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Morphological variants of silent bared-teeth displays have different social interaction outcomes in crested macaques (*Macaca nigra*)

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Abstract

Objectives: While it has been demonstrated that even subtle variation in human facial expressions can lead to significant changes in the meaning and function of expressions, relatively few studies have examined primate facial expressions using similarly objective and rigorous analysis. Construction of primate facial expression repertoires may, therefore, be oversimplified, with expressions often arbitrarily pooled and/or split into subjective pigeonholes. Our objective is to assess whether subtle variation in primate facial expressions is linked to variation in function, and hence to inform future attempts to quantify complexity of facial communication.

Materials and Methods: We used Macaque Facial Action Coding System, an anatomically based and hence more objective tool, to quantify “silent bared-teeth” (SBT) expressions produced by wild crested macaques engaging in spontaneous behavior, and utilized discriminant analysis and bootstrapping analysis to look for morphological differences between SBT produced in four different contexts, defined by the outcome of interactions: Affiliation, Copulation, Play, and Submission.

Results: We found that SBT produced in these contexts could be distinguished at significantly above-chance rates, indicating that the expressions produced in these four contexts differ morphologically. We identified the specific facial movements that were typically used in each context, and found that the variability and intensity of facial movements also varied between contexts.

Discussion: These results indicate that nonhuman primate facial expressions share the human characteristic of exhibiting meaningful subtle differences. Complexity of facial communication may not be accurately represented simply by building repertoires of distinct expressions, so further work should attempt to take this subtle variability into account.

KEYWORDS

facial action coding system, facial expression, macaque, silent bared-teeth, social behavior

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1 | INTRODUCTION

It is widely believed that some human facial expressions are homologous to similar facial movement patterns in other primates, with a popular comparison being that of the human smile to the “silent bared-teeth” expression (hereafter, SBT; van Hooff, 1967) produced by most primates (Preuschoft, 1992, 2000; van Hooff, 1967, 1972). In humans, subtle morphological variants of smiles have been shown to carry different meanings, such as “reward,” “affiliation,” and “dominance” (Martin, Rychlowska, Wood, & Niedenthal, 2017; Rychlowska et al., 2017). While all smiles are defined by the retraction of the lip corners to show the teeth, other accompanying facial movements can change viewers' perception of the facial expression, with “reward” smiles being accompanied by eyebrow raising, “affiliative” smiles by lip pressing, and “dominance” smiles by nose wrinkling and lip raising, among other differences (Martin et al., 2017; Rychlowska et al., 2017). This illustrates that these signals are not necessarily uniform and can be used in a complex manner (Ekman, 1985; Frank, Ekman, & Friesen, 1993; Martin et al., 2017; Rychlowska et al., 2017; Surakka & Hietanen, 1998).

However, in contrast with the research on human facial expressions, little consideration has been given to the potential for subtle variation in primate facial expressions. SBT, for example, has been regarded as a single facial expression both in classic descriptive work (e.g., van Hooff, 1967) and several more recent ethological studies (e.g., Beisner & McCowan, 2014; Flack & de Waal, 2007; Otovic, Partan, Bryant, & Hutchinson, 2014). This assumption has then been carried forward into studies of the evolution of communication. For example, Dobson (2012) counted the number of affiliative facial expressions that different macaques produce, based on descriptions of facial expressions provided by other researchers. Dobson found that, in general, more “socially tolerant” macaques, meaning those with less rigid social structure (i.e., characterized by greater rates of reconciliations and counter-aggressions, lower kin bias among other characteristics) (Thierry, Iwaniuk, & Pellis, 2000), have larger repertoires of affiliative facial expressions. While a useful first step in testing the influence of social factors on the evolution of communication, with a specific focus on facial expressions, this approach is coarse and subjective, requiring pigeonholing facial communicative signals and displays into discrete categories. This is contrary to evidence, for example, that not all primate SBT appear the same: the mandrill (*Mandrillus sphinx*) has a distinct morphological variant of the expression (van Hooff, 1967); whereas in tonkean macaques (*Macaca tonkeana*), SBT and relaxed open-mouth (van Hooff, 1967) expressions appear to occur not as discrete signals but as a graded continuum (Thierry, Demaria, Preuschoft, & Desportes, 1989). This evidence of variability in SBT echoes that observed in human smiles; as stated above, it has been demonstrated that in humans the morphology of a smile is connected to function, implying that the same might be true in other primates. However, few such detailed studies of the connection of form to function of primate facial expressions have yet been undertaken, with some studies finding that SBT performs multiple functions but neglecting to examine the form of the expression in detail (Beisner &

McCowan, 2014; Flack & de Waal, 2007), possibly due to a lack of suitable tools for measuring facial expressions objectively. While descriptive work (e.g., Preuschoft, 1992; van Hooff, 1967, 1972) has always sought to connect form and function of expressions, identification of very subtle variability requires the use of detailed methods.

Many insights into the variability of human facial expressions have been gained by the use of the Facial Action Coding System (FACS; Ekman & Friesen, 1978). This system measures facial expressions in terms of the underlying muscle movements, termed “action units” (AUs). A classic example, the felt smile of enjoyment, known as the “Duchenne” smile, involves raising the cheek through a contraction of the orbicularis oculi muscle (Ekman, Davidson, & Friesen, 1990; Surakka & Hietanen, 1998), which is absent in many forced “non-Duchenne” smiles (but see Krumhuber & Manstead, 2009); the contraction of orbicularis oculi is AU6 in the FACS, while the raising of the lip corners is AU12 and parting of the lips is AU25, hence a Duchenne smile comprises AU6 + 12 + 25 and a non-Duchenne smile involves AU12 + 25 only. Subsequently, FACS has been adapted for use in other primates including chimpanzees (Parr, Waller, Vick, & Bard, 2007), macaques (Julle-Danière et al., 2015; Parr, Waller, Burrows, Gothard, & Vick, 2010), gibbons (Waller, Lembeck, Kuchenbuch, Burrows, & Liebal, 2012), and orangutan (Caeiro, Waller, Zimmermann, Burrows, & Davila-Ross, 2013). This has greatly improved our ability to examine the facial expressions of nonhuman primates in the same terms as those of humans, enabling both within-species (e.g., Waller, Caeiro, & Davila-Ross, 2015; Waller & Cherry, 2012) and between-species (e.g., Waller, Misch, Whitehouse, & Hermann, 2014) comparisons of facial expression composition.

