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Original Citation:

The repertoire and social function of facial displays in Cebus capucinus / A. De Marco; O. Petit; E. Visalberghi. - In: INTERNATIONAL JOURNAL OF PRIMATOLOGY. - ISSN 0164-0291. - STAMPA. - 29:(2008), pp. 469-486.

Availability:

This version is available at: 2158/422261 since:

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27 April 2024

Int J Primatol (2008) 29:469–486
DOI 10.1007/s10764-007-9174-0

The Repertoire and Social Function of Facial Displays in *Cebus capucinus*

A. De Marco · O. Petit · E. Visalberghi

Received: 25 April 2007 / Accepted: 5 July 2007 /
Published online: 21 March 2008
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Abstract Systematic studies on facial displays in capuchins are limited and based mainly on studies of tufted capuchins (*Cebus apella*). Despite the great social-morphological variability within *Cebus* suggesting possible morphological and functional variations in the facial displays of different species, no study has considered thoroughly visual communication in the genus. Our aim was to describe the facial displays of white-faced capuchins and to assess their distribution and communicative function. We observed 15 captive white-faced capuchins in the Primate Centre of the Louis Pasteur University of Strasbourg, for a total of 198 h. We described the following facial displays: relaxed open-mouth, lip-smacking, open-mouth threat-face, silent bared-teeth, open-mouth silent bared-teeth, protruded-lip face, and tongue-out. We never observed the scalp-lifting display, one of the most common displays characterizing tufted capuchins. White-faced capuchins use the majority of facial displays in an affiliative or playful context; only the open-mouth threat-face display is associated with aggressive behaviors. White-faced capuchins lack ritualized signals of submission. The fact that in white-faced capuchins the silent bared-teeth display conveys only a positive message, while in tufted capuchins it signals submission as well as affiliation, supports the covariation hypothesis (Thierry 2004 Social epigenesis. In B. Thierry, M. Singh, & W. Kaummans (Eds.), *Macaque societies: A Model for the study of social organization*, pp. 267–294. Oxford University Press).

Keywords *Cebus* · communication · facial displays · white-faced capuchin

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Introduction

In terms of social systems, the different capuchin species fall along a continuum from α-male despotism (unimale social system) to more relaxed tolerance of the multimale social system (Fragaszy *et al*. 2004; Perry 1998). *Cebus capucinus* live in multimale-multifemale groups, and researchers often describe them as tolerant (Jack 2003; Perry and Rose 1994; Rose 1994). Levels of agonism are very low (Fedigan 1993), and individuals show a high rate of bidirectional aggression and intense conciliatory behaviors (Leca *et al*. 2002). The relationships among males are neutral, tolerant, or highly affiliative (Jack 2003): There is a clear α-male, but the degree to which he asserts his dominance is highly variable (Perry 1998). They have an egalitarian mating system, in which all adult males have access to estrous females and in which they cooperate actively in group defense (Fedigan 1993; Fragaszy *et al*. 2004; Perry 1997). Decision-making processes, such as the initiation of group movement, appear to be distributed among group members, rather than the exclusive domain of high-ranking individuals (Boinski 1993; Boinski and Campbell 1995; Leca *et al*. 2003).

The study of the function of facial displays may reflect the social organization of a primate species and provide further insight into their social relationships. In particular, the silent bared-teeth display is a revealing pattern among Old World primates (Bout and Thierry 2005; Preuschoft1995, 2004; Preuschoft and van Hooff 1997; Thierry 2000;). According to the covariation hypothesis, in *Macaca* the social function of this display covaries with the dominance style of a species (Preuschoft 1995; Thierry 2000): the silent bared-teeth display indicates submission in species with a strict dominance style (*Macaca mulatta*, *M. fuscata*, *M. fascicularis*), whereas it is associated with sociopositive interactions in species with a more relaxed dominance style (*M. tonkeana*, *M. maura*, *M. nigra*). Visalberghi *et al*. (2006) reported that in tufted capuchins the silent bared-teeth display is related both to positive relations and to submission, but their data are not sufficient to prove the existence of such covariation within *Cebus*. In contrast, Perry and Manson (2004) reported that white-faced capuchins lack ritualized signals of submission even though they form dominance hierarchies.

The researchers who have investigated the repertoire of facial displays of *Cebus* have studied *C. apella* (De Marco and Visalberghi 2007; Visalberghi *et al*. 2006; Weigel 1979), while systematic studies on facial communication in *C. capucinus* are very limited (Oppenheimer 1973). Although Weigel (1979) argued that all capuchin species are similar in their visual repertoires of signals, their great morphological variability suggests that morphological differences in facial displays could exist. Indeed there are reports of noteworthy differences. For example, Carosi and Visalberghi (2002) noted that during courtship, whereas *Cebus apella* exhibits eyebrow raising and grin, *C. capucinus* exhibits the duck-face, in which they protrude the lips (Manson *et al*. 1997). Therefore our first aim was to describe the facial displays of white-faced capuchins and to assess their distribution in relation to rank, age, and sex classes of sender or receiver.

According to Preuschoft (2004), dominance style instead of phylogeny is the driving force determining the social function of the silent bared-teeth display in pigtail macaques (*Macaca nemestrina*). Because the dominance style differs across

Cebus sp. (Fragaszy *et al*. 2004; Janson 1986a, b), we expected interspecific functional variations of facial displays also. Consequently, our second aim was to examine the context and social function of the facial displays of white-faced capuchins to test the covariation hypothesis.

