open-mouth threat face is the last display to appear. As Chevalier-Skolnikoff [1974] pointed out, there may be no advantage for neonates to manifest communicative behaviours, such as threat, which could elicit an attack by the receiver. The appearance of positive facial displays earlier than negative ones is certainly advantageous for group-living primates [Redican, 1975].

Communicative Function

Newborns are extremely attractive [Byrne and Suomi, 1995; Silk, 1999]. Group members approach them by performing affiliative behaviours and lip-smacking (fig. 9) as early as during their first day of life, and they do so very frequently for the first 3–4 months, until the infants grow older. At first, the interactions are unilateral, but within a few weeks, infants become more active, respond with affiliative behaviours (touching, licking or nuzzling) and sometimes reciprocate the lip-smacking. In capuchins, as described for stumptail macaques [Chevalier-Skolnikoff, 1974], lip-smacking displays are often performed towards infants nursing or on the nipple. In our opinion, the infant's suckling behaviour was a potent elicitor of lip-smacking. Although difficult to prove, the idea that lip-smacking evolved from suckling behaviour through a process of ritualization is plausible [Hinde, 1966; Chevalier-Skolnikoff, 1974].

We found evidence supporting the view that lip-smacking has an affiliative-reassuring function (see also Weigel [1979] and Visalberghi et al. [2006]), conveying a positive message and promoting affiliative interactions. Our infants often received lip-smacking while asleep [De Marco, pers. observation]; this may suggest that in

Fig. 9. The dominant male performs lip-smacking toward a 4-month-old infant while she is on the nipple of the mother. Drawing by A.D.M.

these cases its function was to inform the mother that the approaching individual had affiliative intentions.

Interestingly we observed that the silent bared-teeth display extends its communicative function as capuchins grow older. In adult subordinate capuchins, the silent bared-teeth display signals submission toward dominant individuals as well as affiliation [Visalberghi et al., 2006]. In infant capuchins, the silent bared-teeth display is always used in affiliative contexts and it conveys a positive message. Only later, during the second year of life, does the silent bared-teeth display begin to signal submission. Also the human smile, regarded as homologous to the silent bared-teeth display [van Hooff, 1972, 1976; Preuschoft, 1995; Preuschoft and van Hooff, 1995b], extends its meaning as children grow older. In children the smile is an expression of real joy and happiness [Darwin, 1872], while later on people learn to smile in formal or tense situations, to greet and to reassure [Eibl-Eibesfeldt, 1972].

The silent bared-teeth display is not very frequent, although it can become so. We noted that during a period in which for medical reasons an infant capuchin and his mother were periodically separated from their group, every time that they were reunited the infant used the silent bared-teeth display as a friendly greeting while approaching its group members with affiliative behaviours [De Marco, 2004].

Fig. 10. a An adult male performs an open-mouth threat face display and accompanies it with a body posture with the tail raised that is typical of adults. **b** Infant (10 months) performing the same display. Note the different extent to which the jaws are opened and the visibility of the canine teeth. Drawings by A.D.M.

Like macaques [van Hooff and Preuschoft, 2003], capuchins do not use the play face during solitary play; this further stresses the importance of its communicative function. Two facial displays, both involving the open mouth, were performed during play interactions: the relaxed open-mouth (in which the upper tooth rows remained covered by the upper lips) and the open-mouth silent bared-teeth displays (in which the opening of the jaws is variable and the upper tooth row is uncovered). These displays are difficult to distinguish since they occur during rapid play interactions [Visalberghi et al., 2006], and it is not clear whether they are different displays or the same of increasing intensity. The remarkable overlapping in the communica-

tive function of these two displays suggests a lack of specificity in their meaning and better supports the latter hypothesis. Evidence that this is the case comes from *Macaca sylvanus,* in which Preuschoft [1992] describes a single open-mouth display (covering or baring the upper tooth rows, in accordance with the different degrees of the display's intensity), and from *Pan paniscus*, in which the open-mouth faces, both the covering and the baring ones, very frequently alternate during play interactions [de Waal, 1988]. According to Bout and Thierry [2005] (see also Thierry et al. [1989]), signal patterns that are morphologically or functionally similar often merge into one another through the evolutionary process.