SBT are produced by many primates. While, as with smiles, these expressions all involve the withdrawal of the upper lip (by AU10, AU12, or a combination of the two) creating parting of the lips (AU25), these can also vary in terms of the degree of withdrawal of the lips, the opening of the jaw, and the presence or absence of movements in other parts of the face. In macaques, SBT is used to signal short-term submission and long-term subordination in less socially-tolerant species such as rhesus macaques (Beisner & McCowan, 2014; de Waal & Luttrell, 1985) and pig-tailed macaques (Flack & de Waal, 2007), and short-term submission in Barbary macaques (Preuschoft, 1992), yet is used more flexibly in more tolerant species including Tonkean macaques (Thierry et al., 1989) and moor macaques (Petit & Thierry, 1992; Thierry, 2000). Crested macaques, *Macaca nigra*, produce SBT in a wide range of contexts including play, affiliation, conflict, and mating, and there is some evidence that morphological variability corresponds to the different contexts. For example, bared teeth with a rhythmic jaw movement seems to be used by males soliciting copulations (Thierry, Bynum, et al., 2000); play may also be characterized by a pronounced stretch of the jaw, as seen in many primates (Preuschoft, 1992; van Hooff, 1967) and other mammals (e.g., canids, Bekoff, 1974; bears, Henry & Herrero, 1974; polecats, Poole, 1978). Dynamic features such as lip-smacking (Thierry, Bynum, et al., 2000; van Hooff, 1967)—the rapid, rhythmic, and repeated bringing together and pulling apart of the lips over a (relatively) closed mouth creating an audible smacking sound—are also common, and are accounted for in the FACS for macaques (MaqFACS; Parr et al., 2010).

The present study aims to use MaqFACS to provide a rigorous quantitative characterization of the morphology of the SBT display in crested macaques at a high level of detail, and to assess whether morphological variation of SBT can be linked to specific behavioral outcomes. We expect that FACS will provide the means sufficient to identify different variants of crested macaque SBT expressions, including both known—for example, the jaw movement described as being used by males in sexual context (Thierry, Bynum, et al., 2000)—and unknown sources of variation, and connect the morphological variability to function of the signals.

2 | MATERIALS AND METHODS

2.1 | Data collection

We studied wild crested macaques in the Tangkoko-Batuangus Nature Reserve in North Sulawesi, Indonesia (1°33'N, 125°10'E). Habituation, long-term life histories, and behavioral data are maintained at this site by the Macaca Nigra Project (MNP; www.macaca-nigra.org). Detailed descriptions of the field site are available elsewhere (Palacios et al., 2012; Rosenbaum, O'Brien, Kinnaird, & Supriatna, 1998). Two groups, numbering 60 (including 21 adult females and 10 adult males) and 80 (20 adult females, 8 adult males) individuals, were followed from dawn to dusk (c. 5:30 a.m.–6:00 p.m.) between September 2010 and April 2011. In total, 37 adult females and 13 adult males were followed in a pseudo-random order using focal animal sampling (Altmann, 1974).

Each observation of an individual lasted 30 min, excluding any time the animal spent out of sight; if an animal was out of sight for up to 15 min the focal was restarted, but if the period exceeded 15 min the focal was abandoned and a new focal began on a different individual. In total, focal animals were followed for 388 hr, with each being followed for at least 6 hr (mean = $7.77 \pm \text{SD } 0.38$ hr). Animals were followed by two researchers: one recording the animal's face with a video camera (Panasonic HDC-SD700, Bracknell, UK) and the other recording data on activity and social interactions. Every time a social behavior occurred, the researcher without the camera recorded a timestamp, the identity of both parties in the interaction, and the type of behavior observed, on a new line of the database. Social interactions often involved several different behaviors, which were each recorded individually. Therefore, it was possible to look at any data file and trace the timing and nature of each social interaction an individual was involved in over a 30-min focal. Whenever the focal animal called, made a facial expression, approached another individual or was itself approached, the researcher operating the video camera activated the "prerecord" setting, meaning that a clip was recorded beginning 3 s before the interaction. Recording was stopped when the participants moved away from each other, began grooming, or engaged in nonsocial behavior such as sitting or foraging. Behavior was coded according to an ethogram based on existing descriptions of macaque behavior (Thierry, Bynum, et al., 2000), on which all researchers were trained by the MNP. Research protocols, developed

in accordance with the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates, were approved by both the Animal Welfare Ethical Review Body of the University of Portsmouth and the Indonesian State Ministry of Research and Technology (RISTEK), and followed in accordance with UK and Indonesian laws.

2.2 | Categorizing behavioral contexts

A total of 476 instances of "SBT" occurred during data collection. However, not all of these instances were captured on camera, and some video clips were not usable due to problems with focus, distance, obstructions, or angle preventing sufficient visibility of the subject's face. In total, 118 expression sequences, that is, clips showing nonneutral facial expressions, were recorded with sufficient quality for FACS coding.

