RESEARCH ARTICLE

The Behavioral Context of Visual Displays in Common Marmosets (Callithrix jacchus)

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Communication is important in social species, and may occur with the use of visual, olfactory or auditory signals. However, visual communication may be hampered in species that are arboreal have elaborate facial coloring and live in small groups. The common marmoset fits these criteria and may have limited visual communication. Nonetheless, some (contradictive) propositions concerning visual displays in the common marmoset have been made, yet quantitative data are lacking. The aim of this study was to assign a behavioral context to different visual displays using pre–post-event–analyses. Focal observations were conducted on 16 captive adult and sub-adult marmosets in three different family groups. Based on behavioral elements with an unambiguous meaning, four different behavioral contexts were distinguished: aggression, fear, affiliation, and play behavior. Visual displays concerned behavior that included facial expressions, body postures, and pilo-erection of the fur. Visual displays related to aggression, fear, and play/affiliation were consistent with the literature. We propose that the visual display “pilo-erection tip of tail” is related to fear. Individuals receiving these fear signals showed a higher rate of affiliative behavior. This study indicates that several visual displays may provide cues or signals of particular social contexts. Since the three displays of fear elicited an affiliative response, they may communicate a request of anxiety reduction or signal an external referent. Concluding, common marmosets, despite being arboreal and living in small groups, use several visual displays to communicate with conspecifics and their facial coloration may not hamper, but actually promote the visibility of visual displays. Am. J. Primatol. 75:1084–1095, 2013.

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INTRODUCTION

In highly social animals, such as primates, communication among conspecifics is crucial [Burrows, 2008]. Evolution of communication systems may have been shaped by ecological and social conditions and different modalities of communication may be differentially suited for specific environmental conditions. Recently, it was shown that New World primates that live in small social groups have facial color patterns that are more complex than those living in large groups [Santana et al., 2012]. It was suggested that the species living in small groups with elaborate facial color patterns may communicate with a restricted number of facial expressions, and that there may be a trade-off between these traits [Santana et al., 2012]. Furthermore, species living in trees are confronted with low visibility, which may render the use of auditory communication more important than visual communication in arboreal species [De La Torre & Snowdon, 2002; Epple, 1968; Martins Bezerra & Souto, 2008; Martins Bezerra et al., 2009; but see Dobson, 2009].

Animals may communicate not only about internal states but also about external referents, eliciting also the appropriate reaction from the receiver in the absence of the stimulus triggering the signal in the sender. Such functionally

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referential signals were first described for vocal communication [vervet monkeys, *Cercopithecus aethiops*; Seyfarth et al., 1980; review: Cásar & Zuberbühler, 2012]. Functionally, referential calls have been interpreted to share qualities with human “words,” yet different views exist concerning the concept’s future usefulness [favorable: Townsend & Manser, 2012; unfavorable: Wheeler & Fischer, 2012]. In contrast, others employ the concept to encompass non-vocal communication, such as the use of favorable or aversial facial expressions to decide which box to open [great apes: Buttelmann et al., 2009; tufted capuchin monkeys, *Cebus apella*: Morimoto & Fujita, 2011, 2012; dogs, *Canis familiaris*: Buttelmann & Tomasello, 2013] and gestures to enlist joint attention [raven, *Corvus corax*: Pika & Bugnyar, 2011], exploring whether the signals contain information that the receiver can use to exhibit the appropriate behavior.

The common marmoset (*Callithrix jacchus*), an arboreal New World monkey living in cooperatively breeding family groups [Lazaro-Perea, 2001] of 3–15 individuals [Ferrari & Lopes Ferrari, 1989; Stevenson & Rylands, 1988], is an example of a species that may be restricted in the use of visual communication. It is a small monkey [±18 cm; Cawthon-Lang, 2005b], consequently making its expressions difficult to distinguish from a distance, especially when combined with living in a low-visibility environment. Indeed, olfactory signals, for example, scent marking [Moynihan, 1967], and auditory communication [DIGBY, 1995; Martins Bezerra & Souto, 2008], including ultrasonic sounds [EPPLIE, 1968; perception of ultrasonic sounds: Osianski & Wang, 2011], are important in the common marmoset. Taken together, this has led to the assumption that marmosets possess a limited repertoire of facial expressions [DOBSON, 2009] and have a “pokerface” [Moynihan, 1967].

Marmosets are, however, capable of making facial expressions. They have quite specialized facial muscles around the nasolabial region and ear that are comparable to the facial muscles of haplorhine primates that display complicated facial expressions, such as macaques and chimpanzees [Burrows, 2008; Burrows et al., 2006]. Other muscles are arranged in a more primitive way, such as the connecting muscle between mouth and ears [Burrows, 2008]. Furthermore, arboreal habitation requires sharp binocular vision [Van Hooff, 1967] and marmosets have the typical primate trait of being highly visual with a well-developed visual nervous system [Stellar, 1960] and are sensitive to visual cues from conspecifics [Snowdon, 2001]. Thus, it is expected that marmosets are physically capable of making and perceiving at least a few facial expressions.

Moreover, common marmosets show pilo-erection of fur on body and tail and have conspicuously colored ear tufts that can be placed at different positions [Moynihan, 1967; Stevenson & Poole, 1976]. Therefore, we may have to broaden the term visual communication from facial expressions to include the use of the entire body as a “visual display.” Several studies have described these visual displays in common marmosets (Table I). The oldest literature suggests visual displays to be meaningless [Moynihan, 1967], but more recent papers assign a function in social behavior contexts to these displays, such as aggression or sex. However, the context in which a particular visual display is used is not always clear (Table I) and quantitative data on the link between a visual display and behavioral context are missing. Thus, although it seems probable that they use visual displays for communication, it has not always been clarified what their message or meaning is (Table I).

