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8   **Social variables exert selective pressures in the evolution and form of primate**

9   **facial musculature**

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16   **Summary:** Mammals use their faces in social interactions more so than any other

17   vertebrates. Primates are an extreme among most mammals in their complex, direct, life-

18   long social interactions and their frequent use of facial displays is a means of proximate

19   visual communication with conspecifics. The available repertoire of facial displays is

20   primarily controlled by mimetic musculature, the muscles that move the face. The form of

21   these muscles is, in turn, limited by and influenced by phylogenetic inertia but here we use

22   examples, both morphological and physiological, to illustrate the influence that social

23   variables may exert on the evolution and form of mimetic musculature among primates.

24 Ecomorphology is concerned with the adaptive responses of morphology to various

25 ecological variables such as diet, foliage density, predation pressures, and time of day

26 activity. We present evidence that social variables also exert selective pressures on

27 morphology, specifically using mimetic muscles among primates as an example. Social

28 variables include group size, dominance "style", and mating systems. We present two case

29 studies to illustrate the potential influence of social behavior on adaptive morphology of

30 mimetic musculature in primates: 1) gross morphology of the mimetic muscles around the

31 external ear in closely related species of macaque (*Macaca mulatta* and *M. nigra*)

32 characterized by varying dominance styles and 2) comparative physiology of the orbicularis

33 oris muscle among select ape species. This muscle is used in both facial

34 displays/expressions and in vocalizations/human speech. We present qualitative

35 observations of myosin fiber-type distribution in this muscle of siamang (*Symphalangus*

36 *syndactylus*), chimpanzee (*Pan troglodytes*), and human to demonstrate the potential

37 influence of visual and auditory communication on muscle physiology. In sum,

38 ecomorphologists should be aware of social selective pressures as well as ecological ones,

39 and that observed morphology might reflect a compromise between the demands of the

40 physical and social environments.

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57 **INTRODUCTION**

58   Vertebrate faces are complex structures that have evolved to simultaneously satisfy

59 multiple functional demands including, but not limited to, dietary functions (procuring and

60 processing nutrients), vision, breathing, and social communication such as olfaction and

61 hearing (Gregory, 1929; Young, 1957; Janvier, 1996). Faces may be conceptualized as

62 consisting of structurally and functionally integrated units based upon these demands but

63 evolution of these units and the face as a whole are constrained by phylogeny and

64 developmental pathways. The evolution of the vertebrate face provided a location where

65 most of the sensory organs and the innovation of dentition could be clustered together,

66 greatly increasing foraging and hunting efficiency relative to invertebrates (Gregory, 1929;

67 Dupret et al., 2014).

68   Mammals evolved features including heterodonty (teeth of different shapes),

69 mammary glands and suckling, an external nose, mobile vibrissae, and mobile external ears,

70 all of which are related to the face (Young, 1957, 1962; Lieberman, 2011). These

71 evolutionary innovations are associated with a shift away from communication centered

72 primarily around chemical senses toward the greater inclusion of auditory and visual

73 communication modes. Increased reliance on auditory and visual communication was also

74 accompanied by reorganizations within the auditory, visual, and olfactory regions of the

75 brain (Northcutt, 2002; Rowe et al., 2011; Kaas, 2013).   While most mammals still use

76 olfaction as a social communication tool (with the probable exception of cetaceans), the

77 production of sometimes elaborate vocalizations/calls, the mammalian cochlea and three-

78 ossicle middle ear, and the development of patterned, brightly colored fur and skin point to

79 the importance of auditory and visual communication among mammals (Young, 1957; Vater

80 et al., 2004; Merritt, 2010; Kermack & Kermack, 2014).