Each expression sequence was categorized for the context in which it was produced, based on the social behavior which was recorded in the focal observation at the time. Video clips were checked again to ensure that there was no conflict between focal recording and behavior visible on the clip, using the same ethogram. If no further social interaction was recorded in the focal observation, any behavior that was visible in the video clip was used to classify interactions (this affected fewer than five expression sequences). Since it was very rare that expression sequences were preceded by other social interactions, they were categorized based on the behavior of both the signaler and receiver immediately following the expression sequence, per Table 1 below. It should be noted that while "Play," "Copulation," and "Submission" sequences were mutually exclusive, each of these could also include affiliative behavior. We used the rule that if any "Play," "Submission," or "Copulation" behavior was present in an interaction we used those categorizations, and if no behavior fitting these categories was present we considered whether "Affiliation" behaviors were present. All categorization was done prior to FACS coding and data analysis; during FACS coding, coders were blind to the category assigned to expression sequences.

In 42 of the expression sequences, no social interaction between the parties followed, and therefore the outcome of the interaction was "no interaction." Since the lack of interaction could be due to several reasons, such as the receiver not seeing a signal, choosing to ignore a signal, or choosing to act on a signal meaning "no response necessary/desired," it is impossible to tie the morphology of the signal to the behavioral outcome in these cases. Therefore, these 42 expression sequences have not been analyzed. This left a total of 76 expression sequences, produced by 23 individuals (all adults), for which FACS data and behavioral data were available. These 76 sequences were then coded by certified MaqFACS coders.

2.3 | Facial movement coding

Facial expression sequences were coded using an adapted version of the FACS for rhesus macaques (MaqFACS; Parr et al., 2010). Despite

TABLE 1 Criteria for categorization of expression sequences

Category	Behavior observed	N sequences	N individuals
Affiliation	Groom, nonaggressive, and nonsexual physical contact or vocalizations, for example, embrace, mutual soft grunt	40	18 (11♀, 7♂)
Copulation	Female present, male inspection, mount, mating	25	9 (9♂)
Play	Play, soft biting, wrestling, expressive run	5	5 (5♀)
Submission	Displacement, flee, crouch, turn away, scream	6	5 (4♀, 1♂)

TABLE 2 Differences noted between crested macaque and rhesus macaque AUs and ADs

AU9	Nose wrinkle	Less clear in crested macaques compared to rhesus macaques, due to differences in skin texture and color. The nose tip appears less mobile than in rhesus macaque, so AU9 does not always cause shortening of the nose. As in rhesus macaques, AU9 does cause deepening of vertical wrinkles and emergence of oblique wrinkles on the nose.
AU18ii	Outer lip pucker	This movement was not observed in crested macaques. Puckering similar to rhesus macaque inner lip pucker (AU18i in MaqFACS) is present, and simply coded AU18.
AD182	Teeth chattering	The jaws oscillate vertically, the lower jaw contacting regularly with the upper jaw but the lips remaining apart. Not described in rhesus macaque FACS.
AD183	Tongue chattering	With lips and jaws parted and relatively static, the tongue flickers up and down between the jaws, contacting each in turn. Not described in rhesus macaque FACS.
AD184	Jaw wobble	With lips and jaws parted, the lower jaw moves up and down rapidly and regularly, with neither jaws nor lips ever meeting. Not described in rhesus macaque FACS.
AD101	Scalp retraction	The hair on the top of the head, including the crest, flattens as the skin is pulled backward. Skin on the forehead and temples appears stretched. Not described in rhesus macaque FACS.
AD59	Head toss	The head is tipped suddenly backward so that the face is turned upward. Not described in rhesus macaque FACS.

Abbreviations: AD, action descriptor; AU, action unit; FACS, Facial Action Coding System.

some differences in facial musculature between crested macaques and rhesus macaques (detailed in Burrows et al., 2016 and in the electronic supplementary material of this paper), and differences in skin color and texture, all individual facial movements displayed by crested macaques could be coded using the AUs in the MaqFACS, though changes were noted in the appearance of two AUs (see Table 2). Following previous versions of the FACS, more complex combinations of movements were coded with action descriptors (ADs), including some newly defined ADs where observed movements did not fit existing definitions given in the MaqFACS (see Table 2). Detailed descriptions of the appearance changes produced by each AU are provided in the electronic supplementary material.

All AUs and ADs coded appear in Table 3, and detailed descriptions of the appearance changes corresponding to these AUs/ADs are presented in the ESM. Two certified MaqFACS users recorded onset and offset of these movements during the 76 expression sequences using the programme BORIS (Friard & Gamba, 2016), with a subset of 13 videos (17.1%) being coded by both researchers for reliability testing. To calculate reliability, we used the same formula used in other versions of FACS (human and nonhuman), per Ekman, Friesen, and Hager (2002):

$$\text{Agreement} = \frac{2 \times (\text{Number of AUs on which coders A and B agreed})}{\text{Total number of AUs scored by the two coders}}$$

Agreement between the two coders was 0.72, which is considered a good level of agreement for FACS reliability coding (Ekman et al., 2002).

The FACS for humans (Ekman et al., 2002; Ekman & Friesen, 1978) includes a 5-point scale for coding intensities of AUs, while the versions of FACS used for nonhuman animals do not. While establishing the suitability of MaqFACS for use with crested macaques, we decided that it was possible to code the intensity of certain AUs (see Table 2), where it was possible to see a difference between minor and major movements, using a binary scale (weak vs. strong actions). Using the standard calculation of FACS reliability (see above; Ekman et al., 2002), agreement on intensities between the coders was 0.75, which is a good level of agreement. All other AUs were coded simply as being present or absent.