Methods

Subjects

We observed a semifree-ranging group of 15 white-faced capuchins (*Cebus capucinus*) at the Primate Centre of the Louis Pasteur University, Strasbourg. The group comprised 2 adult males, 6 adult females (>5 yr), 1 juvenile male, 1 juvenile female (1–2 yr), 1 infant male, and 1 infant female (<1 yr). An infant male and 2 infant females were born during data collection.

The group lived in a *ca.* 0.5-ha^2 wooded park, connected to a 25-m^2 indoor enclosure. During observations, the group did not have access to the indoor area. Commercial primate pellets and water were present *ad libitum* in the indoor enclosure. We provided fresh fruit and vegetables once a week.

Observational Methods

We collected weekly observational data Monday to Friday between 0900 and 1300 h from March to November 2005, for a total of 198 h. To minimize the disturbance effect of multiple observers, De Marco made all the observations.

We used focal individual sampling (Altmann 1974) to score all facial displays the focal subject received or performed and the other species-typical behaviors of the senders and receivers. We grouped the behavior patterns of the interacting individuals into 4 social contexts: affiliative interactions (social grooming, touch, embrace, lick, smell, muzzle, mouth contact, on lap), play interactions (wrestle, play chase, play contact, play bite), submissive interactions (avoid, flight, scream), and aggressive interactions (stare, lunge, chase, slap, bite, overlord). We recorded the behavior of the focal subject on audio tape and later transcribed and coded it. We observed the adults during 15-min sessions for a total of 9 h for each subject; we observed each infant and juvenile during 30-min sessions for a total of 18 h each. We divided each of the sessions of observation into 10-s intervals.

In order to quantify the affiliation between adult group members, we recorded interindividual distances via instantaneous sampling every 5 min for a total of 44 h (Altmann 1974). The number of scans during which the 2 partners were in bodily contact allowed us to provide a quantified assessment of the level of affiliation within each dyad.

Data Analysis

To rank the individuals of the group in a dominance hierarchy we recorded the avoidance behaviors and the unidirectional aggressions of spontaneous events. We used Mat Man program (de Vries 1995; de Vries *et al*. 1993) to calculate the

improved index of linearity (Landau's h' index). We considered only the adults as being hierarchically ordered.

To assess the distribution of facial displays in relation to rank, age, sex, kinship, and affiliation partners, we conducted analysis via nonparametric statistical tests (Spermann correlation coefficient test, Pearson's correlation coefficient test, Mann-Whitney U test) (Siegel and Castellan 1988). We tested matrix correlation via Mat Man (de Vries *et al*. 1993). We set the number of automatic permutations of matrices at 10,000 and used Pearson's correlation coefficient.

To understand the communicative function of a display one should investigate its contextual embedding, its antecedents, and its consequences (Smith 1965). We analyzed the temporal relation between each facial display and another behavior, or class of behaviors, that the sender or the receiver peformed, with the Pre-Post-Event-Histograms program (PPEH©: Preuschoft 1995; Preuschoft and Singer 1995). For each facial display (Event) we analyzed the behaviors occurring 90 s before (Pre) and 90 s after (Post) the occurrence of the facial display.

For each facial display, there is 1) an intrasender sequence, which analyzes the behaviors of the sender in relation to his facial display and 2) an interaction sequence, which analyzes the behaviors of the recipient of the investigated facial display 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 behavior (interaction sequence) provides information about the meaning of the signal (Smith 1965). Moreover, PPEH allowed us also to provide a measurement of reciprocation of each facial display. For each sequence, we summed the number of times a certain behavior occurred at a given 10-s interval for all the sequences involving that facial display. To establish whether the figure deviated significantly from the expected value if the observed instances of the behavior were distributed evenly over all intervals of the time frame, we compared expected and observed rates for the central intervals of the sequences via a Wilcoxon matched-pairs test (Siegel and Castellan 1988). We carried out statistical comparisons only for the intervals –1, 0, +1 to limit the number of tests (Bout and Thierry 2005). In addition, to establish the direction of each facial display, we constructed actor/receiver matrices. We compared the half-matrix of the facial displays performed to those of the facial displays received via Mentel's Z statistic (Mat Man). Probability levels are based on 10,000 random permutations.

Results are significant at $p<0.05$.

Results

We observed the following facial displays: relaxed open-mouth; lip-smacking; open-mouth threat-face; the silent bared-teeth; open-mouth silent bared-teeth; protruded lip-face; and tongue out (Fig. 1). We observed no scalp-lifting display, one of the most common displays of tufted capuchins. Table 1 contains a description of the 7 facial displays in terms of jaw opening, gaze direction, ear position, scalp retraction, and body posture. The table also indicates the names applied to the facial displays by previous researchers (Oppenheimer 1973; Perry 1996).

Fig. 1 Facial displays in white-faced capuchins. (Photos by A. De Marco).