Finally, the open-mouth threat face display first appears in a milder form. As illustrated in figure 10, typically the open-mouth threat face of infant capuchins differs from that of adults. Though adults may open their jaws more or less, their canine teeth are typically in full view or at least visible (see Valenzano [2001] and fig. 10a); in contrast, the canine teeth cannot be prominent when young individuals perform this display because of their smaller size (see Galliari [1985] and fig. 10b) and since infants open their jaws only partially.

According to Preuschoft and van Hooff [1995a], under the condition of egalitarian relations the displays of submission and affiliation and those of appeasement and friendly inclination will converge, and eventually the distinctiveness of play from other sociopositive contexts will be blurred. From an evolutionary point of view, it is possible that the prominent tolerance by adults towards infants in capuchin groups [Fragaszy et al., 2004] influences the development of the social function of displays. Infant capuchins live in a largely benign social world in which they are tolerated and cared for by most members of the group; at this time, 5 out of the 6 facial displays performed by young capuchins are used in affiliative and playful contexts. Only later, during their second year of life, do they face adult rejections [Fragaszy et al., 2004] and begin to use the silent bared-teeth display also as a signal of submission toward dominant individuals.

Target of Facial Displays

Both infant and juvenile capuchin monkeys exchange facial displays especially with their peers while playing with them. In spite of the fact that an infant spends about 57% of the time with its mother during the first year of life [Byrne and Suomi, 1995], the mother is the partner that exchanges the smallest number of facial displays with the infant (for similar findings, see Chevalier-Skolnikoff [1974] and Maestripieri and Call [1996]), possibly because newborns spend most of their time on their mother's back, coming to her belly only for nursing [Fragaszy et al., 2004]. Chevalier-Skolnikoff [1974] argued that during the first weeks of life the communication between mother and infant is almost exclusively in the tactile/sensory mode and that, as the infant matures, while the interactions with the mother continue to be primarily tactile, those with other group members are mostly visual. In fact, for chimpanzees there are also no data concerning how much information is exchanged by means of facial displays from the mother to the infant, though these interactions might be very important in the development of emotional expressions [K.A. Bard, pers. commun.].

It is of interest that young capuchins rarely perform the open-mouth threat face display, the potentially dangerous display, and mostly direct it towards 'things' that cannot strike back, instead of towards group members. The finding that most open-

mouth threat face displays are performed together with similar displays being made by group member(s) supports the idea that this functions to label things (e.g. snake, cats or objects) that more expert individuals consider dangerous [Fragaszy et al., 2004, p. 257]. Social cohesion allows youngsters to 'docket' the outside world and learn to recognize dangerous situations [Suboski, 1990].

As expected since play interactions are highly symmetrical and synchronized [Fagen, 1981; Preuschoft, 1995], the play face is very frequently reciprocated in young capuchins. According to Meltzoff [1993], imitation of facial displays provides chances for the infant to learn their use; young human infants imitate the facial displays of others before recognizing the appropriate context in which they should be performed, and by doing so they learn the context in which the facial display is appropriate. Producing the same facial display at the same time as another group member might make it possible for a young capuchin to learn the context in which the display should be used. Our observational data cannot prove whether this is the case; we only showed that, with the exception of the threat display, young capuchins reciprocate facial displays and that lip-smacking begins to be reciprocated after the first few weeks of life, later than recently described for macaques [Ferrari et al., 2006].

The role played by reciprocation to allow infants to learn the context in which the display should be used should be assessed by ad hoc designed experiments.

When adult capuchins use the silent bared-teeth display to signal submission, the display is unidirectional and not reciprocal, as expected for an indicator of subordinate status [Visalberghi et al., 2006]. In contrast young capuchins use this display bidirectionally and reciprocally. It seems, therefore, that in the tufted capuchins, symmetry of the silent bared-teeth display is, to some extent, related to age, whereas in macaques, it is related to the particular degree of social tolerance found in the different species [Preuschoft and van Hooff, 1995a].

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