During coding, expression sequences were defined as starting when the signaler's face, directed at the recipient, exhibited a change away from neutral expression, and ended when the signaler looked away from the other animal for the final time, or the face returned to

TABLE 3 AUs and ADs coded for crested macaques in the current study. Descriptions of appearance changes and muscular basis are provided in the electronic supplementary material

Action unit/descriptor	Description	Intensity coded?
AU1 + 2	Brow raiser	—
AU6	Cheek raiser	—
AU7	Eyelid tightener	—
AU8	Lips toward each other	—
AU9	Nose wrinkle	—
AU10	Upper lip raiser	Yes
AU12	Lip corner puller	Yes
AU16	Lower lip depressor	Yes
AU18	Lip pucker	—
AU25	Lips parted	—
AU26	Jaw drop	—
AU27	Jaw stretch	—
AU41	Glabella lowerer	—
EAU1	Ears forward	—
EAU2	Ear elevator	—
EAU3	Ear flattener	Yes
AD59	Head toss	—
AD101	Scalp retract	—
AD181	Lipsmack	—
AD182	Teeth chatter	—
AD183	Tongue chatter	—
AD184	Jaw wobble	—

Abbreviations: AD, action descriptor; AU, action unit.

neutral for the final time. If the signaler looked away from the recipient temporarily, before restarting the expression bout, we counted this as one sequence, and discounted the time spent looking away during analysis. Coding was also ended if physical contact such as grooming or mounting began, in order to concentrate on the facial expressions leading to these contacts rather than those produced during that contact. If animals were vocalizing, only movements that persisted beyond the time required to produce a call were coded, per standard FACS methodology (Ekman & Friesen, 1978). Videos were coded every 0.1 s throughout the interaction, with any AUs or ADs present being recorded. Therefore, the final dataset included a calculation of the duration of each AU and AD's presence in each interaction.

We calculated the overall intensity of some AUs (see Table 2) within each interaction using the equation

$$\text{Intensity} = \frac{\text{Time AU expressed at high intensity}}{\text{Total time AU expressed}}$$

We also obtained a measure of variability of expression sequences by calculating the rate (per 10 s) at which the AU combination changed. This measure of variability was selected as it did not

correlate with the duration of the interaction, and the values are in the same order of magnitude as those of other variables, making the output of subsequent analyses clearer.

Therefore, for each expression sequence, we obtained durations of each AU and AD's presence, the intensity of certain AUs, the rate at which intensity changes occurred, and the overall variability of expressions.

2.4 | Statistical analysis

We ran cross-validated linear discriminant analysis using the “lda” function in R (package “MASS,” Venables & Ripley, 2002) with the outcome of the interaction (Affiliation, Copulation, Submission, Play) as the category and including as predictor variables the duration of AUs (corrected for duration of interaction), the variability of expressions produced in an expression sequence, and the intensity of AU10, AU12, and AU26. We restricted the number of predictor variables in the analysis in order to better fit the assumptions of the linear discriminant analysis, which works best with sample sizes larger than the number of variables. To reduce the number of variables, we excluded those AUs that were found at similar, low frequencies in all contexts, and used only one of collinear pairs of variables, leaving a total of 16 possible predictor variables.

Due to the use of multiple video clips per individual, the skewed sex ratios, and the small sample size, assessing the output of the discriminant analysis required comparison to the distribution of outputs obtained by applying the same model to 1,000 randomized datasets (per Mundry & Sommer, 2007), with the randomization restricted to maintain each individual's contribution to each context, in order to reflect the restricted and asymmetrical nature of the sample, and allow for the disproportionate influence of single individuals who contributed multiple examples of facial expressions in certain contexts. Comparison of the output of the discriminant analysis on the observed data to these 1,000 permuted analyses enables greater confidence in the result. By analyzing the contributions of each variable to the discriminant functions, it is possible to identify where the differences between SBT produced in different contexts lie.

Due to the low sample size of expression sequences in both the Play and Submission contexts, we performed two additional analyses to further illustrate our findings. First, we performed a second discriminant analysis using the same methods as the first, but with expressions produced in Play ($n = 5$) and Submission ($n = 6$) contexts removed. Having again excluded those AUs that occurred at similar, low frequencies in both contexts, and removed variables to reduce collinearity, the remaining variables were the same as the original discriminant analysis, except that AD182 (Teeth chatter) was also removed; this AD was absent in both Affiliative and Copulation expression sequences, meaning the model is based on 15 variables in total. We compared the output of the model to the outputs of 1,000 models based on randomized permutations of the dataset, as before.

Actual context	Discriminant analysis classification				% correct
	Affiliation	Copulation	Play	Submission	
Affiliation	30	7	2	1	75.0%
Copulation	12	13	0	0	52.0%
Play	1	1	3	0	60.0%
Submission	2	1	0	3	50.0%
Overall					64.5%

TABLE 4 Confusion matrix of discriminant analysis, also showing rate of successful categorizations

Second, we conducted a bootstrapping analysis to assess whether any AUs or ADs were stereotypical of expressions produced in a particular context. This method is less capable of identifying associations between variables, but very capable of identifying AUs or ADs that appear in one context far more (or less) than other contexts. We compared the frequency of occurrence of each AU in each context with the frequency of that AU in the other three contexts. In order to generate a probability distribution of the occurrence of each AU or AD, we utilized randomized sampling with replacement (Snijders & Borgatti, 1999) to produce 10,000 randomized samples of the database against which to compare our observed data. We varied the size of the randomized samples to match the actual samples against which we were comparing them, so that when analyzing rates of AU27 in expressions for Play context ($N = 5$) we produced 10,000 randomized samples with $N = 5$ to generate the probability distribution. Comparing the mean and standard deviation of the probability distribution to the mean of the observed sample yielded a z value, and examining the number of randomized samples with rates of AU27 greater than or equal to the rate observed in the Play context yielded a p -value, $p = \frac{x}{10,000}$ where x is the number of randomized samples having rate of $AU27 > \text{observed rate of } AU27$. We did this for 10 AUs, 6 ADs, one measure of rate of change, 3 measures of AU intensity, and 3 measures of AU intensity rate of change, for each of the four contexts, giving a total of 92 comparisons (Table 1). Due to the high number of comparisons, we assessed significance using false discovery rate adjustment of p -values (Benjamini & Hochberg, 1995), to reduce the effect of performing multiple comparisons while maintaining a reasonable level of power in the analysis.