The first step to elucidate the communicative and social value of any behavior is to determine in which context it is being displayed. Although context suggests a message of a display, it does not directly give evidence for a communicative function, since it may just be the reaction of one individual to the context, for example, replacement behavior, and not elicit any reactions in other individuals. We therefore analyzed, where possible, sequences of both giving and receiving a certain visual display. If receiving a visual display can be linked to a specific reaction from the receiver, it is an indication that the visual display is used for communication and when indicating an external referent it may even have functional reference.

Understanding social communication improves management of captive primate groups. Visual signals used in social contexts may indicate to us whether groups are socially harmonious or whether welfare problems exist. Since this species is often used in biomedical research, an understanding of the common marmoset’s visual communication system is especially important.

This study aims to assign a social behavioral context to visual displays exhibited by the common marmoset. A “visual display” could entail a facial expression, body posture, and/or the pilo-rection of the fur. Four general “behavioral contexts” were determined by observing a variety of independent behaviors that were known to unambiguously indicate aggression, fear, affiliation, or play. Visual displays were linked to behavioral contexts with the use of pre–post-event-analyses. These analyses compare the frequency of occurrence of a behavioral context in temporal association with a visual display [De Marco et al., 2008; Preuschoft et al., 1995; Visalberghi et al., 2006]. This method has the advantage to statistically validate a connection between a visual display and a behavioral context.

**METHODS**

**Study Subjects**

Three common marmoset family groups, each consisting of eight individuals, were observed at the
| VSB                      | Description                                                                 | A      | D      | F       | G       | P       | S       | O       |
|-------------------------|-----------------------------------------------------------------------------|--------|--------|---------|---------|---------|---------|---------|
| Arched bristle          | The back is arched (bend upwards) while the complete fur is maximally pilo-erected. | + [1; 5] | + [3; 4] |
| Bared teeth             | The lips are retracted so that teeth are visible, although not completely. Gums remain invisible. Upper and lower teeth may be partially parted or remain together. | + [4; 5] |
| Coiled tail             | At least one-third of the tail is coiled.                                   | + [4]  |
| Head tilt               | The head is tilted to either the left or the right while staring at an object or individual. | + [1]  | + [8]a |
| Hind legs               | The marmoset is standing only on its hind legs with arms outstretched. The hind legs are slightly bend or stretched out completely. | + [4]  |
| Hind legs rampant       | Essentially the same behavior as "hind legs," but here hands are touching an object. It seems that the object is used for leaning. | + [4]  |
| Mouth half open         | The mouth is partially opened. The lips are opened a bit, but teeth are not visible or at least not entirely. The lips are not retracted. | + [4]  |
| Open mouth              | The mouth is opened widely, with teeth showing but not accompanied with the retraction of the lips. | + [6]b | + [4]  | + [4]  |
| Pilo-erection anterior  | The fur is pilo-erected on the anterior part of the body.                   | + [4]  | + [4]  |
| Pilo-erection base tail | The fur is pilo-erected on the base of the tail.                           | + [4]  | + [4]  |
| Pilo-erection complete tail | The fur is pilo-erected on the complete tail.                          | + [4]  | + [4]  |
| Side to side            | While fixating an object or individual the head is moved from side to side on the horizontal plane. | + [3; 10] | + [1; 7] |
| Slit stare              | The eyes are narrowed to slits and fixate an object or individual. Often the head is tilted backwards a bit while showing this behavior. | + [4; 7] | + [4]  |
| Stare                   | The marmoset is fixating an object or individual by intensely staring at it. | + [6]c |
| Tongue in-out           | A portion of the tongue is moved in and out of the mouth quickly. May be repeated several times. | + [4]  | + [4]  | + [2]  | + [4; 9] |
| Tufts down              | The tufts are moved partially or completely down on the vertical plane and partially or completely backwards on the horizontal plane, so that the tufts are folded backwards against the marmoset its head. | + [4; 5] |
| Tufts up                | The tufts are rapidly moved back and forth on the horizontal plane.        | + [4]  |
| Tufts up                | The tufts are moved upwards in a higher position than in the "neutral" position. Almost all hairs in the tufts point upwards. | + [4]  |

Note: Distinguished are a context of A: aggression; D: defensive threat; F: fear/anxiety; G: affiliation; P: play; S: sex; and O: other. References: 1. Moynihan [1967, 1970]; 2. Sparks [1967]; 3. Epple [1968]; 4. Stevenson and Poole [1976]; 5. Sutcliffe and Poole [1984]; 6. Digby [1995]; 7. Cilia and Piper [1997]; 8. Kaplan and Rogers [1999, 2006]; 9. Gerber and Schnell [2004]; 10. Barros et al. [2007].

*aExploratory behavior.

*bCombined with stare.

*cCombined with open mouth.
Biomedical Primate Research Centre in Rijswijk, the Netherlands. Marmoset breeding pairs typically produce twin offspring every 5 months [Sutcliffe & Poole, 1984]. The groups consisted of one breeding pair and three generations of its twin offspring. Sixteen adults (>14 months) or sub-adults (>9–14 months) [cf., Cawthon-Lang, 2005a] from three different family groups were observed for this study (Table II). We excluded infants and juveniles, since their behavior may differ from that of adults and sub-adults [as found for vocalizations, see Martins Bezerra & Souto, 2008; Martins Bezerra et al., 2009]. Dominance within a group is thought to be age-dependent, with older individuals occupying a higher dominance position than younger (immature) ones [Sutcliffe & Poole, 1984].