The protruded-lip face occurred only once: it was in the context of reconciliatory mount. Owing to the low rate at which the capuchins performed it, we did not include it in the statistical analysis. We also omitted from the analysis the tongue-out display because only infants and a single adult male performed it, usually while he was displaying peculiar behaviors. Moreover, the tongue-out display did not seem to be performed toward other(s), i.e., as a form of communication (Perry, *pers. comm*.).

Sociodemographic Variables

Table 2 contains the frequencies (per individual per hour) scored for each display performed and received by each sex-age class. There is a statistically significant effect of age on the frequency of certain facial displays. The open-mouth threat-face display, both performed and received, correlates positively with age (Spearman correlation, respectively: r_s=0.67, r_s=0.59; N=15, p<0.05). Thus adults performed and received more open-mouth threat-face displays than juveniles did. In contrast, performances of the relaxed open-mouth display and reception of the lip-smacking and silent bared-teeth displays are significantly negatively correlated with age (Spearman correlation, respectively: r_s=–0.68, r_s=–0.83, r_s=–0.59; N=15, p<0.05).

There is no statistically significant difference between males and females in the frequency of each facial display performed and received.

The analysis of the occurrence of 121 avoidance behaviors and of 31 unidirectional conflicts allowed us to rank the adults (Landau's linearity index h' corrected for unknown relationships = 0.88, p<0.004). We compared the frequency of each facial display performed and received according to hierarchical rank. There is no significant correlation. However, subjects directed only 13% of avoidance toward the α-male.

Table 1 Facial displays of tufted capuchins

Facial display	Mouth, jaws	Gaze	Ears	Eyebrows	Body posture	Other names
Relaxed open-mouth (ROM)	Mouth opened in an oval shape by retraction of the corners of the mouth and gaping of the jaws	Directed toward R when A and R are not in contact: Usually averted when they are in contact	Normal, sometimes retracted	Normal	Variable	Open mouth (Oppenheimer 1973)
Lip-smacking (LPS)	Jaws rhythmically, weakly lowered and raised: No retraction of the corners of the mouth	Usually directed at R from an oblique angle	Normal	Normal	Variable	
Open-mouth threat-face (OMTF)	Wide opening of the mouth, baring the teeth in a complete retraction of the corners of the mouth	Intense staring toward R	Retracted	Lowered into a frown	A is standing and thrusts his body toward R: Tail is not raised. Sometimes associated to overlord	Open mouth, bared teeth (Oppenheimer 1973; Perry 1996)
Silent bared-teeth (SBT)	Mouth closed, baring of upper and lower teeth. Retraction of the corners of the mouth	Directed at R	Normal, sometimes retracted	Lowered into a frown	Variable	Grin (Oppenheimer 1973)
Open-mouth silent bared-teeth (OSBT)	Mouth opened by retraction of the corners of the mouth. Teeth exposed.	Directed at R	Normal, sometimes retracted	Normal	Variable	
Protruded-lip face (PLF)	Mouth closed, lips tensed together and protruded	Usually staring toward R	Normal	Normal	Usually dancing movements or mounted position	Protruded-lips (Oppenheimer 1973; Perry 1996)
Tongue-out (TO)	Mouth opened and tongue widely protruded, touching the chin	Normal	Normal	Normal	Variable	

For each facial display, we provide information about gaze, position of the ears, jaws and scalp, and body posture, and stress how it differs from the neutral facial expression. We also report if other authors previously described the facial display and the name given to it. (R = recipient, A = Actor).

Table 2 Frequencies (per individual per hour) of each facial display performed (a) and received (b) in each sex-age class

	SBT	ROM	LPS	OSBT	OMTF
(a)					
Adult male (N=2)	0.30±0.27	0.58±0.51	0.67±0.47	0.39±0.55	0.61±0.23
Adult female (N=6)	0.14±0.15	0.37±0.50	0.67±0.28	0.29±0.36	0.88±0.57
Young male (N=3)	0.18±0.18	6.52±3.67	0.96±0.26	0.28±0.28	0.09±0.08
Young female (N=4)	0.08±0.11	2.94±2.25	0.32±0.33	0.10±0.16	0.10±0.11
(b)					
Adult male (N=2)	0.14±0.12	2.22±2.36	0.11±0.00	0.39±0.47	1.5±0.86
Adult female (N=6)	0.02±0.04	0.84±0.60	0.06±0.05	0.18±0.21	0.40±0.25
Young male (N=3)	0.41±0.61	5.92±5.22	1.81±2.43	0.39±0.34	0.54±0.47
Young female (N=4)	0.18±0.13	1.86±2.06	0.86±0.37	0.17±0.19	0.04±0.08

To investigate whether kinship could influence the exchange of facial displays, we distinguished 3 degrees of closeness in maternal kin relationships: non-kin, far-kin (same matrilineal), and close-kin (mother/offspring). For each facial display, we compared the matrix, in which we implemented the 3 types of kin dyads, with the matrices of hourly frequencies. There is a negative correlation for the lip-smacking display (Pearson's correlation coefficient = –0.117, p=0.024), which means that unrelated dyads exchanged more lip-smacking than close-kin did. In contrast, there is no significant correlation for the other facial displays.

Finally, we investigated whether affiliation between adult partners could influence the exchange of facial displays. Based on comparison of the matrix of hourly frequencies of bodily contacts with matrices of hourly frequencies of each facial display, there is no statistically significant effect of affiliation for any of them.