3 | RESULTS

The discriminant analysis correctly classified facial expressions by context significantly above chance level (Tables 4 and 5). Figure 1 shows example expressions from each of the four contexts.

Expression sequences produced in copulation and affiliation contexts were relatively similar, yet affiliation expressions were categorized correctly 75% of the time, and copulation expressions were categorized correctly 52% of the time (Table 4). Expression sequences in the copulation context generally show higher loadings in LD2 and, particularly, in LD3 (Figure 3). AD184 (jaw wobble) has a strong positive influence on these two LDs (Figure 2) and was found almost exclusively in copulation context. Higher rates of AU26 (jaw drop)

TABLE 5 Results of discriminant analysis of the (a) full dataset and (b) copulation and affiliation expressions, compared to distributions produced by separate analyses of 1,000 randomized datasets for each case

	Full dataset	Copulation and affiliation only
N	76	65
Expected correct ^a	30.83 ± 4.403	35.68 ± 4.325
Actual correct	49	46
p	<.001	.004

^aMean \pm SD of 1,000 analyses of randomized weighted permutations of each dataset.



FIGURE 1 Examples of silent bared-teeth expressions produced in the four contexts. Clockwise from top-left: affiliation, play, submission, copulation

and AU43 (eye closure), and greater variability in intensity of AU12 (lip corner puller) may also have led to higher values of LD3 in the copulation context. Since AU9 contributes positively to LD2 and LD3

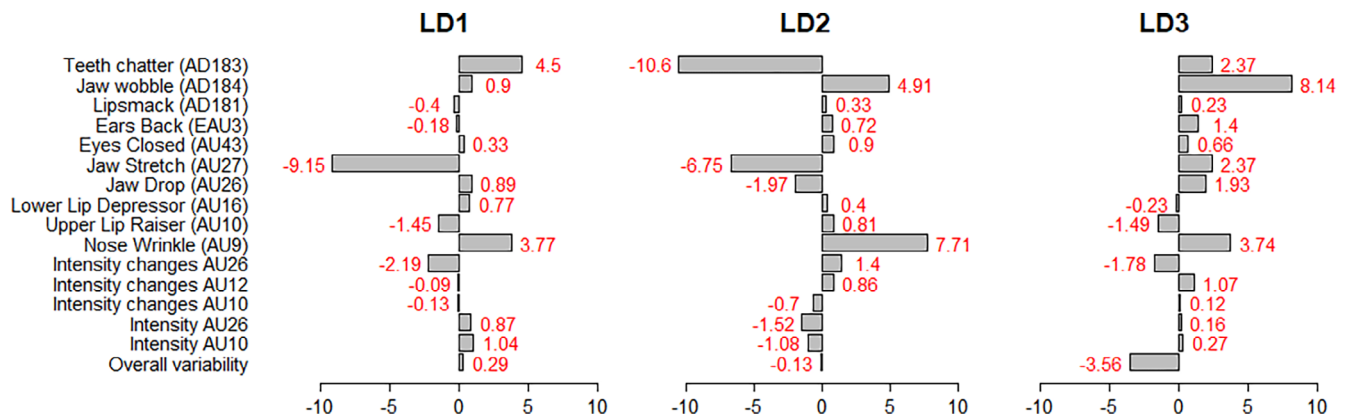


FIGURE 2 Relative contributions of variables to linear discriminants

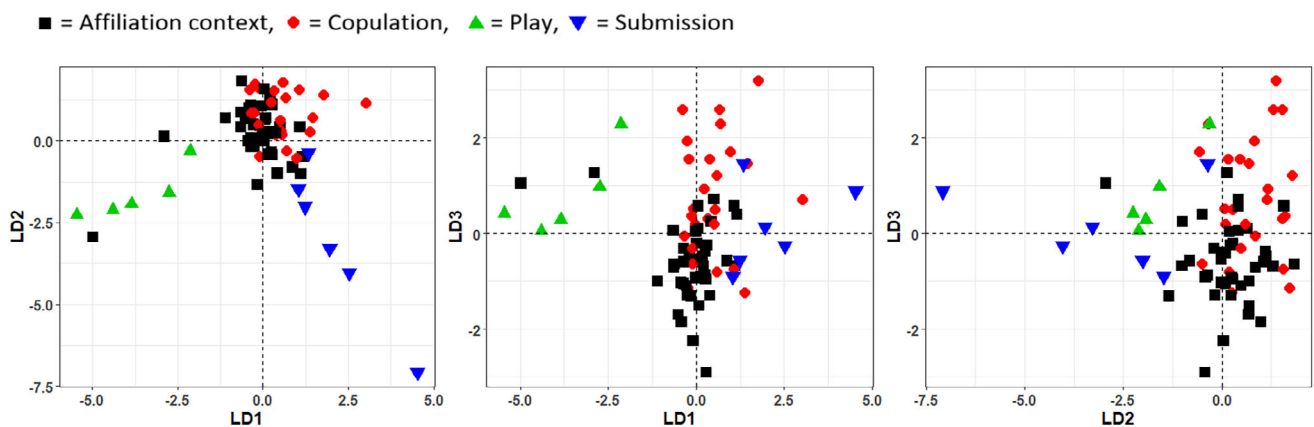


FIGURE 3 Values of linear discriminant functions (LD1, LD2, LD3) for every expression sequence, by context

(Figure 2), and this AU occurred in 6 of 25 expressions (24%) in copulation context but only 4 of 40 expressions (10%) in affiliative context, this may also have had an impact on the successful classification of these expressions.

