

# 1 **Higher social tolerance is associated with more complex facial** 2 **behavior in macaques**

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17 Coding System, macaque

## 18 **Abstract**

19 The social complexity hypothesis for communicative complexity posits that animal societies with  
20 more complex social systems require more complex communication systems. We tested the so-  
21 cial complexity hypothesis on three macaque species that vary in their degree of social tolerance  
22 and complexity. We coded facial behavior in >3000 social interactions across three social contexts  
23 (aggressive, submissive, affiliative) in 389 animals, using the Facial Action Coding System for  
24 macaques (MaqFACS). We quantified communicative complexity using three measures of uncer-  
25 tainty: entropy, specificity, and prediction error. We found that the relative entropy of facial be-  
26 havior was higher for the more tolerant crested macaques as compared to the less tolerant Barbary  
27 and rhesus macaques across all social contexts, indicating that crested macaques more frequently  
28 use a higher diversity of facial behavior. The context specificity of facial behavior was higher  
29 in rhesus as compared to Barbary and crested macaques, demonstrating that Barbary and crested  
30 macaques used facial behavior more flexibly across different social contexts. Finally, a random  
31 forest classifier predicted social context from facial behavior with highest accuracy for rhesus and  
32 lowest for crested, indicating there is higher uncertainty and complexity in the facial behavior of  
33 crested macaques. Overall, our results support the social complexity hypothesis.

## 34 **Introduction**

35 Animals must overcome a range of environmental and ecological challenges to survive and re-  
36 produce, with group-living species having to overcome additional social challenges to maximize  
37 fitness. Communicative signals can be used to navigate a number of different social situations  
38 and may need to become more elaborate as social complexity increases. The social complexity  
39 hypothesis for communicative complexity encapsulates this idea, proposing that animal societies  
40 with more complex social systems require more complex communication systems [1].

41 The social complexity hypothesis has become a topical issue in recent years, with questions regard-  
42 ing the definitions, measurement, and selective pressures driving both social and communicative  
43 complexity [2,3]. Social complexity as experienced by group members can be affected by the level  
44 of differentiation of social relationships, where complexity increases as social relationships become  
45 more differentiated [4,5]. In a socially complex society individuals interact frequently with each  
46 other in diverse ways and in many different contexts [1]. If the types of interactions that individuals  
47 have is constrained, for example, by dominance or kinship, then social complexity decreases [1].  
48 Social complexity is also affected by the predictability or consistency of social interactions [5,6].  
49 When the behavior of social partners is unpredictable, such as when the dominance hierarchy is un-  
50 stable, individuals likely perceive the social environment as more complex [6]. These operational  
51 definitions of social complexity are valuable to advance the study of social complexity but are not  
52 easy to quantify with a single measure [7].

53 Similarly, communicative complexity is also difficult to quantify. Many studies have used the  
54 number of signalling units as a measure of communicative complexity [2]. While a useful mea-  
55 sure, it is not always apparent what a signaling unit is. For example, calls are sometimes graded on  
56 a continuous scale without a clear separation between different call types [8]. Fewer studies have  
57 investigated the complexity of non-vocal communication [1,2], but similar issues exist. One previ-  
58 ous study quantified the repertoire of facial behavior in macaques by the number of discrete facial  
59 expressions that a species displays and found that it was positively correlated with conciliatory

60 tendency and counter-aggression across species [9]. However, classifying facial expressions into  
61 discrete categories (e.g., bared-teeth display) does not capture the full range of expressiveness and  
62 meanings that the face can convey. For example, subtle morphological variations in bared-teeth  
63 displays are associated with different outcomes of social interactions (e.g., affiliation versus sub-  
64 mission) in crested macaques (*Macaca nigra*) [10]. A better approach is to quantify facial behavior  
65 at the level of individual facial muscle movements [11], which can be done using the Facial Action  
66 Coding System (FACS) [12]. In FACS, visible muscle contractions in the face are called Action  
67 Units and allow for a detailed and objective description of facial behavior [11,12]. Indeed, facial  
68 mobility, as defined by the number of Action Units that a species has, is positively correlated with  
69 group size across non-human primates [13]. However, isolated muscle movements still do not ac-  
70 count for the full diversity of facial behavior because facial muscles often contract simultaneously  
71 to produce a large variety of distinct facial expressions.

72 One promising avenue to approximate complexity in living organisms is to quantify the uncertainty  
73 or predictability of a system [14,15], which are general properties of complex systems [16,17].  
74 Shannon's information entropy [18] is a measure of uncertainty that can be applied to animal com-  
75 munication. Conceptually, entropy measures the potential amount of information that a communi-  
76 cation system holds, rather than what is actually communicated [18,19]. Entropy increases along  
77 two dimensions: (i) with increasing diversity of signals, and (ii) as the relative frequency of signal  
78 use becomes more balanced. For example, a system with three calls can hold more information  
79 than a system with one call and thus would have higher entropy. Likewise, a system with three  
80 calls used with equal frequency will have a higher entropy than another system that expresses one  
81 call more frequently than the two others. Uncertainty increases with entropy because each com-  
82 municative event has the potential to derive from a greater number of units. The relative entropy,  
83 or uncertainty, of different systems can be compared by calculating the ratio between the observed  
84 and maximum entropy of each system.