Communicative Function and Direction of Facial Displays

Relaxed open-mouth display Juveniles performed and received the relaxed open-mouth display more frequently than the older individuals did. Youngsters performed 91.4% and received 75.0% (corrected for the number of subjects in the respective age class) of the 561 observed relaxed open-mouth displays. Displays of the relaxed open-mouth are significantly associated with playful behaviors both in the intrasender sequences (interval 0: n=9, t=45, p<0.05, Wilcoxon matched-pairs test, 1- tailed) and in the interaction sequence (interval 0: n=10, t=55, p<0.05, Wilcoxon matched-pairs test, 1-tailed: Fig. 2a; Table 3). The display is also significantly associated with affiliative behaviors both when performed (interval 0: n=9, t=45, p<0.05, Wilcoxon matched-pairs test, 1-tailed) and when received (interval 0: n=11, t=61, p<0.05, Wilcoxon matched-pairs test, 1-tailed: Fig. 2b; Table 3). The display is bidirectional (Mantel's Z test, r=0.944, p=0.0001, 2-tailed) and the PPEH shows that the relaxed open-mouth display is highly reciprocal (interval 0: n=10, t=55, p< 0.05, Wilcoxon matched-pairs test, 1-tailed). In fact, the receiver responded to a relaxed open-mouth display with the same display within the same 10-s interval in a significant number of cases (Fig. 2c and Table 3). There is no association between the relaxed open-mouth display and submissive and agonistic behaviors (Table 3).

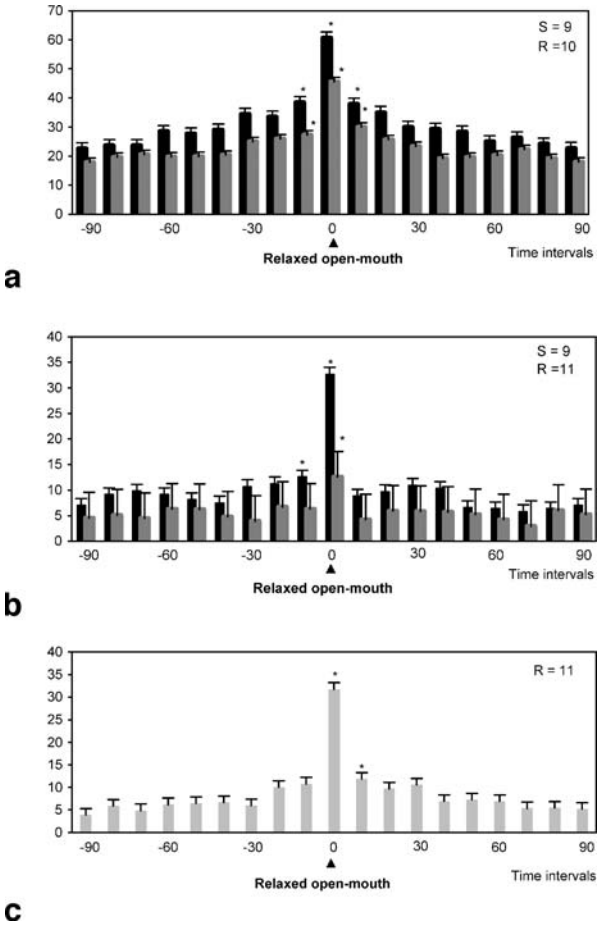

Fig. 2 Relaxed open-mouth display. Behavioral sequences in: play context **(a)**, affiliative context **(b)**, and when partners exchange the relaxed open-mouth display **(c)**. The relaxed open-mouth display occurs at interval 0 (on the abscissa); time intervals at 10 s extend from 90 s before the occurrence of the relaxed open-mouth display until 90 s after it. Intrasender sequences (black bars) and interaction sequences (dotted bars) show the frequencies of behaviors performed by the sender and receiver of the display, respectively. S indicates the number of senders and R indicates the number of receivers present in the analysis.

Lip-smacking We observed 151 lip-smacking displays. Juveniles performed 46.8% of the scored lip-smacking displays and received 94.1% of them (corrected for the number of subjects in the respective age class). The display is significantly associated with affiliative behaviors both when performed (interval 0: $n=11$, $t=66$, $p<0.05$, Wilcoxon matched-pairs test, 1-tailed) and when received (interval 0: $n=5$, $t=15$, $p<0.05$, Wilcoxon matched-pairs test, 1-tailed: Fig. 3; Table 3). It was bidirectional (Mantel's Z test, $r=0.581$, $p=0.0004$, 2-tailed) but it was not exchanged reciprocally. There is no significant association between lip-smacking performed and received within the same 10-s interval or with playful, submissive, or agonistic behaviors (Table 3).