Affiliation expressions have lower values of LD3 (Figure 3), which may be due to the effects of higher variability (Expression changes per 10 s) of affiliative expressions, and the relatively lower rates of EAU3, AU43, AU26, and AD184 observed in this context, on this linear discriminant (Figure 2).

Expression sequences produced in play contexts were correctly categorized 60% of the time (Table 4). Play expressions have low values of LD1, produced by high rates of AU27 (jaw stretch)—every SBT produced in this context ($n = 5$) incorporated this AU, which was only involved in 5 of 71 expressions produced in nonplay contexts. Values of LD2 are average to high (Figure 3), due to lower expression variability (expression changes per 10 s), the absence of teeth chattering, and higher rates of AU10 (upper lip raiser; Figure 2).

Expression sequences produced during submission were correctly categorized 50% of the time (Table 4). Submission expressions have lower values of LD1 and LD2 (Figure 3), predominantly caused by the frequent presence of AD182 (teeth chattering) in this context (Figure

2). Relatively low rates of EAU3 (ears flattened), high intensities of AU10 (upper lip raise) and AU26 (jaw drop), and a lack of variation in intensity of AU10, AU12 (lip corner puller) and AU26 also contribute to this categorization (Figure 2).

The second discriminant analysis, including only expression sequences produced in Affiliation and Copulation contexts, also categorized expression sequences at above-chance accuracy (Table 5). Overall model accuracy was 70.8% (see ESM Table S2 for confusion matrix). As with the output of the first discriminant analysis, it is again apparent (see ESM) that AD184 (Jaw wobble, present in 12 expressions) and AU9 (Nose wrinkle, present in 5 expressions) were strong contributors to the classification of Copulation expressions; AU27 (Jaw stretch, present in 5 expressions) and high overall variability were the strongest contributors to the classification of Affiliation expressions (ESM Figures S1 and S2).

The bootstrapping analysis (see Table 6) identified that rates of AD184 (Jaw wobble) were higher in copulation context than expected by chance ($z = 3.12, p < .0001$). In play context, rates of AU27 (Jaw stretch) were higher than expected ($z = 3.80, p < .0001$), as were rates of EAU3 (ear flattener; $z = 1.17, p = .036$). AD182 (Teeth chatter) only occurred in submission context ($p < .0001$). In this context, intensity

TABLE 6 Results of bootstrapping analysis to identify AU-context combinations with above-chance occurrence rates (only cases with adjusted $p < .1$ are shown; full results for all AU-context combinations available in ESM Table S1)

Context	Variable name	FACS code	Observed occurrence (mean \pm SD)	Expected occurrence (mean \pm SD)	Z	Adjusted p^a
Copulation	Jaw wobble	AD184	0.07 \pm 0.13	0 \pm 0.02	3.12	<.0001 ^b
Play	Jaw stretch	AU27	0.38 \pm 0.11	0.02 \pm 0.09	3.8	<.0001 ^b
	Ears flat	EAU3	0.9 \pm 0.14	0.51 \pm 0.33	1.17	.036 ^b
Submission	Lip raiser intensity	AU10 (Int)	0.89 \pm 0.17	0.5 \pm 0.35	1.12	.058
	Lip corner puller intensity	AU12 (Int)	0.94 \pm 0.14	0.53 \pm 0.38	1.11	.036 ^b
	Jaw drop intensity	AU26 (Int)	0.63 \pm 0.2	0.22 \pm 0.33	1.25	.084
	Teeth chatter	AD182	0.15 \pm 0.21	0 \pm 0	na ^c	0 ^b

Abbreviation: AU, action unit.

^aAdjusted p -values based on the false discovery rate calculation (Benjamini & Hochberg, 1995).

^bSignificant at .05 significance level.

^cz cannot be calculated when the mean and SD of the comparison sample are both zero.

of AU12 (Lip corner puller) was higher than chance level ($z = 1.11$, $p = .036$), and intensities of AU10 (Upper lip raiser; $z = 1.12$, $p = .058$) and AU26 (Jaw drop; $z = 1.25$, $p = .084$) were also high, though not sufficiently to achieve statistical significance once p -values were corrected for multiple comparisons. In affiliation context, no AUs or ADs occurred at above-chance rates. Table 6 shows a subset of the results of the bootstrapping analysis (those cases where corrected $p < .1$); full results are available in the ESM.

4 | DISCUSSION

We found that SBT expressions produced in different contexts were discriminated successfully above chance level, using a robust randomization procedure. Thus, facial expressions that differed subtly in appearance also differed in social outcomes. Expressions produced in some contexts were characterized by particular AUs or ADs, while other distinctions were made using measurements of the intensity of AUs, and the overall variability of expression sequences. The results of the bootstrapping analysis demonstrate that some AUs and ADs are characteristic of only one context: Jaw stretch (AU27) and Ear flattener (EAU3) for play, Jaw wobble (AD184) for copulation, and Teeth chatter (AD182) for submission. Higher intensity of movement was also generally characteristic of submission. Looking beyond these isolated stereotypes, distinction between the different contexts, particularly copulation and affiliation, is likely to depend on tendency rather than stereotypy. These two contexts were distinguished at above-chance rates, but their distinction depended on the combination of several tendencies across multiple AUs, rather than one or two AUs forming a clear indicator. The results also demonstrate the ability of MaqFACS to produce data that can be used to assess the differences between facial expressions reliably and objectively.