85 The predictability and uncertainty of a communication system is also affected by how flexibly sig-  
86 nals are used across different social contexts [5]. For instance, if signal A is always used in an

87 aggressive context and signal B is always used in an affiliative context, then it is easy to predict  
88 the context from the signal. Conversely, if signals A and B are used in both contexts, then pre-  
89 dictability is lower, and complexity is higher. Extremely rare signals do not substantially affect  
90 the predictability of a system regardless of whether they have high or low specificity since they are  
91 seldom observed in the majority of social interactions. Therefore, predictability is highest when  
92 signals are both highly context-specific and occur in that context often. Additionally, predictabil-  
93 ity can be measured directly by training a machine learning classifier to predict the social context  
94 that a given signal was used in. Differences in prediction error would approximate the relative  
95 uncertainty and complexity, with accuracy being lower in more complex systems. However, as  
96 complexity lies somewhere between order and randomness [15,19], we should still be able to pre-  
97 dict the social contexts better than chance, even in a complex system.

98 Studying closely related species offers a robust means of testing the social complexity hypothesis  
99 due to their homologous communication systems. For this reason, macaques (genus *Macaca*) are  
100 excellent taxa to test the social complexity hypothesis. All species have a similar social organiza-  
101 tion consisting of multi-male, multi-female groups, but vary in social style in ways that are highly  
102 relevant to predictions of the social complexity hypothesis. The social styles of macaques consist  
103 of several covarying traits that can be ordered along a social tolerance scale ranging from the least  
104 (grade 1) to most tolerant (grade 4) [20,21]. Social interactions for the least tolerant species, such  
105 as rhesus (*M. mulatta*) and Japanese (*M. fuscata*) macaques, are generally more constrained by a  
106 steep linear dominance hierarchy [22] and kinship [23–25]. Additionally, severe agonistic inter-  
107 actions are more frequent [25], instances of counter-aggression and reconciliation after conflicts  
108 are rare [22,25], and formal signals of submission are commonly used [26,27]. Combined, these  
109 behavioral traits indicate that agonistic interactions of the least tolerant species are more stereo-  
110 typed and formalized. Thus, the outcome of such interactions is more certain, whereas the opposite  
111 is true for the most tolerant species, such as crested and Tonkean (*M. tonkeana*) macaques. The  
112 unpredictability in the outcome of agonistic interactions of tolerant macaques likely results in a  
113 social environment that is perceived as more complex by individuals [6], where more subtle means

114 of negotiation during conflicts may be necessary.

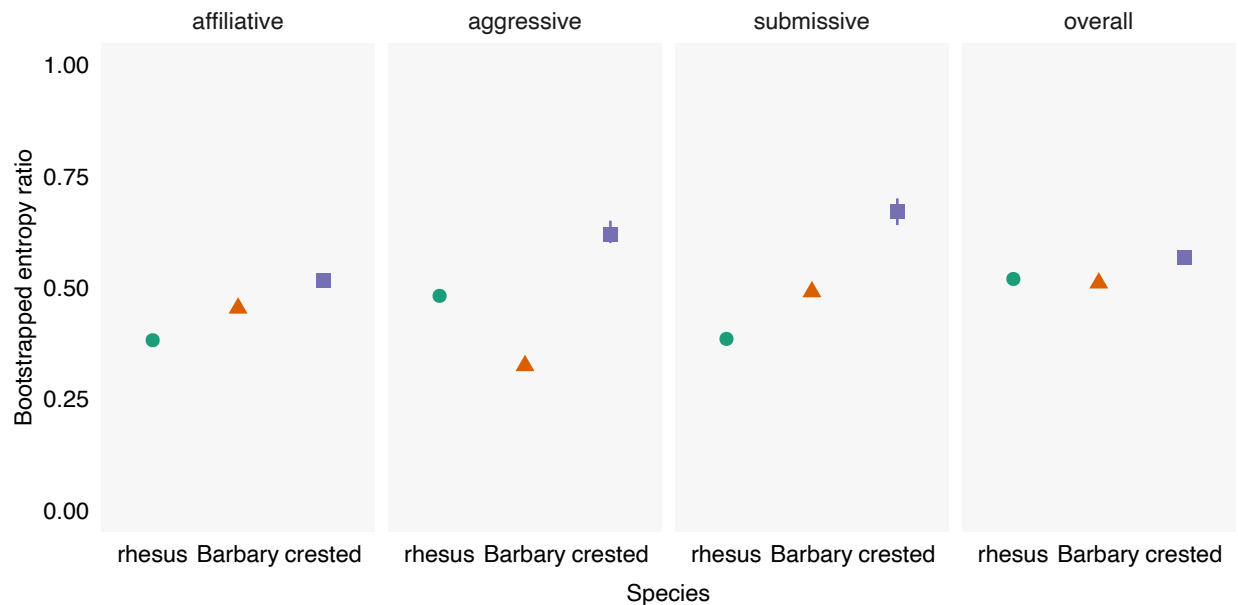
115 In this study we compared the facial behavior of three macaque species that vary in their degree  
116 of social tolerance and, therefore, social complexity: rhesus (least tolerant), Barbary (*M. sylvanus*,  
117 mid-tolerant), and crested macaques (most tolerant). For macaques (and primates in general), the  
118 face is central to communication and is a key tool in allowing individuals to achieve their social  
119 goals by communicating motivations, emotions and/or intentions [28,29]. We coded facial behav-  
120 ior at the level of individual visible muscle movements using FACS and recorded all observed  
121 unique combinations, rather than classifying facial expressions into discrete categories. Based on  
122 the social complexity hypothesis [1], we expected that tolerant species would have higher com-  
123 municative complexity, given that their social relationships are less constrained by dominance and  
124 have higher overall uncertainty in the outcome of agonistic interactions. Specifically, we predicted  
125 the following: (1) relative entropy of facial behavior will be lowest in the rhesus and highest in  
126 crested macaques, (2) context specificity of facial behavior will be highest in rhesus and lowest  
127 in crested macaques, and (3) social context can be predicted from facial behavior most accurately  
128 in rhesus and least accurately in crested macaques. For all three metrics, we expected Barbary  
129 macaques to lie somewhere in between the rhesus and crested macaques.