Animals were housed in an inside enclosure of 2 × 2 × 3 m connected to an outside enclosure of 2 × 2 × 3 m. Standard enrichment, such as branches, boxes, baskets, garden ropes, fire hoses, and nets, were always present in the cages. In addition, a different additional play object was presented every week. The cages were equipped with bio floors containing crickets and other insects that were available for the marmosets [Vernes & Louwerse, 2010]. The marmosets were fed monkey chow (Sniff®) in the morning and this was replenished if necessary at the end of the afternoon. As a complement Arabic gum, fruit, raisins, biscuits, or puffed wheat with honey were given once a day. Water was available ad libitum.

**Observations**

Pre–post event observations concern the significant association in time between a visual display (the event at point zero) and a particular behavioral context by comparing behavioral rates at specific time points with a baseline. Therefore, interactions between individuals were followed in detail, including who gives and who receives the behavior, and these were collected with focal observations.

Focal observations [Box, 1975; Martin & Bateson, 1993] were collected during a 4-month period (December 2010–March 2011). Observations were carried out between 09.30–12.00 and 13.00–15.30 hr. The timing of the observations was balanced over the day, to exclude effects of time of the day. Subjects were observed on average 293 min (mean: 293.13 min, standard deviation: 4.43 min). The focal observations of December and January were 10 min long, those in February and March were 20 min (see below for an explanation). Two weeks before the observation period started, the marmosets were habituated to the observer (RAdB) sitting in front of their cage.

The ethogram used in this study was based on published descriptions of common marmoset behavior [Barros et al., 2007; Cilia & Piper, 1997; Digby, 1995; Epple, 1968; Gerber & Schnell, 2004; Kaplan & Rogers, 1999, 2006; Moynihan, 1967, 1970; Sparks, 1967; Stevenson & Poole, 1976; Sutcliffe & Poole, 1984; see also www.marmosetcare.com]. Two types of behavior were distinguished. First, we identified behavior that can be unequivocally related to one behavioral context, distinguishing four contexts: aggressive, fear, affiliation, and play behavior. These behaviors were either actions or vocalizations that in the literature were assigned to a specific behavioral context. We did not observe sexual behavior in the observation period and, therefore, could not distinguish a sexual context. Second, we identified "visual displays," entailing a facial expression, body posture, and/or the (partial) pilo-rectio of the fur (Table I; Fig. 1; Supplementary Video).

The behavioral context “aggression” consists of both intra-group and inter-group aggressive behavior (i.e., chase, cuff, fight, lift tail, push, slap/claw, snap bite, uninhibited bite, chatter, tsetsetse, twitter,

**TABLE II. Groups and Subjects Observed**

| Name | Sex | Birth date | Age category |
|------|-----|------------|--------------|
| AL   | M   | Not known  | Adult        |
| SP   | F   | Not known  | Adult        |
| BO   | F   | 12-6-2009  | Adult        |
| QU   | M   | 12-6-2009  | Adult        |
| HA   | F   | 18-4-2010  | Sub-adult    |
| LA   | F   | 18-4-2010  | Sub-adult    |
| PA   | F   | 20-9-2010  | Infant       |
| TR   | F   | 20-9-2010  | Infant       |
| GE   | M   | 23-1-2004  | Adult        |
| JU   | F   | 6-5-2004   | Adult        |
| CL   | M   | 12-4-2009  | Adult        |
| KE   | M   | 12-4-2009  | Adult        |
| HO   | M   | 12-6-2010  | Juvenile     |
| MA   | F   | 12-6-2010  | Juvenile     |
| FO   | M   | 15-11-2010 | Infant       |
| GU   | M   | 15-11-2010 | Infant       |
| MU   | F   | Not known  | Adult        |
| ZA   | M   | Not known  | Adult        |
| BA   | M   | 9-8-2009   | Adult        |
| NE   | F   | 9-8-2009   | Adult        |
| FI   | F   | 6-1-2010   | Sub-adult    |
| GI   | F   | 6-1-2010   | Sub-adult    |
| OD   | M   | 6-7-2010   | Infant       |
| PI   | F   | 6-7-2010   | Infant       |

*Day-Month-Year format used.
receiving of: cringe, escape, squeal, withdrawal posture and scream). Intra-group aggression was seen in all three social groups, but occurred at low rates. However, all groups regularly responded aggressively to neighboring groups. The characteristic “twitter” vocalization, indicating intergroup aggression [Epple, 1968; Martins Bezerra & Souto, 2008], was heard often. Inter- and intra-group aggression were collapsed into one context, in order to obtain sufficient aggressive interactions for statistical analyses. The behavioral context “fear” consisted of behavior that indicated submission, fear or anxiety (i.e., cringe, escape, flee, mob, scratch, self-groom, startle response, wet dog shake, withdrawal posture, alarm call, egg and egg, squeal, scream, tsik, receiving of: chase, cuf, snap bite, push, slap/claw, and uninhibited bite). “Affiliation” was comprised of behavior that was considered friendly or positive social behavior (i.e., allogroom, approach, being together, body rub, carry infant, follow, grooming invitation, huddle, hug, lick, nuzzle rub, share food, suckle and transfer infant). Lastly, “play” included behavior seen in play (i.e., bounce, extricate, grip, mock bite, object play, play chase, play escape, play invitation, play wrestle, sliding on side, somersault, and stalk).