Play expressions were characterized by jaw stretching (AU27)—every example of play involved this AU. This fits with existing descriptions of “play face,” which is an exaggerated jaw stretch exhibited by many carnivores (e.g., canids, Bekoff, 1974; bears, Henry & Herrero,

1974; polecats, Poole, 1978) and primates (e.g., Tonkean macaques, Thierry et al., 1989; gorillas, Waller & Cherry, 2012) before and during play. Yet these expressions were only categorized successfully 60% of the time. This may be because five other (i.e., not preceding play) expressions also involved AU27, meaning that the analysis would risk miscategorizing all of those if it depended more fully on the single AU to categorize play expressions. It is important to note that it is not possible to know the animal's intention in producing an expression (see Townsend et al., 2017 for a review of intentionality in animal signaling), only to document the behavior preceding and following the expression; all instances of AU27 may have been produced with the intention of play, and the invitation rejected in those five other instances.

Submissive context was characterized by the presence of teeth-chatter (AD182), and by a high level of intensity of lip movements (AU10 and AU12). Teeth-chatter, described by van Hooff (1967) as similar to lipsmacking but with lips retracted, and by Thierry, Bynum, et al. (2000) as a rapid alternation between SBT and lipsmacking, has previously been identified as being used in submission contexts in other macaques, but not crested macaques (Thierry, Bynum, et al., 2000).

Copulation expressions involved above-average rates of AD184 (Jaw wobble), which has previously been described as part of sexual signaling in this species. These expressions were also more likely to involve AU9 (Nose wrinkle), but this AU only occurred in 10 of 76 interactions; AU9 is difficult to detect due to the dark, smooth skin of crested macaques (see Table 2), and may only be detectable in certain individuals or intense actions. Affiliative SBT were identified partly due to their higher variability, while expressions that preceded copulation tended to have relatively high intensity of AUs, and low overall variability.

Increases in variability and intensity of facial movements would both be expected to cause increased conspicuousness of the expression. In potentially costly situations, increased intensity may be favored as a means of avoiding ambiguity: confusing aggression with playfulness, or miscommunication of submission, could be very harmful to an animal's health, while expressions indicating intention to

copulate could also be under similar selection for clarity to avoid ambiguity. Usage of intense facial movements, including jaw stretch (AU27), in play may prevent confusion for the partner, as is suggested for the more exaggerated play face displayed by gorillas engaged in intense rather than gentle play (Waller & Cherry, 2012). For affiliative interactions, confusion should not be so costly, and so more subtle signals, with a commensurate reduction in measurable intensity, may be expected. Thus, expressions produced in affiliative contexts may be under less severe pressure to conform to a stereotype, leading to the more variable and less intense forms detected by this study. However, it could also be argued that variability itself can be conspicuous and may be favored in more serious situations: facial expressions produced in copulation and submission context each contained a dynamic element (jaw-wobble and teeth-chatter, respectively) at above-average rates, which could serve to make these displays more conspicuous to a potential partner or an approaching dominant individual. The lipsmacking display, produced in a range of mainly affiliative contexts (Micheletta, Engelhardt, Matthews, Agil, & Waller, 2013; van Hooff, 1967), is also dynamic but presumably less conspicuous than teeth-chatter, in which the teeth are bared. Comparison of the visibility of facial expressions formed of different AU combinations could give useful insights into this aspect of facial communication.

5 | LIMITATIONS

Since the intention of signalers is difficult to infer from observing behavioral outcomes (but see Townsend et al., 2017), it is possible that in some cases where affiliation is the recorded outcome of the interaction, the signaler's intention was play or copulation. While AU27 was used in all expressions preceding play, it also occurred in 7% of other interactions—it is arguable that in these examples the signaler may have intended to play with the recipient but was refused. Similarly, in interactions where a male directed an expression toward a female, it is possible that he intended to copulate with her, but she proceeded only to groom him, leading to the categorization of affiliation. Using preceding behavior to categorize interactions was impossible, since SBT appeared to begin encounters rather than ending them—very few interactions involved any preceding behavior apart from an approach by either party. Furthermore, a potential issue with categorization was that the categories are broad, and not strictly mutually exclusive. For example, hip-holding (Affiliative) might occur after backing away into a crouch (Submission), embracing (Affiliative) during a pause in wrestling (Play), and grooming (Affiliative) after inspecting a presenting female (Copulation). However, these affiliative behaviors usually occurred after one or more of the stereotypical behaviors listed in Table 1, and in each, the interaction was categorized under the appropriate nonaffiliative context. In future, it might be possible to compare subcategories such as “submission with affiliation” and “submission with no affiliation.”

Another potential source of uncertainty in our data is that since unimodal communication is uncommon (Partan & Marler, 1999; Slocombe, Waller, & Liebal, 2011) other communication modes, such

as body posture and gesture, are also likely to have had an impact on the observed outcomes of social interactions. While vocalizations are commonly produced alongside facial expressions, and are known to impact the outcome of friendly interactions in other primates (e.g., Davila-Ross, Jesus, Osborne, & Bard, 2015), none were detected during the expression sequences.