## 130 **Results**

### 131 **Entropy of facial behavior**

132 To compare the relative uncertainty in the facial behavior of macaques, we defined facial behavior  
133 by the unique combination of Action Units (facial muscle movements) that occurred at the same  
134 time. We calculated the entropy ratio for each species and social context, defined as the ratio  
135 between the observed entropy and the expected entropy if Action Units were used randomly. Values  
136 closer to 0 indicate that there is low uncertainty (e.g., when only a few facial movements are used  
137 frequently) and values closer to 1 indicate high uncertainty (e.g., when many facial movements are

138 used frequently). To determine whether the entropy ratios for each species differed within social  
139 context, we calculated the entropy ratio on 100 bootstrapped samples of the data, resulting in a  
140 distribution of possible values. The bootstrapped entropy ratio of facial behavior differed across  
141 species and within social contexts (Figure 1). In an affiliative context, the entropy ratio was highest  
142 for crested, then Barbary, and lowest for rhesus macaques (crested: mean = 0.52, range = 0.50–  
143 0.53; Barbary: mean = 0.45, range = 0.45–0.46; rhesus: mean = 0.38, range = 0.37–0.39). In an  
144 aggressive context, the entropy ratio was highest for crested, then rhesus and lowest for Barbary  
145 macaques (crested: mean = 0.62, range = 0.60–0.65; Barbary: mean = 0.32, range = 0.32–0.33;  
146 rhesus: mean = 0.48, range = 0.47–0.49). In a submissive context, the entropy ratio was highest for  
147 crested, then Barbary, and lowest for rhesus macaques. (crested: mean = 0.67, range = 0.64–0.70;  
148 Barbary: mean = 0.49, range = 0.48–0.50; rhesus: mean = 0.38, range = 0.37–0.39). Overall, across  
149 all contexts, including when the context was unclear, the entropy ratio was highest for crested, and  
150 similar for Barbary and rhesus macaques (crested: mean = 0.57, range = 0.56–0.58; Barbary: mean  
151 = 0.51, range = 0.51–0.51; rhesus: mean = 0.52, range = 0.51–0.52; Figure 1).



152

153 **Figure 1:** Bootstrapped entropy ratio of facial behavior across social contexts for three species of  
154 macaques. The entropy ratio was calculated on 100 bootstrapped samples of the data by dividing  
155 the observed entropy by the expected entropy if Action Units were used randomly for each social

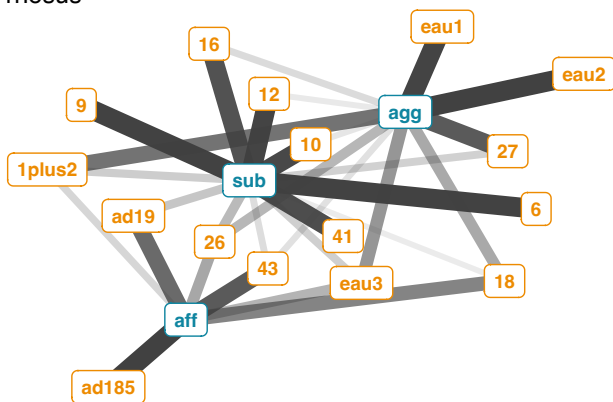
156 context. The entropy ratio ranges from 0 to 1, with higher values indicating higher uncertainty.  
157 Symbols and whiskers indicate mean and range of bootstrapped values.

## 158 **Context specificity of facial behavior**

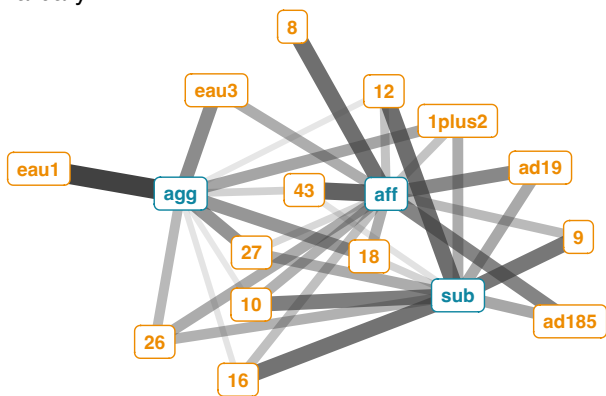
159 We calculated the context specificity for all possible combinations of Action Units. Here we re-  
160 port specificity for combinations that were observed in at least 1% of observations per species and  
161 social context because extremely rare signals do not affect the predictability of a system substan-  
162 tially, regardless of whether they have high or low specificity. Specificity for each Action Unit  
163 combination was defined as the number of times it was observed in one context divided by the  
164 total number of times it was observed across all contexts. When considering single Action Units,  
165 some were observed in only one context, but most were observed at least once in all three contexts  
166 for all three species (Figure 2). On average, single Action Units were observed in fewer contexts  
167 for rhesus (mean degree = 1.9), compared to Barbary (mean degree = 2.4), and crested macaques  
168 (mean degree = 2.6). The specificity of all Action Unit combinations used in an affiliative context  
169 was highest for the rhesus macaques, then Barbary, and lowest for crested macaques (rhesus: mean  
170 = 0.80, SD = 0.28, n = 69; Barbary: mean = 0.63, SD = 0.26, n = 450; crested: mean = 0.37, SD  
171 = 0.26, n = 327; Figure 3a). The specificity of Action Unit combinations used in an aggressive  
172 context was highest for rhesus, then crested, and lowest for Barbary macaques (rhesus: mean =  
173 0.71, SD = 0.35, n = 83; Barbary: mean = 0.44, SD = 0.38, n = 64; crested: mean = 0.51, SD =  
174 0.30, n = 281). The specificity of Action Unit combinations used in a submissive context was also  
175 highest for rhesus, then crested, and lowest for Barbary macaques (rhesus: mean = 0.93, SD = 0.18,  
176 n = 312; Barbary: mean = 0.61, SD = 0.18, n = 297; crested: mean = 0.70, SD = 0.21, n = 595).  
177 The majority (>50%) of Action Unit combinations used by rhesus macaques had high specificity  
178 (>0.8) in all three social contexts, whereas only a minority (<50%) of Action Unit combinations  
179 used by Barbary and crested macaques had high specificity (Figure 3b).