Visual displays concern facial expressions that is movement of tufts, eyes, mouth, or tongue; body postures that is arching back, raising body, and pilo-reaction on the whole or part of the tail or back (Table I). For all but one of these visual displays at least one behavioral context has been reported in the literature, but often more than one context has been suggested, indicating that no clear consensus exists on their meaning (Table I).

Observations were conducted using The Observer (version XT 9.0). Data were entered in the format: focal animal; the behavior; recipient of behavior. The behavior could either be a visual display or aggressive, fear, affiliation and play behavior defining a context. For both these context-defining behaviors and visual displays the direction was noted that is “giving” or “receiving”. However, of seven visual displays (i.e., “coiled tail,” “head tilt,” “hind legs,” “hind legs rampant,” “side to side,” “tongue in-out”), the head and visual attention of the sending individual were typically not aimed at another individual and, therefore, it was difficult to determine whether these behaviors were directed to one specific individual. Therefore, only “giving” and not “receiving” these visual displays was analyzed.

Analyses

The aim of the pre–post-event analysis was to test whether certain visual displays were found in
close association with the presence or absence of behavior defining a particular context, following the methods of Preuschoft et al. [1995]. When a visual display was recorded during a focal observation, a time window of 3 min before and 3 min after the visual display was examined to calculate the baseline rate of behavior determining each context (Fig. 2). The time window was subdivided into blocks of 10 sec. We used 0/1 sampling to note in each “10-sec block” if any behavior that was part of a behavioral context was absent or present. These behaviors included both state and point behaviors. Thus, although several behaviors of one behavioral context could be displayed within a 10-sec block, the maximum score for each context in each time block was 1. The counting was done separately for all focal animals and for all behavioral contexts and visual displays.

The timing of a visual display within a focal observation varied, and sometimes we did not observe the full 3 min before or after the visual display was seen. Therefore, we sometimes analyzed incomplete time frames with only the full 3 min before or after the physical appearance. Instead of discarding these data, we corrected for the number of times each 10-sec block was observed. To do so, all 10-sec block counts were divided by the number of times that block was observed. To increase the number of visual display observations with a full 6 min block, we conducted focal observations of 20 min in the second half of the study.

For each visual display, we calculated per individual for each 10-sec block the rate of each behavioral context. Next, we calculated for each 10-sec block the average rate for all individuals that showed a particular visual display. Subsequently, the “baseline” rate for each of the four behavioral contexts was calculated by averaging the absence or presence of behavior over all 10-sec blocks of all

![Graph](Fig. 2. This figure provides the detailed presentation of the PPE analysis for the visual display “arched bristle.” Box plots indicate the median of the distribution in the rate of aggression. Each box plot represents 10 sec. The visual display is given at time 0. Before and after this visual display, the X-axis displays eighteen 10-sec blocks, totaling 3 min. For each 10-sec block the median of the distribution of behavior signifying this context, in this case aggressive behavior, is provided with a box plot. The baseline frequency of the behavioral context was calculated from these data and is indicated here by the black line. Figures 3 and 4 provide the base line and the box plots from 10-sec block —2 to 2. The horizontal line indicates the average rate, “*” indicates a significant difference from the average.)
animals over the 6 min time span surrounding the visual display (the solid line in the figures). We regarded 6 min as long enough for a rapid-moving animal such as the common marmoset to represent a reliable baseline.

We analyzed whether certain behavioral contexts were more often or less often seen in close temporal association with the visual displays. We concentrated the analysis on the five 10-sec blocks that directly surrounded the visual display (−20 sec, −10 sec, 10 sec in which the element was shown, plus 10 sec and plus 20 sec), as Preuschoft et al. [1995] has shown that these points were specifically important in indicating the relation between a visual display and behavioral context. The division into 10-sec blocks also gave us the opportunity to note quick responses to a visual display. Henceforth, these surrounding 10-sec blocks will be referred to as time −2, −1, 0, 1, and 2.

We tested for animals for each of the five surrounding blocks to see whether the mean frequency of a particular behavioral context was significantly higher than the baseline. The variation between animals was taken into account by comparing the frequency for each animal separately with the baseline of the behavioral context. Thus, the chance of a bias due to outliers in the data was minimized. All individual values were compared to the baseline using a Wilcoxon-signed rank test (PSAW Statistics 18). The significance level was set at 0.05, however, since for each visual display five tests were done for each social behavior context, a Bonferroni correction was applied resulting in an alpha value of 0.01.

Fig. 3. Box plots indicate the median of the distribution in the rate of fear behavior in the 20 sec preceding and following a: giving and b: receiving “pilo-erection complete tail.” Each box plot represents 10 sec. The visual display “pilo-erection complete tail” is a: given or b: received at time 0. The horizontal line indicates the average rate, * indicates a significant difference from the average.

Fig. 4. Box plots indicate the median of the distribution in the rate of play behavior in the 20 sec preceding and following a: giving and b: receiving “open mouth.” Each box plot represents 10 sec. The visual display “open mouth” is a: given or b: received at time 0. The horizontal line indicates the average rate, * indicates a significant difference from the average.
Only visual displays where results had a $P$-value smaller than 0.01 (significant) or 0.05 (trend) are mentioned. All statistical tests were two-tailed.

RESULTS

The various visual displays were displayed by a differing number of subjects (Table III). Thirteen visual displays were exhibited by most or all individuals (between 13 and 16 individuals). Some visual displays were not shown by a sufficient number of individuals or were not frequently enough observed to yield meaningful results. Five visual displays were exhibited by most or all individuals (between 13 and 16 individuals). Some visual displays were not shown by a sufficient number of individuals or were not frequently enough observed to yield meaningful results. Five visual displays were exhibited by most or all individuals (between 13 and 16 individuals). Some visual displays were not shown by a sufficient number of individuals or were not frequently enough observed to yield meaningful results.