The small sample sizes for expression sequences produced in play and submission contexts are a concern. However, the bootstrapping analysis showed that these two contexts differ starkly in the rates of certain AU/ADs: AU27 (jaw stretch) for Play, AD184 (teeth chatter) in submission context. Likewise, a second discriminant analysis (see ESM) conducted using data from only affiliation and copulation contexts was still capable of distinguishing these contexts at above-chance rates. While there was significant sex skew between the different contexts, notably with “copulation” expressions only produced by males, and “play” expressions only produced by females, this is taken into account in the permutation analysis. Since the sex skews of the 1,000 randomized datasets mirror those of the original dataset, neither this skew, nor any other characteristics of the individuals producing the expressions, can explain the good performance of the discriminant analysis in categorizing expressions by context. It should also be noted that while a perfect discriminant analysis would enable identification of stereotypical AU combinations for each context; these expressions—particularly those produced in affiliation and copulation contexts—are too similar to enable such a neat outcome. They share the dominant features of lip withdrawal (AU10 and AU12) and mouth open (AU25), and other AUs are not exclusive to either context, and so the differences between them are tendencies rather than characteristics.

6 | IMPLICATIONS

Aside from the findings that jaw stretching precedes play, and teeth chattering precedes submission, which are not unexpected (see Preuschoft, 1992; van Hooff, 1967, 1972), this work has also enabled the identification of other tendencies of facial movement that distinguish SBT produced in different contexts. These results indicate a level of subtle variability in the appearance of primate SBT that has not previously been quantified, and indicate that SBT should not necessarily be treated as a single expression either with a single fixed function (as in rhesus macaques, per de Waal & Luttrell, 1985) or with the function being decided by context (per Beisner & McCowan, 2014; Flack & de Waal, 2007), unless detailed morphological analyses have been conducted to rule out appearance changes as an alternative, parsimonious explanation. It is likely that similar results apply to other facial expressions; however, this will require further investigation. Primate SBT is purportedly homologous to the human smile (Preuschoft, 1992; van Hooff, 1972), which has been shown to vary morphologically between contexts, with “reward,” “affiliative,” and “dominant” smiles being produced through different AU combinations (Rychlowska et al., 2017). Other nonhuman primates, including the gorilla (Waller & Cherry, 2012) and chimpanzee (Parr et al., 2005; Vick

& Paukner, 2010), also display meaningful subtle variability in certain facial expressions. The findings of the current study appear to reflect a similar characteristic of variability in crested macaque SBT.

Since tests of the social complexity hypothesis (SCH; Freeberg, Dunbar, & Ord, 2012) involve quantification of communicative complexity, these findings should call into question the use of simple repertoires of facial expressions as measures of complexity in these tests (e.g., Dobson, 2012). Categorizing facial expressions into simple repertoires (e.g., Dobson, 2012) is a useful first step to quantify facial expression complexity, but this approach ignores any variation within facial expressions; this extra variability could have a huge impact on the actual complexity of communication without being sufficient to be picked up in the repertoire. The finding that crested macaque SBT vary subtly according to the context begs the question of whether this is also the case for other facial expressions, and/or for other species. The use of high-definition analytical tools such as the FACS could enable the creation of new measures of complexity of facial expressions, which would enable more effective tests of the SCH to be conducted. Crested macaques are classified among the most socially-tolerant of macaques, due to their relatively high rates of post-conflict reconciliation (Petit, Abegg, & Thierry, 1997; Thierry et al., 2008) and bidirectional conflict (Thierry et al., 2008), which indicate that dominance relationships are relatively less rigid, though this may reflect only characteristics of interactions between females (Reed, O'Brien, & Kinnaird, 1997). These characteristics are said to signify a high level of social complexity (Dobson, 2012; Thierry, 2007). It is therefore likely, per the SCH (Freeberg et al., 2012), that this species will exhibit greater complexity of communication, manifesting as greater variability of facial expressions, compared to other macaques. If it was found that other tolerant (Thierry et al., 2008) macaque species show similar variation in SBT, but less-tolerant species do not, this would constitute evidence to support the SCH. Finding variability in the SBT of less-tolerant species could also yield great insights into the relative importance of the form and context of signals. In studies of rhesus macaques (Beisner & McCowan, 2014) and pig-tailed macaques (Flack & de Waal, 2007), the authors presented evidence that SBT carried different meaning, shown by different behavioral outcomes, according to whether they were produced in a "peaceful" or "conflict" context. The demonstration in the current paper of the importance of subtle morphological variation, which was not considered in the previous studies, indicates that it may not only be the context only that affects the function of these signals, but rather the morphology of the expression itself that facilitates the different function. Detailed study of the morphology of SBT in rhesus and pigtailed macaques would help to answer this question.

We have demonstrated that FACS can be used to classify crested macaque SBT according to behavioral context, at above-chance levels. By identifying the physical characteristics of expressions that underlie these distinctions, we have confirmed some preexisting ideas about crested macaque facial expressions as well as gaining some new insight. This finding illustrates the potential for FACS to provide new understanding of the connection between form and function of facial expressions in nonhuman primates, and the potential importance of

subtle variation to this field of study. The results call into question the classification of SBT as a single static signal, imply that subtle variability in facial movements may play an important role in facial communication, and support a reassessment of the methods used to quantify complexity of facial communication in comparative studies.

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CONFLICT OF INTEREST

The authors declare there are no conflicts of interest.

AUTHOR CONTRIBUTIONS

Peter R. Clark performed video coding, cleansed and analyzed data, wrote the paper, and produced tables and figures. **Jérôme Micheletta** collected video clips and behavioral data. **Bridget M. Waller** and **Jérôme Micheletta** contributed significantly to the writing of the paper. **Antje Engelhardt** and **Muhammad Agil** provided material and logistical support. **Eglantine Julle-Danière** and **Peter R. Clark** adapted MaqFACS for use with crested macaques. **Anne M. Burrows** provided anatomical expertise. All authors reviewed drafts of the paper.

DATA AVAILABILITY STATEMENT

The data and R code that support the findings of this study are available in figshare at <http://doi.org/10.6084/m9.figshare.c.5047724>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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