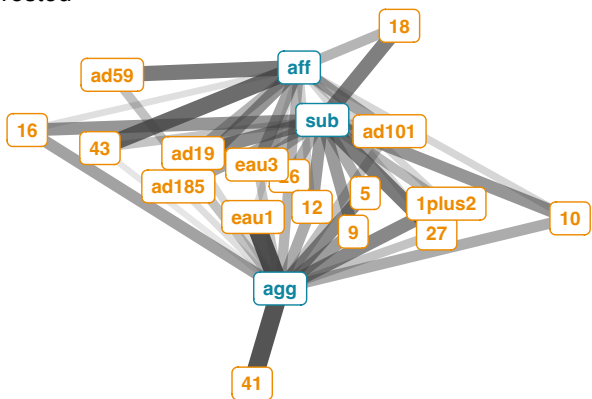
rhesus



Barbary



crested

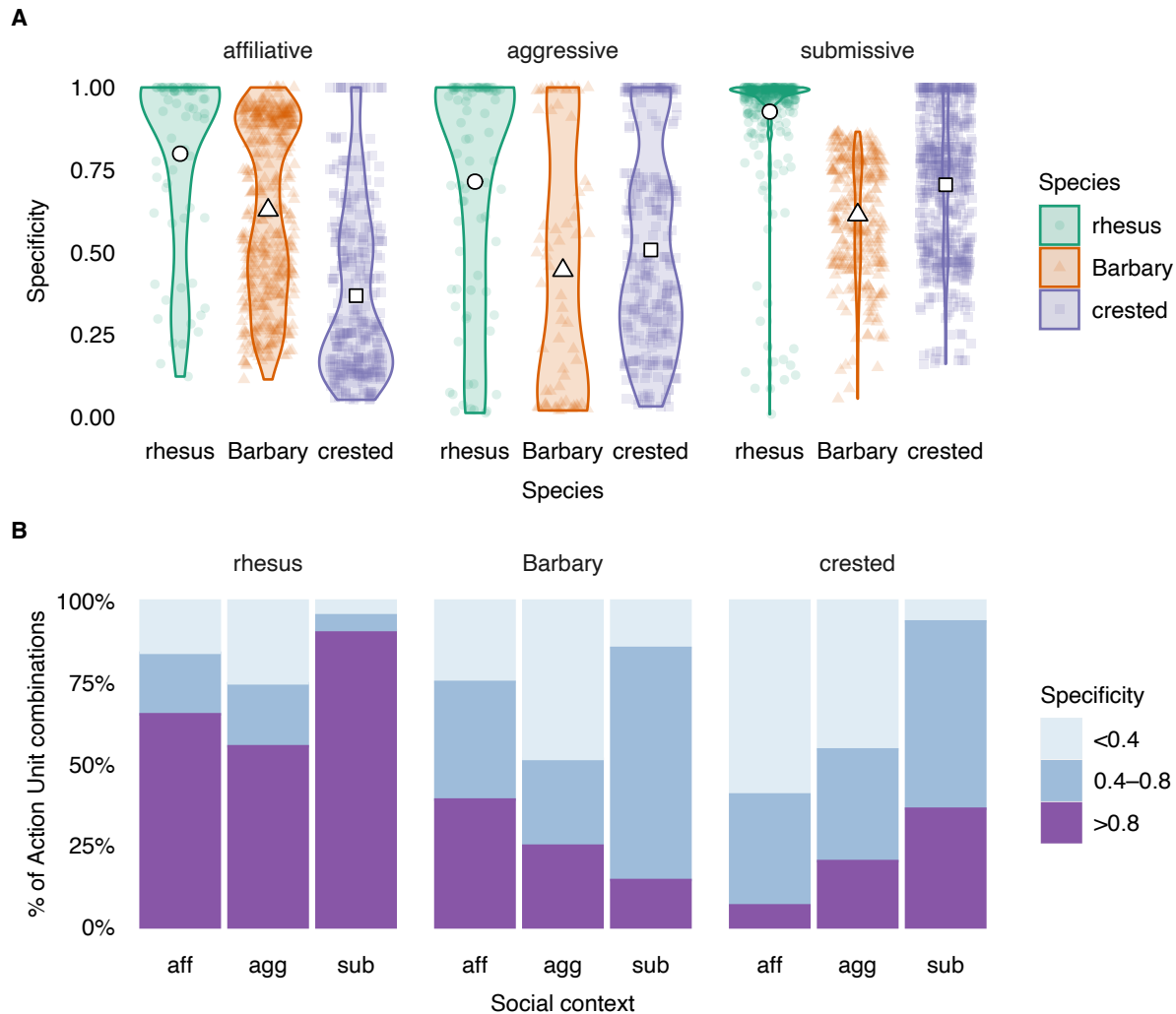


Specificity: — 0.25 — 0.50 — 0.75

180

181 **Figure 2:** Bipartite network of single Action Units (orange) and social context (blue) for three  
182 species of macaques. Edges are shown for Action Units that occurred in at least 1% of obser-

183 variations per context. Edge thickness and transparency are weighted by specificity, which ranges  
 184 from 0 (indicating an Action Unit is never observed in a context) to 1 (indicating an Action Unit  
 185 is only observed in one context). Context abbreviations: agg = aggressive, aff = affiliative, sub =  
 186 submissive.



187

188 **Figure 3:** Specificity of Action Unit combinations that were used in at least 1% of observations per  
 189 species per social context. Specificity ranges from 0 (indicating an Action Unit is never observed  
 190 in a context) to 1 (indicating an Action Unit is only observed in one context). **(A)** Distribution  
 191 of Action Unit combination specificity. Width of violin plots indicate the relative density of the  
 192 data. Colored symbols indicate unique Action Unit combinations. White symbols indicate mean  
 193 specificity. **(B)** Proportion of Action Unit combinations used with high (>0.8), moderate (0.4–

194 0.8) or low ( $<0.4$ ) specificity. Context abbreviations: agg = aggressive, aff = affiliative, sub =  
195 submissive.

## 196 **Predicting social context from facial behavior**

197 A random forest classifier was able to predict social context (affiliative, aggressive or submissive)  
198 from facial behavior with a better accuracy than expected by chance alone for all three species  
199 of macaques. The classifier was most accurate for rhesus ( $\kappa = 0.92$ ), then Barbary ( $\kappa =$   
200  $0.68$ ), and least accurate for crested macaques ( $\kappa = 0.49$ ). The confusion matrices for model  
201 predictions are shown in table S1.

## 202 **Discussion**

203 We investigated the hypothesis that complex societies require more complex communication sys-  
204 tems [1] by comparing the complexity of facial behavior of three species of macaques that vary in  
205 their degree of social tolerance and complexity. We defined facial behavior by the unique combina-  
206 tions of muscle movements visible in the face. Doing so allows for a much more precise description  
207 of facial behavior and captures subtle differences that are lost if facial expressions are classified as  
208 discrete categories. We quantified communicative complexity using three measures of uncertainty  
209 and predictability: entropy, context specificity, and prediction error. Collectively, our results sug-  
210 gest that the complexity of facial behavior is higher in species with a more tolerant—and therefore  
211 more complex—social style; complexity was highest for crested, followed by Barbary, and low-  
212 est in rhesus macaques. In light of what we know about the differences between macaque social  
213 systems, our results support the predictions of the social complexity hypothesis for communicative  