Visual Displays Related to Aggression

Two visual displays were related to the aggression context: “arched bristle” and “tufts up”. For the “arched bristle” signal (Fig. 2), the rate of aggressive behavior was significantly higher than baseline at time $-1$ and time 0 ($t = -1$, $n = 14, P = 0.003$; $t = 0$, $n = 14, P = 0.004$). For “give tufts up,” the rate was significantly higher than baseline at time 0 ($t = 0$, $n = 16, P = 0.006$) and a trend was found at time $-1$ and time $-2$ ($t = -1$, $n = 16, P = 0.03$; $t = -2$, $n = 16, P = 0.049$).

Visual Displays Related to Fear

Three displays showed a trend in relation with fear behavior, namely “pilo-rection of the complete tail,” “pilo-rection of the tail tip,” and “tufts down”. We found that “pilo-rection of the complete tail” ($t = -1$, $n = 16, P = 0.04$; $t = 0$, $n = 16, P = 0.02$; Fig. 3a), “pilo-rection of the tip of the tail” ($t = -1$, $n = 16, P = 0.04$) and “tufts down” ($t = 1$, $n = 16, P = 0.04$) tended to be related to the frequency of fear behavior.

Visual Displays Related to Affiliation

Individuals receiving “pilo-rection of the complete tail,” “pilo-rection of the tail tip,” and “tufts down,” the three visual displays related to fear behavior, were giving affiliative behavior in response. Receiving “pilo-rection complete tail” was significantly related to affiliative behavior at time 0 ($n = 13, t = 0, P = 0.003$) and tended to relate at time 1 and time 2 ($n = 13, t = 1, P = 0.02$; $n = 13, t = 2, P = 0.02$; Fig. 3b). Receiving “pilo-rection tip tail” tended to be related to higher frequencies at time 2 ($n = 11, t = 2, P = 0.03$). Receiving “tufts down” was significantly related to affiliation at time 0 and time 2 ($n = 13, t = 0, P = 0.006$; $n = 13, t = 2, P = 0.009$) and a trend was found at time 1 ($n = 13, t = 1, P = 0.04$).

| Visual display        | N, display giving/receiving observed | N, individuals giving/receiving display | Average rate giving (range) of all 16 individuals/hr | Average rate receiving (range) of all 16 individuals/hr |
|-----------------------|--------------------------------------|----------------------------------------|-------------------------------------------------------|--------------------------------------------------------|
| Arched bristle        | 311/18                               | 14/10                                  | 4.0 (0–15.9)                                          | 0.2 (0–0.8)                                           |
| Bared teeth           | 27/1                                 | 6/1                                    | 0.3 (0–3.9)                                          | 0.0 (0–0.2)                                           |
| Coil tail             | 122/–                                | 16/–                                   | 1.6 (0.4–3.7)                                        | —                                                      |
| Head tilt             | 549/–                                | 16/–                                   | 7.0 (2.6–13.8)                                       | —                                                      |
| Hind legs             | 63/–                                 | 13/–                                   | 0.8 (0–2.4)                                          | —                                                      |
| Hind legs rampant     | 194/–                                | 7/–                                    | 2.5 (0–37.4)                                         | —                                                      |
| Mouth half open       | 40/1                                 | 10/1                                   | 0.5 (0–3.5)                                          | 0.0 (0–0.2)                                           |
| Open mouth            | 108/80                               | 11/10                                  | 1.4 (0–6.2)                                          | 1.0 (0–3.1)                                           |
| Pilo-rection anterior | 21/2                                 | 9/2                                    | 0.3 (0–1.0)                                          | 0.0 (0–0.2)                                           |
| Pilo-rection base tail| 67/4                                 | 14/3                                   | 0.9 (0–4.6)                                          | 0.1 (0–0.4)                                           |
| Pilo-rection complete tail | 320/47                          | 16/13                                  | 4.1 (0.2–20.1)                                       | 0.6 (0–2.0)                                           |
| Pilo-rection tip tail | 142/25                               | 16/11                                  | 1.8 (0.2–9.7)                                        | 0.3 (0–1.0)                                           |
| Side to side          | 32/–                                 | 14/–                                   | 0.4 (0–1.7)                                          | —                                                      |
| Slit stare            | 36/5                                 | 13/4                                   | 0.5 (0–1.7)                                          | 0.1 (0–0.4)                                           |
| Stare                 | 94/0                                 | 15/0                                   | 1.2 (0–8.5)                                          | —                                                      |
| Tongue in-out         | 763/–                                | 16/–                                   | 9.8 (2.8–15.5)                                       | —                                                      |
| Tufts down            | 306/54                               | 16/13                                  | 3.9 (0.6–11.0)                                       | 0.7 (0–2.1)                                           |
| Tufts flick           | 10/1                                 | 6/1                                    | 0.1 (0–0.8)                                          | 0.0 (0–0.2)                                           |
| Tufts up              | 133/17                               | 16/10                                  | 1.7 (0.6–4.3)                                        | 0.2 (0–1.0)                                           |
In addition, giving “open mouth” was related to affiliative behavior. Affiliative behavior tended to be higher than baseline at time $-1$ and $0$ (n = 11, $t = -1$, $P = 0.026$; n = 11, $t = 0$, $P = 0.021$).