81 　　　The advent of mammalian apomorphies related to the face is associated with the

82 most mobile and ornamentally patterned faces among all vertebrates. Mammals have the

83 ability to deform the facial mask (including movement of the vibrissae) and the external ears

84 via contraction of the mimetic muscles (Young, 1957; Burrows, 2008). These muscles exist

85 in various forms among all vertebrate classes and they are derived from the second (hyoid)

86 branchial arch with innervation from the 7th cranial nerve, the facial nerve (e.g., Larsen,

87 2001; Sperber, 2010). Mammalian mimetic musculature is unique among other vertebrates

88 in their attachments directly into the soft, mobile dermis of the face, including the cartilages

89 of the external ears and external nose (Noden, 1984; Gibbs et al., 2002; Burrows, 2008;

90 Diogo et al., 2008).   Non-mammalian vertebrates use these muscles in breathing and

91 feeding functions but in mammals they also take on new roles in assistance with gathering

92 sensory information, making facial displays or expressions during social interactions, moving

93 the external ears, and changing the size of the openings for the external nose, eyes, and

94 mouth (Burrows, 2008; Diogo et al., 2008).

95   Primates, especially anthropoids, are dependent upon visual communication more

96   so than most other mammalian orders and it often occurs via facial displays (Dominy &

97   Lucas, 2001; Regan et al., 2001; Jacobs, 2009; Liebal et al., 2013). Indeed, the evolution of

98   trichromatic vision and the high visual acuity within Old World primates have been linked at

99   least in part to their elaborate use of visual communication, including skin and fur

100   pigmentation and facial displays (e.g., Dominy & Lucas, 2001; Gilad et al., 2004; Veillieux &

101   Kirk, 2004; Setchell et al., 2006; Kamilar et al., 2013).

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105   *Primate Facial Displays as Visual Communication*

106   Visual communication among conspecifics within Primates is part of maintaining

107   social groups, social bonds, reproduction, and many aspects of daily life, especially so

108   among the diurnal species (Liebal et al., 2013). Primates generate visual communication

109   signals in the face and these signals include skin coloration/patterning and facial

110   expressions/displays (Santana et al., 2012, 2014; Liebal et al., 2013). Skin coloration and

111   patterning make up the "external morphology" of the face (Santana et al., 2012). External

112   morphology provides cues on identity, both at the species and individual levels, and is

113   important in assigning identity for recognition of kin, individuals, and mate recognition

114   (Gauthier & Logothetis, 2000; Higham et al., 2012; Santana et al., 2012). Regarding facial

115   coloration, a recent study revealed the influence of ecological factors on facial

116   pigmentation, showing that species living in tropical, dense and humid forest of Africa tend

117   to have darker faces than species living elsewhere (Santana et al. 2013).

118   "Internal facial morphology" consists of the mimetic musculature and its motor

119   supply, branches of the facial nerve (Santana et al., 2012). Mimetic musculature is

120   responsible for generating facial displays or facial expressions (Burrows & Cohn, 2014).

121   These displays assist in regulating and maintaining social bonds and the social group by

122   cuing conspecifics on the emotional and behavioral intentions of the sender (Morimoto &

123   Fujita, 2011; Liebal et al., 2013). Facial displays/expressions are achieved by deforming the

124   facial mask to reveal the emotional state or behavioral intent of the sender (Schmidt &

125   Cohn, 2001; Burrows, 2008; Burrows & Cohn, 2014). Meanings of these displays are usually

126   inferred from both the accompanying behaviors within the sender (such as loud

127   vocalizations) or the behavioral responses of the receiver (such as fleeing).

128   Comparing facial display repertoires among primate species (and non-primate,

129   mammalian species) can be useful for conceptualizing the evolution of facial

130   displays/expressions, social behaviour, and the evolution of human social behavior.

131   Development of the Facial Action Coding System (FACS) for a variety of mammalian species

132   allows for objective comparisons of facial displays. FACS is an anatomically based

133   observational coding system (Ekman et al., 2002, Ekman and Friesen, 1978) that was first

134   developed for use in human facial expression analysis. FACS uses numbers to refer to

135   specific units of movement (Action Units: AUs), each based on a specific mimetic muscle

136   contraction or combination of muscle contractions. As it is anatomically based, FACS lends

137   itself well to modification across species as any commonalities between the faces of

138   different species can be used as a starting point. FACS has now been modified for use with

139   chimpanzees (ChimpFACS: Vick et al., 2007), rhesus macaques (MaqFACS: Parr et al., 2010),

140   gibbons and siamangs (GibbonFACS: Waller et al., 2012), orangutans (OrangFACS: Caeiro et

141   al., 2013), domestic dogs (DogFACS: Waller et al., 2013), domestic cats (CatFACS: Caiero et

142 al., in prep) and horses (EquiFACS: Wathan et al., 2015). Development of similar systems

143 across a wider range of species (both primates and non-primates) is essential to make large

144 scale, multi-species comparisons. Thus, an understanding of the mimetic musculature can

145 inform our understanding of social behavior among species.