Table 3 Facial displays performed and received by white-faced capuchins

context	facial display	*n*	expected	time interval								
				–1			0			+1		
				observed	*t*	*p*	observed	*t*	*p*	observed	*t*	*p*
affiliative	ROM-sender	9	9.96	12.6	43	.007	32.7	45	.004	8.78	15	ns
	ROM-receiver	11	5.56	6.27	44.5	ns	12.5	61	.013	4.18	15	ns
	LPS-sender	11	1.39	3.18	65	.002	4.36	66	.001	2.73	65	.002
	LPS-receiver	5	4.28	5.8	12.5	ns	8.8	15	.021	7.4	15	.021
	OMTF-sender	8	1.74	1.25	18	ns	.38	0	ns	.75	9	ns
	OMTF-receiver	7	1.11	1.43	19	ns	.71	6	ns	1	11	ns
	OSBT-sender	5	1.17	1.6	8	ns	4	15	.022	2	11	ns
	OSBT-receiver	5	1.27	2.4	6	ns	3.2	14	.040	2.4	14	.040
Play	ROM-sender	9	30.5	38.4	45	.004	60.7	45	.004	37.9	44	.005
	ROM-receiver	10	23.1	27.3	45	.004	45.6	55	.002	30	54	.003
	LPS-sender	8	.75	.88	18	ns	1	20	ns	.88	21	ns
	LPS-receiver	5	.76	1.6	12	ns	.4	4	ns	1	9	ns
	OMTF-sender	3	.75	1	3	ns	1	3	ns	0	0	ns
	OMTF-receiver	2	_	_	_	ns	_	_	ns	_	_	ns
	OSBT-sender	4	1.11	1	4	ns	1.25	5	ns	2	8	ns
	OSBT-receiver	5	.91	1.4	9	ns	1.8	12	ns	2	14	.04
submissive	ROM-sender	3	.012	0	0	ns	0	0	ns	.33	3	ns
	ROM-receiver	2	_	_	_	ns	_	_	ns	_	_	ns
	LPS-sender	1	_	_	_	ns	_	_	ns	_	_	ns
	LPS-receiver	0	_	_	_	ns	_	_	ns	_	_	ns
	OMTF-sender	2	_	_	_	ns	_	_	ns	_	_	ns
	OMTF-receiver	3	1.04	1.67	3	ns	3.33	.17	ns	3.67	5	ns
	OSBT-sender	2	_	_	_	ns	_	_	ns	_	_	ns
	OSBT-receiver	2	_	_	_	ns	_	_	ns	_	_	ns
aggressive	ROM-sender	5	.29	.8	9	ns	.8	5	ns	.6	5	ns
	ROM-receiver	5	.43	1.2	12	ns	.4	5	ns	.6	5	ns
	LPS-sender	0	_	_	_	ns	_	_	ns	_	_	ns
	LPS-receiver	0	_	_	_	ns	_	_	ns	_	_	ns

Table 3 (continued)

context	facial display	*n*	expected	time interval								
				–1			0			+1		
				observed	*t*	*p*	observed	*t*	*p*	observed	*t*	*p*
	OMTF-sender	10	6.41	10.6	48	.016	20.1	55	.002	9.4	45	.036
	OMTF-receiver	4	4.45	9.5	10	ns	10	9	ns	3.5	2	ns
	OSBT-sender	1	_	_	_	ns	_	_	ns	_	_	ns
	OSBT-receiver	0	_	_	_	ns	_	_	ns	_	_	ns
reciprocity	ROM	10	8.54	10.8	41	ns	31.8	55	.002	11.9	47	.023
	LPS	3	.3	1.33	3	ns	1	3	ns	0	0	ns
	OMTF	4	3.37	8.25	10	.034	9.5	9	ns	3	3	ns
	OSBT	3	.63	1.67	3	ns	4.33	6	ns	2.67	5	ns

For each facial display, we assessed whether there was a significant relationship between the facial display and the behavior of the sender (intrasender sequence) and the receiver (interaction sequence) We carried out comparisons between expected and observed rates for time intervals –1, 0, and + 1 (Wilcoxon matched-pairs test, 1-tailed). The last row indicates whether the receiver has reciprocated the display by performing the same display within the same 10-s interval.

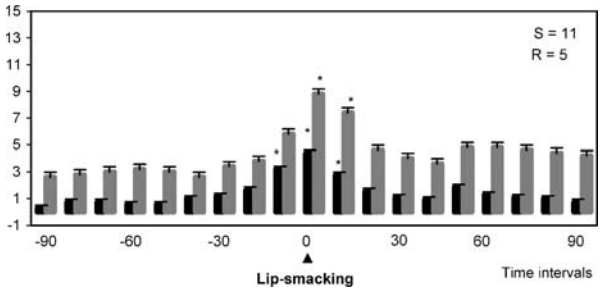

Fig. 3 Lip-smacking display. Behavioral sequence in the affiliative context. Lip-smacking occurs at interval 0 (on the abscissa); time intervals at 10 s extend from 90 s before the occurrence of the lip-smacking display until 90 s after it. Intrasender sequences (black bars) and interaction sequences (dotted bars) show the frequencies of the affiliative behaviors performed by the sender and receiver of the display, respectively. S indicates the number of senders and R indicates the number of receivers present in the analysis.