Visual Displays Related to Play

Both giving and receiving an “open mouth” were related to a play context. Play behavior tended to be shown more often than baseline at time $-1$ and time 1 of “give open mouth” (n = 11, $t = -1$, $P = 0.032$; n = 11, $t = 1$, $P = 0.021$) and at time 0 and time 1 of “receive open mouth” (n = 10, $t = 0$, $P = 0.009$; n = 10, $t = 1$, $P = 0.012$; Fig. 4a and b).

Visual Displays Not Related to a Particular Context

Several visual displays that were observed frequently enough and in a sufficient number of individuals to enable statistical analyses did not show a significant relation with any behavioral context, namely “coiled tail,” “head tilt,” “hind legs,” “pilo-erection base tail,” “stare,” and “tongue in-out.”

DISCUSSION

Visual Displays Related to an Aggressive Context

The giving of “arched bristle” and “tufts up” were found in an aggressive context. Therefore, they seem to indicate an internal aggressive intent. It is consistent with the literature that “tufts up” is an aggressive signal [references for the discussed contexts of visual displays are provided in Table 1]. “Arched bristle” can also be considered an aggressive signal, which is consistent with earlier reports in marmosets and owl monkeys, Aotus trivirgatus [Moynihan, 1967].

Visual Displays Related to a Fear Context

Several visual displays tended to be related to fear, namely “pilo-erection complete tail,” “pilo-erection tip tail,” and “tufts down.” In earlier studies, “pilo-erection complete tail” had been related to both aggression and fear when approached by an unfamiliar object or individual. Our study indicates that this visual display is only related to fear, not to aggression. This suggests that this visual display is context specific. Giving “pilo-erection tip tail” has been described in the literature [Moynihan, 1967], but has not explicitly been related to a particular behavioral context. Our results indicate that it may be a signal of fear. Giving “tufts down” has been described as a reaction to novelty, a reaction to aggression or avoiding aggression. This is consistent with the fear context found in our study.

None of the visual displays related to fear was significantly more often given in reaction to aggression. This may be due to the way we measured aggression: intra- and inter-group aggression were lumped into one context. If these visual displays are related to only one of these types of aggression, in particular to intra-group aggression, we may not have had sufficient data to show such a relationship. Moreover, the context fear was composed of behavior indicating submission, fear, and anxiety, but could not be subdivided due to sample size. A more detailed analysis may further specify the meaning of these visual displays.

Visual Displays Related to an Affiliative and/ or Play Context

Giving open mouth was related to both an affiliative and play context. Also receiving “open mouth” was related to the play context. Likewise, in the literature this behavior is considered play behavior. This is consistent with reports on other New World monkeys, where the similar relaxed open mouth display is found in a play context [Cebus apella: Visalberghi et al., 2006; Cebus capucinus: De Marco et al., 2008]. Moreover, this relaxed open mouth display exhibits visual similarities with the relaxed open mouth display of Old World monkeys and apes [i.e., open mouth, retracted lips, and teeth partly visible: van Hooff, 1967] that is also associated with play behavior and often called the “play face.” This suggests a homology between the play-related open mouth display of common marmosets and capuchin monkeys with the play-face of Old World monkeys and apes.

Receiving the fear and anxiety signals “pilo-erection complete tail,” “pilo-erection tip tail,” and “tufts down” was related to an affiliative context. Therefore, giving a signal of fear seemed to elicit affiliative behavior in the receiver. These observations are new for common marmosets, since no such reports in the literature were found. This may be similar to what has been found in rooks, where a partner returning from a fight receives affiliation from its mate [Seed et al., 2007], constituting consolation that is an uninvolved by-stander gives affiliation to the loser of a fight [De Waal and Van Roosmalen, 1979]. Reconciliation that is between-opponent affiliation after a fight, also typically occurs in a situation of post-conflict anxiety [Aureli et al., 2002]. Although reconciliation has been reported for common marmosets [Westlund et al., 2000], it is unclear whether they engage in consolation. Moreover, we could not determine whether this fear was caused by aggression, outside frightening influences such as birds and loud sounds or a reaction to anxiety. In addition, it was not established whether common marmosets react to the visual displays, or to accompanying acoustic or
olfactory signals. Therefore, it is not clear whether we should consider this affiliative reaction to fear as reconciliation, third-party affiliation or a reaction to anxiety. Moreover, whether this behavior indeed functions to reduce tension, like play in common marmosets [Norscia & Palagi, 2011] and brown lemurs [Palagi & Norscia, 2011], remains to be studied. However, these positive reactions to anxious individuals may represent a sensitivity to other’s needs, consistent with the common marmosets’ cooperative breeding system and their general prosocial attitude to group members [Burkart & van Schaik, 2010].

**Visual Displays Lacking a Clear Context**

Several visual displays were not related to a particular behavioral context. Both “head tilt” and “tongue in-out” were performed by all individuals and were often observed. Still, no specific social context seemed to be related to these signals, neither with an increase nor a decrease of the related behavior. Also the literature is ambivalent on the social context of these two visual displays.

For “head tilt” both an aggressive and an exploratory function have been proposed. However, our results are not consistent with an aggressive function of “head tilt”. Our results cannot support an exploratory context, since our data did not test the prevalence of visual displays in such a context. However, this interpretation is consistent with our impression that this behavior is often shown when unfamiliar persons walk in front of the animals’ enclosures or when new situations arise. Whether exploration of novel situations is indeed the context of this behavior remains to be investigated.

For “tongue in-out” four social contexts have been invoked: aggression, fear, affiliation, and for newly mated pairs a sexual context. However, we did not find an association of this behavior with a specific context, ruling out aggression, fear, and affiliation. Since we did not observe sexual behavior during the observation period, we cannot rule out a sexual context for this behavior. We believe that future research should pay attention to this behavior, since there may actually be two types of “tongue in-out” behavior [Fred Batenburg, personal observation]: a modest version, where the tongue is stuck out only slightly (see Supplementary Video), and an extreme version, where the tongue seems protruded at maximum length, occasionally with a trembling tip.