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147   *Primate Social Systems*

148   Most primates are highly social (e.g., Schultz, 1969). They interact frequently and

149 regularly with other group members beyond the family unit. However, different taxa within

150 the order Primates use social behaviour in highly contrasting ways (Schultz, 1969; Burrows,

151 2008).

152   Prosimians (the lorises, galagos, lemurs, and tarsiers) are typically understood as

153 being the least gregarious of all primate species. They are mostly nocturnal, arboreal,

154 relatively small-bodied (with small faces), and have a relatively low brain size to body size

155 ratio compared to anthropoids (Hill, 1953, 1955; Schultz, 1969; Martin, 1990; Sussman,

156 1999). Some of these species live as individual adults that have overlapping ranges, such as

157 in mouse lemurs (*Microcebus*), dwarf lemurs (*Cheirogaleus*), tarsiers (*Tarsius*), lorises (*Loris*,

158 *Nycticebus*),and some galagos (*Galago*, *Otolemur*). In this type of social system direct,

159 proximate encounters occur that may be either affiliative or agonistic (friendly or

160 aggressive) and it is known that some of these encounters involve facial displays (Bearder &

161 Doyle, 1974; Charles-Dominique, 1977; Martin, 1990; Andrès et al., 2003; Nash, 2003;

162 Kessler et al., 2012; Eichmueller et al., 2013). These prosimian species may form small

163 groups that consist of a mother, her infant, and an adult daughter, taxa such as the mouse

164 lemurs.   While these primate species do not form large social groups they still typically

165 come together in mixed sex sleeping groups, a behavior that has been linked to both

166   temperature regulation and safety against predators (Radespiel et al., 2003;

167   Rasoloharijaona et al., 2008; Biebouw et al., 2009). While facial displays have been

168   documented in some of these taxa (e.g., Charles-Dominique, 1977), auditory

169   communication (via elaborate long- and short-distance calls) and olfactory communication

170   figure prominently in these species (Martin, 1990; Sussman, 1999; Liebal et al., 2013).

171   The diurnal lemurs can be strikingly different from lorises, galagos, nocturnal lemurs

172   (mouse lemurs and dwarf lemurs), and tarsiers. Taxa such as the large-bodied sifakas

173   (*Propithecus* spp.) and ring-tailed lemurs (*Lemur catta*) are diurnal, more often terrestrial,

174   and can form relatively large multi-male/multi-female groups (up to 16 individuals) in a

175   polygamous setting (Richard, 1985; Gould, 1997). Polygamy, the ability of one individual to

176   control reproductive access to multiple individuals of the opposite sex, typically takes the

177   form of polygyny within primates, the ability of one male to control access to multiple

178   females (Fleagle, 2013). However, within some of the diurnal lemurs it takes the form of

179   polyandry, one female controlling reproductive access to multiple males (Sussman, 1999).

180   *L. catta* has a complex dominance hierarchical system along the matriline (a system where

181   social rank is determined based upon kinship to the dominant female). Facial displays of

182   submission and aggression have been documented in *Propithecus* and *L. catta* in the wild

183   (Jolly, 1965; Richard & Heimbuch, 1975).

184   Anthropoids consist of the New World monkeys (platyrrhines), Old World monkeys

185   (catarrhines), and apes. They are the best understood in terms of visual communication by

186   way of facial displays. Anthropoids are typically larger-bodied (with larger faces) than

187   prosimians, are almost all diurnal and more often terrestrial, and often form big social

188   groups (Sussman, 2000; Ankel-Simons, 2001; Fleagle, 2013).

189   Social group sizes within anthropoids can be quite large from 40 individuals up to

190   groups that consist of over 300 individuals (Dunbar, 1991; Rowe, 1996). These species

191   usually form multi-male/multi-female polygynous groups with one dominant male and

192   agonistic (aggressive) encounters can be frequent. Anthropoids use olfactory

193   communication but the olfactory structures, as well as olfactory regions of the brain, are

194   reduced relative to prosimians (Martin, 1990). Vocalizations (both short- and long-distance

195   varieties) are also used in anthropoids but there is strong evidence that visual

196   communication via facial displays is the primary means of proximate, social communication

197   (Liebal et al., 2013).