Open-mouth threat-face display We did not consider the open-mouth threat-face displays directed to external stimuli outside cages, but instead focused on the displays performed during social interactions among group members. In capuchins, the open-mouth threat-face display has several degrees of intensity. It lasts for some time, from a few s up to nearly a min, and it is typically associated with a frozen threatening body posture. White-faced capuchins performed 15.3% of the open-mouth threat-face jointly with another individual in their typical overlord position (Fig. 1; Fragaszy *et al*. 2004; Oppenheimer 1973). Adults performed 89.0% and received 72.0% of the 73 observed open-mouth threat-face display, corrected for the number of the subjects in the respective age class. The open-mouth threat-face display is significantly associated with agonistic behaviors performed by the sender of the display (interval 0: $n=10$, $t=55$, $p<0.05$, Wilcoxon matched-pairs test, 1-tailed: Fig. 4; Table 3). In contrast, for the receivers of open-mouth threat-face display there is no significant association with either agonistic or submissive

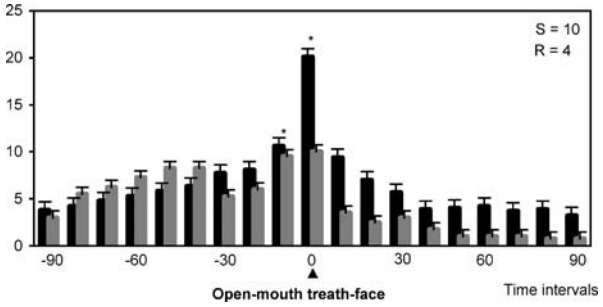

Fig. 4 Open-mouth threat-face display. Behavioral sequence in an agonistic context. The open-mouth threat-face display occurs at interval 0 (on the abscissa). Time intervals at 10 s extend from 90 s before the occurrence of the open-mouth threat-face display until 90 s after it. Intrasender sequences (black bars) and interaction sequences (dotted bars) show the frequencies of the agonistic behaviors performed by the sender and receiver of the display, respectively. S indicates the number of senders and R indicates the number of receivers present in the analysis.

behaviors. Subjects exchanged the display bidirectionally (Mantel's Z test, r=0.439, p=0.0003, 2-tailed) and reciprocally (interval –1: n=4, t=10, p<0.05, Wilcoxon matched-pairs test, 1-tailed). There is no association between open-mouth threat-face displays and affiliative or play behaviors (Table 3).

Silent bared-teeth display. We observed 37 silent bared-teeth displays. Infants and juveniles performed 41.9% of them and they received 84.8% of them (corrected for the number of the subjects in the respective age classes). The α-male and the α-female received, respectively, only 4.7% and 9.4% of all silent bared-teeth displays. Due to the low rate at which the capuchins performed the display it was impossible to compare for each subject the expected and observed rates via the Wilcoxon matched-pairs test. Therefore, we cumulated the data for all individuals performing it and assessed whether the total number of occurrences scored for each interval deviated significantly from the value expected on average over the 3 min time period via a binomial test (Preuschoft 1995). Our results show that when a subject received a silent bared-teeth display, it was engaged in affiliative behaviors (interval 0: p< 0.05). When it exhibited the display, the association with affiliative behaviors approached statistical significance (p=0.057; Fig. 5). The display was neither bidirectional nor reciprocal. PPEH analysis indicated that silent bared-teeth displays are not associated with play and submissive behaviors or occur in response to received aggression.

Open-mouth silent bared-teeth display We observed a total of 47 open-mouth silent bared-teeth displays. Infants and juveniles performed 34.7% of the silent bared-teeth displays and received 52.0% of them (corrected for the number of subjects in the respective age classes). The display is significantly associated with affiliative behaviors both when performed (interval 0: n=5, t=15, p<0.05, Wilcoxon matched-pairs test, 1-tailed) and when received (interval 0: n=5, t=14, p<0.05, Wilcoxon matched-pairs test, 1-tailed: Fig. 6; Table 3). For the receivers of open-mouth silent bared-teeth displays there is a significant association with play behaviors (interval + 1: n=5, t=14, p<0.05, Wilcoxon matched-pairs test, 1-tailed). Further, we observed an adult female engaged in agonistic behaviors while performing the display. The

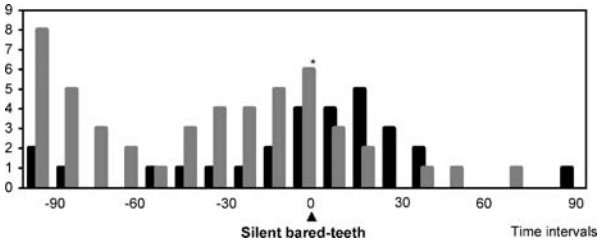

Fig. 5 Silent bared-teeth display. Behavioral sequence in an affiliative context. The silent bared-teeth display occurs at interval 0 (on the abscissa); time intervals at 10 s extend from 90 s before the occurrence of the silent bared-teeth display until 90 s after it. Intrasender sequences (black bars) and interaction sequences (grey bars) show the frequencies of the affiliative behaviors performed by the sender and receiver of the display, respectively.

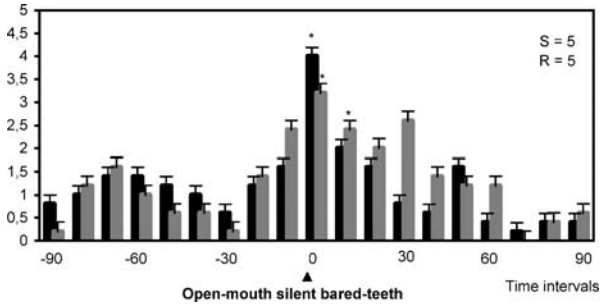

Fig. 6 Open-mouth silent bared-teeth display. Behavioral sequence in an affiliative context. The open-mouth silent bared-teeth display occurs at interval 0 (on the abscissa); time intervals at 10 s extend from 90 s before the occurrence of the open-mouth silent bared-teeth display until 90 s after it. Intrasender sequences (black bars) and interaction sequences (grey bars) show the frequencies of affiliative behaviors performed by the sender and receiver of the display, respectively. S indicates the number of senders and R indicates the number of receivers present in the analysis.

open-mouth silent bared-teeth display was bidirectional (Mantel's Z test, r=0.542, p=0.0003, 2-tailed), but subjects did not exchange it reciprocally (Table 3).