To our knowledge, this distinction has not been made in the literature. In our study, we observed modest exposure of the tongue in all kinds of situations and we could not assign it to a specific behavioral context. It is possible that the extreme version is specifically linked to a sexual context. Alternatively, we propose that “tongue in-out” may represent exploratory behavior. Common marmosets use scent marking [Epple, 1970; Lazaro-Perea et al., 1999; Moynihan, 1967] and olfactory communication is important. Therefore, “tongue in-out” behavior may concern olfactory or vomeronasal sampling of the environment.

Also for “coiled tail” a sexual context has been proposed and could not be confirmed. However, during our study “coiled tail” was regularly observed and displayed by all individuals, including non-paired group members, and the coiling of the tail was only seen when sitting passively together on a branch. Taking these factors into consideration, it is proposed that tail coiling is an expression of comfort or relaxation. Therefore, it is potentially a behavior that may indicate that individuals in the group are relaxed.

For a number of other visual displays that were not often observed, we failed to find contexts. The visual display “hind legs” has been proposed to relate to fear, “stare” to aggression and “pilo-erection base tail” to defensive threat. Our analyses did not yield a significant effect. The three visual displays were performed less than a hundred times and this may have rendered the power of the analyses too low.

**Communication With Visual Displays**

Visual displays may function to communicate, where the display is elicited in a specific situation and the receiver reacts in a particular way. “Open mouth” seems to communicate friendly or playful intent, since receivers often react with play. Similarly, senders of fear displays may signal a request for affiliation. Interestingly, fear signals may concern functional referential signals, where the recipient draws inferences about the fear experienced by the signaler, involving a facial expression. Other New World monkeys [capuchin monkeys: Morimoto & Fujita, 2011], great apes [Buttellmann et al., 2009], and dogs [Buttellmann & Tomassello, 2013] can also use emotional facial expressions, to elicit specific behavior from recipients. Alternatively, a single external factor may have caused fear in the signaler and affiliation in the receiver. Although it is difficult to exclude this option in the current dataset, the absence of affiliative behavior preceding a fear context makes the alternative explanation less likely. Therefore, visual displays connected to a fear context possibly act as a functional referential signal.

Although our study confirmed that some of the visual displays are related to aggression, no clear reaction to these signals was found. This may relate to their function: we considered intra- and inter-group aggression together. Inter-group aggression, however, was more prevalent, but we only monitored reactions of group members. Therefore, we may have missed how individuals of neighboring groups reacted to these aggressive signals.
Altogether, several visual displays seem to have a communicative function, although for a number of visual displays this remains to be established. Common marmosets use these facial expressions and body postures to communicate with group members. This counters the suggestion that New World monkeys living in arboreal habitats [e.g., Martins Bezerra et al., 2009; Moynihan, 1967] do not use visual displays. Similarly, the suggestion that primates living in small groups and those with complex facial color patterns use fewer facial expressions compared to species living in large groups and species with limited facial color patterns is also not supported [Santana et al., 2012]. Actually, the white ear tufts of this species, that contribute to the complexity of facial color patterns, may serve to make facial expressions more conspicuous instead of hampering them [pace Santana et al., 2012], consistent with the proposal of ritualized displays in classic ethology. The use of the whole body and conspicuously colored parts of the face are consistent with the proposed necessity for elaborated displays of a small species living in an arboreal habitat, potentially countering the proposal of Santana et al. [2012]. Comparative research to investigate this proposal is necessary.

CONCLUSION

This study has shown that common marmosets use elaborate visual displays and part of these signals may function to communicate with conspecifics. Although we could not assign a context to all observed visual displays, the context for a number of these signals was found, partly reconﬁrming, yet also partly limiting or even adjusting the contexts proposed in the literature. Visual displays can function to communicate and, most intriguingly, fear-related visual displays elicit friendly behavior, consistent with the cooperative breeding system found in marmosets, and potentially constitute referential signals. Marmosets have been illustrated as "pokerfaced" [Moynihan, 1967] or as having a limited repertoire of facial expressions [Santana et al., 2012]. Indeed, their visual displays do not concentrate on the face, but instead their conspicuously white ear tufts and their entire body are integrated. Therefore, their communicative repertoire may not be smaller than in primates that mainly use facial expressions. Actually, the complexity of their facial color patterns may not hamper, but facilitate their facial expression.