198   In polygamous (both polyandrous and polygynous) societies, social interactions are

199   more frequent and proximate than in the nocturnal prosimians (Liebal et al., 2013). Due in

200   part to the more complex and frequent social interactions that typify anthropoids relative to

201   prosimians, anthropoids have a higher brain size to body size ratio than prosimians and part

202   of the relatively increased brain size is located in regions associated with the neurobiology

203   of facial processing (Dunbar, 1989; Burrows, 2008; Parr, 2011; Fleagle, 2013).

204   Apes (the lesser apes: gibbons and siamangs; and the greater apes: orangutans,

205   gorillas, bonobos, and chimpanzees, along with humans) are all diurnal, large-bodied

206   species that mostly live in big groups that are mostly characterized by polygynous systems

207   (Goodall, 1986; Bartlett, 2008; Fleagle, 2013). While social relationships may be more fluid

208   than in Old World monkeys, social interactions in apes are typified by complex facial display

209   repertoires (e.g., Ekman et al., 2002, Ekman and Friesen, 1978; Goodall, 1986; Vick et al.,

210   2007; Waller et al., 2012; Caiero et al., 2013).

211   Monogamous relationships within primates are rare (Clutton-Brock, 1974; Fleagle,

212   2013; Liebal et al., 2013). Owl monkeys (the New World *Aotus* spp.), the sole nocturnal

213 anthropoid, are typically monogamous but our best understanding of primate monogamy

214 may be the gibbons (*Hylobates* spp.) and siamangs (*Symphalangus* spp). Due in part to their

215 frequent use of monogamy, opportunities for proximate social interactions with a high

216 number of individuals are lower in lesser apes than in the polygamous greater ape species

217 (Waller et al., 2012; Fleagle, 2013). Along those lines, recent studies demonstrated that

218 gibbons and siamangs have fewer mimetic muscles than their close relatives the

219 chimpanzees (Burrows et al., 2011; Diogo et al., 2012b) and fewer facial displays (Waller et

220 al., 2012).

221   Orangutans (*Pongo* spp.) are a special case among apes. These are large-bodied,

222 arboreal primates and they live relatively solitary lifestyles compared to the other great

223 apes (e.g., Galdikas, 1988). However, like all primates, they exploit the social group

224 throughout their life histories. Orangutans may form travel bands (where individuals feed

225 and travel together when fruit is abundant), temporary aggregations (where individuals

226 feed together but travel separately when fruit, their main food source, is scarce), and

227 consortships (where a sexually receptive female travels in coordination with a male for a

228 defined period of time). Typically, mothers and immature offspring travel together and may

229 include an older daughter and her offspring in the group. It is especially noteworthy that

230 orangutans may form larger groups depending upon the specific study site and fruit

231 availability (Knott, 1998; van Schaik, 1999; Knott & Kahlenberg, 2010). Despite the large

232 cheek flanges that some mature males form and the relatively low frequencies of social

233 interactions with multiple individuals, orangutans have been documented to produce about

234 the same number of facial displays as chimpanzees, but fewer than humans (Waller et al.,

235 2013).

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237   *Ecomorphological Relationships in Primate Mimetic Musculature*

238   Primates present a wide range of facial morphology, skin and fur coloration, and use

239   of facial displays (Schultz, 1969; Liebal et al., 2013). Santana and colleagues (2014)

240   demonstrated that interspecific variation in facial coloration is associated with degree of

241   facial mobility within diurnal anthropoids. Species with multi-colored faces tended to have

242   the lowest range of facial displays and species with more "plain" faces tended to have the

243   highest range of facial displays. Body size and face size also influence facial display

244   repertoire. Dobson (2009a) found that anthropoids with small faces tended to have fewer

245   facial displays than anthropoids with larger faces, most likely due to improved visual acuity

246   in large-bodied (and large-faced) anthropoids.