214 complexity.

215 The entropy ratio of facial behavior was highest in crested compared to Barbary and rhesus  
216 macaques, both overall and within each social context (affiliative, aggressive, submissive). This

217 result suggests that crested macaques use a higher diversity of facial signals within each social  
218 context more frequently, resulting in the higher relative uncertainty in their use of facial behavior.  
219 Information theory defines information as the reduction in uncertainty once an outcome is learned  
220 [18]. By this definition, our data suggest that the facial behavior of crested macaques has the  
221 *potential* to communicate more information, compared to Barbary and rhesus macaques, although  
222 this would need to be explicitly tested in future studies. Our findings are in line with predictions  
223 of the social complexity hypothesis [1] given the differences in social styles between tolerant and  
224 intolerant macaques. In tolerant macaque societies, social interactions are less constrained by  
225 dominance [22] such that rates of counter aggression and reconciliation post-conflict are higher  
226 [25,30]. Thus, there is a greater variability in the kind of interactions that individuals have,  
227 potentially requiring the use of more diverse facial behavior to achieve social goals, particularly  
228 during conflicts. Similarly, strongly bonded chimpanzee (*Pan troglodytes*) dyads exhibit a larger  
229 repertoire of gestural communication than non-bonded dyads, presumably due to the former  
230 having more varied types of social interactions [31].

231 The overall entropy ratio of rhesus and Barbary macaques was similar, suggesting that they have  
232 similar communicative capacity using facial behavior. However, the entropy ratio differed when  
233 compared within social contexts; while relative entropy was higher for Barbary macaques in af-  
234 filiative and submissive contexts, it was higher for rhesus macaques in aggressive contexts. One  
235 possible explanation may be due to the use of stereotyped signals of submission and dominance in  
236 each species. For example, subordinate rhesus macaques regularly exhibit stereotyped signals of  
237 submission (silent-bared-teeth), whereas dominant Barbary macaques regularly exhibit stereotyped  
238 threats (round-open-mouth) [26,27]. Frequent use of a stereotyped signal within a context reduces  
239 the overall diversity of signals, resulting in a lower entropy ratio for submission and aggression in  
240 rhesus and Barbary macaques, respectively. It has been suggested that in societies with high power  
241 asymmetries between individuals, such as in rhesus macaques, spontaneous signals of submission  
242 serve to prevent conflicts from escalating as well as increasing the tolerance of dominant individuals  
243 toward subordinates [27]. In societies with more moderate power asymmetries, such as in Barbary

244 macaques, subordinates may be less motivated to spontaneously submit and thus dominants may  
245 need to assert their dominance with formalized threats more frequently [27].