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REFERENCES

Aureli F, Cords M, van Schaik CP. 2002. Conﬂict resolution following aggression in gregarious animals: a predictive framework. Anim Behav 64:325–343.
Barros M, Giorgetti M, Vieira Souto AA, et al. 2007. Persistent anxiety-like behavior in marmosets following a recent predatory stress condition: reversal by diazepam. Pharmacol Biochem Behav 86:705–711.
Box HO. 1975. Quantitative studies of behaviour within captive groups of marmoset monkeys (Callithrix jacchus). Primates 16:155–174.
Burkart JM, van Schaik CP. 2010. Cognitive consequences of cooperative breeding in primates? Anim Cogn 13:1–19.
Burrows AM. 2008. The facial expression musculature in primates and its evolutionary signiﬁcance. BioEssays 30:212–225.
Burrows AM, Waller BM, Parr LA, Bonar CJ. 2006. Muscles of facial expression in the chimpanzee (Pan troglodytes): descriptive, comparative and phylogenetic contexts. J Anat 208:153–167.
Buttelmann D, Tomasello M. 2013. Can domestic dogs (Canis familiaris) use referential emotional expressions to locate hidden food? Anim Cogn 16:137–145.
Buttelmann D, Call J, Tomasello M. 2009. Do great apes use emotional expressions to infer desires? Dev Sci 12:688–698.
Cásar C, Zuberbühler K. 2012. Referential alarm calling behaviour in New World primates. Curr Zool 58:680–697.
Cawthon-Lang KA. 2005a. Primate factsheets: common marmoset (Callithrix jacchus). Behavior. Available online at: http://pin.primate.wisc.edu/factsheets/entry/common_marmoset/behav [accessed December 2010].
Cawthon-Lang KA. 2005b. Primate factsheets: common marmoset (Callithrix jacchus). Taxonomy, morphology & ecology. Available online at: http://pin.primate.wisc.edu/factsheets/entry/common_marmoset/taxon [accessed March 2012].
Cilia J, Piper DC. 1997. Marmoset conspeciﬁc confrontation: an ethologically-based model of anxiety. Pharmacol Biochem Behav 58:85–91.
De La Torre S, Snowdon CT. 2002. Environmental correlates of vocal communication of wild pygmy marmosets, Cebuella pygmaea. Anim Behav 63:847–856.
De Marco A, Petit O, Visalberghi E. 2008. The repertoire and social function of facial displays in Cebus capucinus. Int J Primatol 29:469–486.
De Waal FBM, Van Roosmalen A. 1979. Reconciliation and consolation among chimpanzees. Behav Ecol Sociobiol 5:55–66.
Digby L. 1995. Social organization in a wild population of Callithrix jacchus: II Intragroup social behaviour. Primates 36:361–375.
 Dobson SD. 2009. Socioecological correlates of facial mobility in nonhuman Anthropoids. Am J Phys Anthropol 139: 413–420.
Epple G. 1968. Comparative studies on vocalization in marmoset monkeys (hapalidae). Folia Primatol 8:1–40.
Epple G. 1970. Quantitative studies on scent marking in the marmoset. Folia Primatol 13:48–62.
Ferrari SF, Lopes Ferrari MA. 1989. A re-evaluation of the social organization of the Callitrichidae, with reference to the ecological differences between genera. Folia Primatol 52:132–147.
Gerber P, Schnell CR. 2004. Behavioral and cardiophysiological responses of common marmosets (Callithrix jacchus) to confrontations with opposite-sexed strangers. Primates 45:187–196.
Kaplan G, Rogers LJ. 1999. Parental care in marmosets (Callithrix jacchus jacchus): development and effect of anogenital licking on exploration. J Comp Psychol 113: 269–276.

Kaplan G, Rogers LJ. 2006. Head-cocking as a form of exploration in the common marmoset and its development. Dev Psychobiol 48:551–560.

Lazaro-Preuschoft S, Gevers E, van Hooff JARAM. 1995. Functional differentiation in the affiliative facial displays of longtailed macaques (Macaca fascicularis). In: Preuschoft S, editor. Laughter and smiling in macaques: an evolutionary perspective. Utrecht: Utrecht University. p 57–88.

Santana SE, Alfaro JL, Alfaro ME. 2012. Adaptive evolution of facial colour patterns in neotropical primates. Proc R Soc B 279:2204–2211.

Seed AM, Clayton NS, Emery NJ. 2007. Post-conflict third party affiliation in rooks Corvus frugilegus. Curr Biol 17:152–158.

Seyfarth RM, Cheney DL, Marler P. 1980. Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. Science 210:801–803.

Snowdon CT. 2001. Social processes in communication and cognition in callitrichid monkeys: a review. Anim Cogn 4:247–257.

Sparks J. 1967. Allogrooming in primates: a review. In: Morris D, editor. Primate ethology. Chicago: Aldine. p 236–266.

Stellar E. 1960. The marmoset as a laboratory animal: maintenance general observation of behavior and simple learning. J Comp Physiol Psychol 53:1–10.

Stevenson MF, Poole TB. 1976. An ethogram of the common marmoset (Callithrix jacchus jacchus): general behavioural repertoire. Anim Behav 24:428–451.

Stevenson MF, Rylands AB. 1988. The marmosets, genus Callithrix. In: Mittermeier RA, Rylands AB, Coimbra-Filho AF, da Fonseca GAB, editors. Ecology and behavior of neotropical primates. vol 2. Washington, DC: World Wildlife Fund. p 131–222.

Sutcliffe AG, Poole TB. 1984. Intragroup agonistic behavior in captive groups of the common marmoset Callithrix jacchus jacchus Int J Primatol 5:473–489.

Townsend SW, Manser MB. 2012. Functionally referential communication in mammals: the past, present and the future. Ethology 119:1–11.

Van Hooff JARAM. 1967. The facial displays of the Catarrhine monkeys and apes. In: Morris D, editor. Primate ethology. Chicago: Aldine. p 236–266.

Vernes MK, Louwerse AL. 2010. BPRC’s enrichment manual for macaques and marmosets. Rijswijk: BPRC.

Visalberghi E, Valenzano DR, Preuschoft S. 2006. Facial displays in Cebus apella. Int J Primatol 27:1689–1707.

Westlund K, Ljungberg T, Borefelt U, Abrahamsson C. 2000. Post-conflict affiliation in common marmosets (Callithrix jacchus jacchus). Am J Primatol 52:31–46.

Wheeler BC, Fischer J. 2012. Functionally referential signals: a promising paradigm whose time has passed. Evol Anthropol 21:195–205.

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