Discussion

White-faced capuchins use 6 distinct facial displays to communicate: relaxed open-mouth, lip-smacking, open-mouth threat-face, silent bared-teeth, open-mouth silent bared-teeth, and protruded-lip face. Tufted capuchins exhibit the same facial displays (Visalberghi *et al*. 2006; Weigel 1979). However, *Cebus capucinus* perform lip-smacking and the silent bared-teeth displays in a milder form and open-mouth threat-face displays are of longer average duration than in *C. apella*. Moreover, white-faced capuchins do not perform the scalp-lifting display (a quick raising of the scalp and the eyebrows) or exhibit movements of the scalp in association with other facial displays. Contrarily, scalp-lifting is one of the most common displays characterizing sexual behavior in tufted capuchins (Carosi and Visalberghi 2002), and scalp retraction often occurs in association with other facial displays (De Marco and Visalberghi 2007; Visalberghi *et al*. 2006). For example, during threat displays tufted capuchins raise their eyebrows dramatically, whereas white-faced capuchins lower them into a mild frown (Freese and Oppenheimer 1981). Capuchins, like other primate species, possess distinctive facial markings, such as hair patterns and skin coloration, that make them easily identifiable belonging to the same species and that emphasize differences between facial displays (Chevalier-Skolnikoff 1973; Fragaszy *et al*. 2004). According to Weigel (1979), the faces of tufted capuchins have conspicuously contrasting areas that accentuate the display of retracting the forehead. The typically prominent tufts, which are raised up and backwards into a fluttering movement, emphasize the scalp-lifting display. Moreover, when retraction of the scalp occurs simultaneously with other facial displays such as silent bared-teeth or lip-smacking, the displays are more salient and function more effectively to catch the attention of a conspecific (Visalberghi *et al*. 2006). The lack of scalp-lifting

in white-faced capuchins can be accounted for the different characteristics of hair patterns and skin colors and by the differing degree of mildness of repertoire of the facial displays between the 2 species.

Sociodemographic variables had little influence on the distribution of the facial displays: white-faced capuchins exchange facial displays whatever their degree of kinship, affiliation or dominance. The findings are consistent with results of previous studies showing that white-faced capuchins have high levels of interindividual tolerance in social interactions (Fedigan 1993; Leca *et al.* 2002, 2003; Perry 1996; Rose 1997) and that positive social interactions are more frequent and more distributed than in tufted capuchins (Leca *et al.* 2007). According to the covariation hypothesis, interconnections between traits constrain the expression of behavioral patterns and any significant variation in a single character induces a set of correlated changes (Thierry 2000, 2004). For example, in *Macaca*, the covariation between traits characterizes the expression of many social patterns, such as conflict management, dominance asymmetry, kinship networks, and group cohesiveness (Petit *et al.* 1992, 1997; Preuschoft and van Schaik 2000; Thierry 1990; Thierry *et al.* 1997). In capuchins, the form of fur-rubbing behaviors appears to covary with their differing dominance styles (Leca *et al.* 2007); the high frequency of social and distributed fur rubbing in white-faced capuchins and the high frequency of solitary fur rubbing related to dominance and kinship in tufted capuchins might be associated with the different social relationships in the 2 species. Likewise, in capuchins, the social function of facial displays appears to covary with the specific style of social relationships. One could characterize social relationships of white-faced capuchins as being open and tolerant (Leca *et al.* 2002, 2007), and they perform all facial displays, with the exception of the threat face, to communicate affiliation or playfulness.

When considering the social function of each facial display, the relaxed open-mouth typically accompanies social play in primates (Preuschoft and van Hooff 1997; Redican 1975; van Hooff 1967, 1972; van Hooff and Preuschoft 2003). In this respect, white-faced capuchins are not an exception. In fact, play face was the most frequent facial display, mostly by young capuchins. Subjects exchanged the relaxed open-mouth display bidirectionally as well as reciprocally: usually, during play interactions, both partners give the relaxed open-mouth display at the same time.

Researchers had not reported lip-smacking in white-faced capuchins (Oppenheimer 1973), in contrast to tufted capuchins (Weigel 1979; Visalberghi *et al.* 2006; De Marco and Visalberghi 2007), probably because it is not easy to observe in white-faced capuchins, which perform it in a very mild form, typically when very close to their partners. In primates, the lip-smacking display may occur in a very wide variety of social circumstances, including grooming, copulation, greeting, and antagonism (Redican 1975).We noted that in white-faced capuchins lip-smacking conveys a positive message and promotes affiliative interactions. It is directed almost exclusively toward infants and juveniles; it is bidirectional, but often it is not reciprocated. In general, non-kin and far-kin exchange more lip-smacking displays than close-kin do, as in tufted capuchins (De Marco and Visalberghi 2007). Among white-faced capuchins, the mother is the partner that exchanges the smallest number of lip-smacking displays with her offspring.