246 While the entropy ratio captures the uncertainty of facial behavior used within a social context,  
247 context specificity captures the uncertainty generated when the same facial behavior is used flexi-  
248 bly across different social contexts. Overall, the context specificity of facial behavior was higher  
249 for the intolerant rhesus macaques as compared to the more tolerant Barbary and crested macaques  
250 across all three social contexts. This pattern occurred for both the mean specificity values and the  
251 proportion of Action Unit combinations used that had high ( $>0.8$ ) specificity. Similarly, a previous  
252 study demonstrated that vocal calls of tolerant macaques are less context specific than in intoler-  
253 ant macaques [32]. There was not a clear difference in specificity between Barbary and crested  
254 macaques; specificity was higher for Barbary macaques in affiliative contexts, similar for both  
255 species in aggressive contexts, and higher for crested macaques in submissive contexts. These dif-  
256 ferences in context specificity of communicative signals across macaque species may be related  
257 to differences in power asymmetry in their respective societies, particularly as it relates to the risk  
258 of injury. For macaques, bites are far more likely to injure opponents than other types of contact  
259 aggression (e.g., grab, slap) and thus provide the best proxy for risk of injury [21]. The percentage  
260 of conflicts involving bites is much higher in the less tolerant rhesus macaque, compared to the  
261 more tolerant Barbary and crested macaques who have similar low rates of aggression involving  
262 bites [25,33]. Risky situations may promote the evolution of more conspicuous, stereotypical sig-  
263 nals to reduce ambiguity [34]. Indeed, intolerant macaques such as the rhesus more commonly use  
264 formal signals of submission [26,27]. In our study, rhesus macaques used facial behavior with high  
265 specificity across all contexts but particularly in submissive contexts. If the same facial behavior  
266 (or signal in general) is used in multiple social contexts, its meaning may be uncertain and must  
267 be deduced from additional contextual cues [35]. When facial behavior is highly context specific,  
268 there is less uncertainty about the meaning of the signal and/or intention of the signaler. In a society  
269 where the risk of injury from aggression is high, it may be adaptive for individuals to use signals that  
270 are highly context specific or ritualized to reduce uncertainty about its meaning. By contrast, the

271 lower risk of injury in Barbary and crested macaques may allow room for more nuanced exchanges  
272 of information during conflicts as well as higher rates of reconciliation post conflict [25,30].

273 In all three species of macaques, at least some facial muscle movements had low specificity and  
274 were therefore used across multiple social contexts that likely differed in valence. This finding is  
275 in line with the idea that communicative signals in primates are better interpreted as the signaler  
276 announcing its intentions and likely future behavior [36,37], and not necessarily as an expression  
277 of emotional state [28,29,36,38].

278 We found that a random forest classifier was least accurate at predicting social context from facial  
279 behavior for crested, followed by Barbary, and then rhesus macaques. The behavior of complex  
280 systems is generally harder to predict than simpler ones [16,17]. Thus, the relatively poorer perfor-  
281 mance of the classifier in crested macaques suggests that they have the most complex facial behav-  
282 ior. Nevertheless, the classifier was able to predict social context from facial behavior with better  
283 accuracy than expected by chance alone for all three species of macaque, including the crested.  
284 This result confirms the assumption that facial behavior in macaques is not used randomly and  
285 most likely has some communicative or predictive value [39]. Completely random systems are not  
286 considered complex [19], but the communications systems of living organisms are unlikely to be  
287 observed as random. Therefore, measuring uncertainty becomes a good proxy for complexity [14].

288 In addition to social complexity, it is possible that other factors are related to the complexity of  
289 facial behavior. For example, primates with a larger body size have greater facial mobility [13,40],  
290 which could allow for greater complexity of facial behavior. However, differences in mean body  
291 mass across the three macaques species of this study are small (rhesus: 6.5 kg; Barbary: 11.5  
292 kg; crested: 7.4 kg) [41] with substantial overlap in body weight across adult individuals of the  
293 different species [42], and so it is unlikely to explain the differences in the complexity of facial  
294 behavior that we report in this study. The degree of terrestriality could also influence the evolution  
295 of facial signals due to more limited visibility in the canopy. However, differences in facial mobility  
296 across terrestrial and non-terrestrial primates are not significant once body size is controlled for

297 [13]. Furthermore, all three species included in this study have comparable levels of terrestriality,  
298 spending the majority (52-72%) of the time on the ground [43–45]. Spatial spread and predation  
299 pressure could potentially also influence the use of facial signals. For example, when group spread  
300 is higher, reliance on facial signals could be lower, or when predation pressure is higher, reliance  
301 on facial signals could be higher. There are currently no reliable data on predation pressure and  
302 spatial spread of the three species in their natural habitat but it could be a good avenue for future  
303 studies.

304 Our results on the complexity of facial behavior in macaques is mirrored by previous studies show-  
305 ing that the complexity of vocal calls is similarly higher in tolerant compared to intolerant macaques  
306 [32,46]. Although not all macaque facial expressions have a vocal component, vocalizations are  
307 fundamentally multisensory with both auditory and visual components, where different facial mus-  
308 cle contractions are partly responsible for different-sounding vocalizations [47]. Indeed, some areas  
309 of the brain in primates integrate visual and auditory information resulting in behavioral benefits  
310 [48]. For example, macaques detect vocalizations in a noisy environment faster when mouth move-  
311 ments are also visible, where faster reaction times are associated with a reduced latency in auditory  
312 cortical spiking activity [49]. Combined, these findings suggest that the evolution in the complex-  
313 ity of vocal and facial signals in macaques may be linked and the same may be true of primates in  
314 general. For instance, humans not only have the most complex calls (language) and gestures, but  
315 most likely use the most complex facial behavior as well, given that their general facial mobility  
316 is highest among primates (most Action Units) [12,50]. In lemurs (Lemuriformes), the repertoire  
317 size of vocal, visual, and olfactory signals positively correlate with group size and each other, sug-  
318 gesting that complexity in all three communicative modalities coevolved with social complexity  
319 [51]. While the complexity of different communication modalities is likely interlinked and cor-  
320 related with each other, future studies would ideally integrate signals from all modalities into a  
321 single communicative repertoire for each species. While collecting and analyzing data on multiple  
322 modalities of communication has historically been a challenge, such endeavors would be an im-  
323 portant next step in the study of animal communication [52]. By breaking down signaling units to

324 their smallest components, as we have done for facial behavior in this study, we may be able to  
325 define a “signal” by temporal co-activation of visual, auditory, and perhaps even olfactory cues,  
326 which would provide the most comprehensive picture of animal communication.

## 327 **Methods**

### 328 **Study subjects and data collection**

329 Behavioral data and video recordings were collected on one adult male and 31 adult female rhesus  
330 macaques (*M. mulatta*), on 18 adult male and 28 adult female Barbary macaques (*M. sylvanus*),  
331 and 17 adult male and 21 adult female crested macaques (*M. nigra*). See supplementary text for  
332 further details.

333 For all study groups and subjects, focal animal observations [53] lasting 15-30 minutes were con-  
334 ducted throughout the day in a pseudo-randomized order such that the number of days and time of  
335 day that each individual was observed was balanced. Videos of social interactions were recorded  
336 with a recording camera (Panasonic HDC-SD700, Bracknell, UK) during focal animal observations  
337 as well as *ad libitum*. Social behavior, including grooming, body contact, and agonistic interactions  
338 were recorded using a handheld smartphone or tablet with purpose-built software (rhesus: Animal  
339 Behavior Pro [54]; Barbary: CyberTracker (<http://cybertracker.org>), crested: Microsoft Excel).

### 340 **Facial behavior and social context coding**

341 Facial behavior was coded at the level of observable individual muscle movements using the Fa-  
342 cial Action Coding System (FACS) [12], adapted for each species of macaque (MaqFACS): rhesus  
343 [55], Barbary [56], crested [10]. In FACS, individual observable muscle contractions are coded as  
344 unique Action Units (AU; e.g., upper lip raiser AU10). Some common facial movements where  
345 the underlying muscle is unknown are coded as Action Descriptors (AD; e.g., jaw thrust AD29). In



346 MaqFACS, the lip-pucker AU18 has two subtle variations normally denoted as AU18i and AU18ii  
347 [55,56]. However, it was often difficult to reliably distinguish between these two subtle variations  
348 when coding videos, and so the lip-pucker was simply coded as AU18. We added a new Action De-  
349 scriptor 185 (AD185) called jaw-oscillation, to denote the stereotyped movement of the jaw up and  
350 down. When combined with existing Action Units of lip movements, the jaw-oscillation AD185  
351 allows for a more detailed and accurate coding of some facial behaviors that would otherwise be  
352 labeled as lipsmack (AD181), teeth-chatter, or jaw-wobble [10,55]. A complete list of Action Units  
353 and Action Descriptors coded in this study is given in table S2.

354 We coded facial behavior of adult individuals but included their interactions with any other group  
355 member regardless of age or sex. Each social interaction was labeled with a context; aggressive,  
356 submissive, affiliative, or unclear. We did not consider interactions in a sexual context because data  
357 for the rhesus macaques were only collected during the non-mating season. Social context was la-  
358 beled from the point of view of the signaler based on their general behavior and body language (but  
359 not the facial behavior itself), during or immediately following the facial behavior. An aggressive  
360 context was considered when the signaler lunged or leaned forward with the body or head, charged,  
361 chased, or physically hit the interaction partner. A submissive context was considered when the  
362 signaler leaned back with the body or head, moved away, or fled from the interaction partner. An  
363 affiliative context was considered when the signaler approached another individual without aggres-  
364 sion (as defined previously) and remained in proximity, in relaxed body contact, or groomed either  
365 during or immediately after the facial behavior. In cases where the behavior of the signaler did not  
366 match our context definitions, or displayed behaviors belonging to multiple contexts, we labeled  
367 the social context as unclear. Social context was determined from the video itself and/or from the  
368 matching focal behavioral data, if available. Videos were FACS coded frame-by-frame using the  
369 software BORIS [57] by AVR, CP and PRC, who are certified FACS and MaqFACS coders. Table  
370 1 shows the number of social interactions per species and context from which FACS codes were  
371 made.

372 **Table 1:** Total number of social interactions per species and social context that were MaqFACS  
373 coded.