The silent bared-teeth display occurs less frequently in the white-faced capuchin group. In Old World primates, it conveys different messages according to the gradient of

dominance in the species. In species with high-power asymmetry and a despotic dominance style the silent bared-teeth display indicates formal subordination (*Macaca fascicularis*, Preuschoft *et al*. 1995; *M. mulatta*, de Waal and Luttrell 1985; *M. nemestrina*, Preuschoft 2004), whereas in species with a more relaxed dominance style it signals peaceful intentions and serves to initiate sociopositive interactions (*M. tonkeana*, de Waal 2003; Preuschoft 1995; Thierry 2000;Thierry *et al*. 1989). In tufted capuchins, the silent bared-teeth display signals submission when performed toward high-ranking individuals (Visalberghi *et al*. 2006; Weigel 1979). We observed that white-faced capuchins use the silent bared-teeth display exclusively for affiliative interactions and often perform it toward young individuals. Therefore, white-faced capuchins seem to lack a facial display to indicate subordination even though they live within a dominance hierarchy (*cf*. Perry and Manson 2004). According to the power asymmetry hypothesis (Preuschoft and van Hooff 1995, 1997), the finding that in white-faced capuchins the silent bared-teeth display conveys an affiliative message provides further support for the view that capuchins have relaxed social relationships (Leca *et al*. 2002, 2003, 2007; Jack 2003; Perry and Rose 1994; Rose 1994). However, because tufted capuchins use the silent bared-teeth differently and it is possibly related to group composition (Visalberghi *et al*. 2006), firm conclusions require systematic observations of more groups of both species.

The open-mouth threat-face is the only white-faced capuchin display associated with a non-sociopositive context. It is associated with a typical frozen threat posture, in which the white areas of the face, the shoulders, and the chest are fully exposed

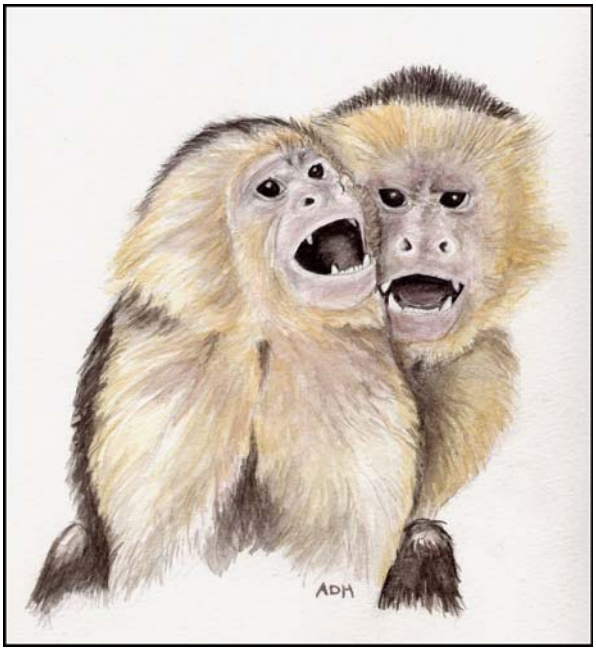

Fig. 7 Two adult individuals perform an open-mouth threat-face display jointly, in the typical overlord position. (Drawing by A. De Marco).

(Oppenheimer 1973), and the tail is not raised (*pers. obs*.). Performed mostly by adults, it sometimes occurs jointly with ≥1 individual(s) riding on the back of the partner, or embracing it, and aligning their heads in an overlord position (Fig. 7; Fragaszy *et al*. 2004; Oppenheimer 1973). The finding that white-faced capuchins exchange the open-mouth threat-face bidirectionally and reciprocally, whereas tufted capuchins do not (Visalberghi *et al*. 2006), further stresses the relaxed dominance relationships of the latter species.

In future studies, one should consider the open-mouth silent bared-teeth display whose social function in the white-faced capuchins ranged from affiliative/play contexts to agonistic ones.

In conclusion, the communicative functions of white-faced capuchin facial displays agree with their typically relaxed interindividual relationships. Our data suggest covariation between the social function of facial displays and social organization of *Cebus capucinus* and *C. apella*. However, to test the covariation hypothesis properly we need further interspecific comparative studies on social behavioral patterns in other groups of the same species and in other capuchins, as has been done with macaques. This is particularly important because capuchins, like macaques (Thierry 2000), show great variability in genetic, life-history, and social characteristics (Fragaszy *et al*. 1990, 2004), and such variability is likely to be reflected by systematic differences in the shape and function of their facial displays.

Acknowledgments We thank the Primate Centre of the Louis Pasteur University of Strasbourg, which hosted the *Cebus capucinus* group we studied. We thank Signe Preuschoft for providing us with Pre-Post-Event Histogram (PPEH) and Cécile Schweitzer for occasional assistance in data collection. We also thank Bernard Thierry for fruitful comments. We received financial support from grant RBNE01SZB4 from FIRB/MIUR. We also thank Lewis Halsey, who provided assistance in language editing of the manuscript.

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