Species	Context	N interactions	N subjects
rhesus	affiliative	193	29
	aggressive	413	32
	submissive	318	31
	unclear	121	30
Barbary	affiliative	683	43
	aggressive	585	44
	submissive	529	34
	unclear	603	45
crested	affiliative	241	35
	aggressive	62	23
	submissive	25	18
	unclear	107	25

## 374 **Statistical analyses**

375 Prior to analyses, MaqFACS data were formatted as a binary matrix with Action Units and Action  
376 Descriptors (hereafter simply Action Units) in the columns. Each row denoted an observation time  
377 block of 500ms, where if an Action Unit was active during this time block, it was coded 1 and coded  
378 0 if not. Thus, each row contained information on the combination of facial muscle movements  
379 that were co-activated within a 500ms time window. All statistical analyses were conducted in R  
380 (version 4.2.1) [58].

381 The observed entropy for each social context was calculated using Shannon's information entropy  
382 formula [18]:

$$H = - \sum_i^n p_i \log p_i$$

383 where  $n$  is the number of unique Action Unit combinations and  $p$  is the probability of observ-  
384 ing each Action Unit combination in each social context. The expected maximum entropy was  
385 calculated by randomizing the data matrix while keeping the number of active Action Units per  
386 observation (row) the same. This process was repeated 100 times and the mean of the randomized  
387 entropy values was used as the expected entropy. Therefore, the expected entropy indicated the  
388 entropy of the system if facial muscle contractions occurred at random, while keeping the com-  
389 bination size of co-active muscle movements within the range observed in the data. The entropy  
390 ratio was calculated by dividing the observed entropy by the expected (maximum) entropy. To  
391 determine whether the entropy ratios for each species differed within social context, the entropy  
392 ratio was calculated on 100 bootstrapped samples of the data, resulting in a distribution of possible  
393 entropy ratios. If the distribution of bootstrapped entropy ratios did not overlap, the differences  
394 between entropy ratios were considered to be meaningful.

395 We calculated the specificity with which Action Unit combinations are associated with a social con-  
396 text within each species using the function “specificity” from the R package “NetFACS” (version  
397 0.5.0) [59]. Due to an imbalanced number of observations across social contexts, contexts with  
398 fewer observations were randomly upsampled prior to the specificity calculation. During the up-  
399 sampling procedure all observations of the minority contexts were kept, and new observations were  
400 randomly sampled to match the number of observations in the majority context. This procedure  
401 corrects for any bias in the specificity results from an imbalanced dataset (see fig. S1). Specificity  
402 is the conditional probability of a social context given that an Action Unit combination is observed,  
403 and ranges from 0 (when an Action Unit combination is never observed in a context) to 1 (when  
404 an Action Unit is only observed in one context). Low specificity values indicate that Action Units  
405 were used flexibly across multiple contexts whereas high values indicate that Action Units were  
406 used primarily in a single context. Specificity was calculated for all Action Unit combination sizes

407 ranging from 1 to 11 (the maximum observed combination size) co-active Action Units. When  
408 reporting context specificity results, we excluded Action Unit combinations that occurred in less  
409 than 1% of observations within a social context because extremely rare signals do not impact the  
410 predictability of a communication system regardless of whether specificity is low or high. There-  
411 fore, excluding rare Action Unit combinations removes noise from the specificity results. We report  
412 the mean specificity of Action Unit combinations per social context and the proportion of Action  
413 Unit combinations that have high, moderate, or low specificity. For single Action Units we plotted  
414 bipartite networks that show how Action Units are connected to social context weighted by their  
415 specificity.

416 To predict social context from the combination of Action Units we fit a random forest classifier us-  
417 ing the “tidymodels” R package (version 1.0.0) [60] using the function “ran\_forest” with the engine  
418 set to “ranger” [61], 500 trees, 4 predictor columns randomly sampled at each split, and 10 as the  
419 minimum number of data points in a node required for splitting further. The data were randomly  
420 split into a training set (70%) and a test set (30%), while keeping the proportion of observations  
421 per social context the same in the training and test sets. Due to an imbalanced number of obser-  
422 vations across social contexts, contexts with fewer observations were over-sampled in the training  
423 set using the SMOTE algorithm [62] to improve the classifier predictions. To assess the classifier  
424 performance, we report the kappa statistic, which denotes the observed accuracy corrected for the  
425 expected accuracy [63]. Kappa is 0 when the classifier performs at chance level and 1 when it  
426 shows perfect classification. Kappa values between 0 and 1 indicate how much better the classi-  
427 fier performed than chance (e.g., kappa of 0.5 indicates the classifier was 50% better than chance).  
428 Kappa is a more reliable estimate of model performance than accuracy alone when the relative  
429 sample size for each context is imbalanced, as was the case with our data.

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## 439 **Ethics**

440 This work adhered to the Guidelines for the treatment of animals in behavioral research and teach-  
441 ing [64] and was approved by the Animal Welfare and Ethical Review Body of the University of  
442 Portsmouth (AWERB, approval number: 919B). The AWERB uses UK Home Office guidelines  
443 on the Animals (Scientific Procedures) Act 1986 when assessing proposals and adheres to the reg-  
444 ulations of the European Directive 2010/63/EU. The German Primate Center also complies with  
445 the European Directive 2010/63/EU, as well as with the provisions of the German Animal Welfare  
446 Act.

## 447 **Data availability**

448 The data and R code used for all statistical analysis is available on GitHub, [https://github.com/](https://github.com/avrincon/macaque-facial-complexity)  
449 [avrincon/macaque-facial-complexity](https://github.com/avrincon/macaque-facial-complexity).

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