247   Ecomorphology is concerned with the relationships between morphological form of

248   any individual and the environment of that individual.   Skeletal and dental morphologies

249   across primate species have been shown to be adaptive to environmental factors. For

250   example, dentition within primates that are primarily seed-eaters, gum and sap-eaters and

251   fruit feeders shows unique morphological features linked to acquiring and processing these

252   particular foods (e.g., Hylander, 1975; Lambert et al., 2004; Burrows & Nash, 2010; Burrows

253   et al., 2015). Mandibular morphology has similarly been linked to dietary niche across a

254   range of primate taxa (e.g., Ross & Wall, 2000; Ravosa et al., 2007; Mork et al., 2010). These

255   ecomorphological relationships have mainly been conceptualized as a focus on the

256   functional interactions and adaptive responses between morphology and the

257   physical/ecological environment (such as density of leaf cover, temperature, and dietary

258   niche).   However, physical and ecological features of environments are not the only factors

259   that need to be considered in ecomophological relationships, especially within primates.

260   Ecomorphological pressures shaping primate mimetic musculature include dietary

261   niche, foliage density, etc. (Liebal et al., 2013). However, mimetic musculature also adapts

262   to ecomorphological pressures focusing on the social environment (Schmidt & Cohn, 2001).

263   Social environments are crucial in imposing constraints, selective pressures, and adaptive

264   niches for exploitation within primates (e.g., Dunbar, 1989, 1998, 2009). For example,

265   diurnal anthropoids who live in large social groups have the highest range of facial displays

266   relative to those that live in smaller groups (Dobson, 2009b). Linking broad social behaviors

267   to specific morphologies might not always be straightforward, but for mimetic muscle

268   morphology there is a clear and direct link between morphology and social communication

269   with conspecifics since contraction of the musculature leads directly to the facial display.

270   Whereas other social behaviors (such as approach and avoidance) might be hard to link to

271   specific morphologies, facial displays/expressions are overtly linked to mimetic muscle

272   anatomy (Burrows & Cohn, 2014). As such, variation in these muscles, both at the gross and

273   microanatomical levels, is likely to result in differences in facial display/expression behavior.

274   Much of our previous understanding of mimetic musculature and its evolution in

275   primates was rooted solely in phylogeny. Huber (1931) held that facial expression

276   musculature was the simplest and least complex in prosimians (complexity here referring to

277   number of individual muscles, relative sizes, interconnections, and attachment sites). Under

278   this "phylogenetic" model, complexity of mimetic muscle morphology increased in a simple

279   linear, step-wise fashion up the phylogenetic scale until humans, where the ultimate in

280   complexity was achieved.   This view has traditionally also been applied to facial display

281   repertoire with the most simple, undifferentiated displays being rooted in the prosimians,

282   ever increasing in a step-wise, linear fashion up to humans, where the most complex,

283   subtle, and graded displays are found.

284   This "phylogenetic model" of morphology has recently been challenged. Work in

285   wide phylogenetic, ecological, and social environment ranges of primates (and some non-

286   primate mammals) has shown that social environment variables play a considerable role in

287   the adaptive morphology of mimetic musculature (Burrows & Smith, 2003; Burrows et al.,

288   2006, 2009, 2011; Burrows, 2008; Diogo et al., 2008, 2012a, b; Diogo & Wood, 2012; Rogers

289   et al., 2009; Diogo et al., 2014).   Clearly, a simple, linear phylogenetic model of primate

290   mimetic musculature evolution is inaccurate and incomplete.

291   Neurobiological evidence also indicates that there are considerable socioecological

292   variables involved in the evolution of facial displays among primate species. Sherwood

293   (2005) examined facial nerve neuron number across a wide phylogenetic range of primates,

294   including social group size as a variable and correcting for body size difference. This study

295   demonstrated that species that live in large, complex social groups had more facial nerve

296   neurons than species that live in small social groups, indicating more potential control over

297   mimetic musculature. Additionally, Sherwood et al. (2005) found relatively greater volume

298   of facial nerve nuclei in the great apes and humans compared to all other Old World

299   primates, suggesting increased differentiation of the facial muscles and greater utilization of

300   the visual channel in social communication. Lastly, Dobson (2012a) showed that neocortex

301   size (the area of the brain that includes regions devoted to social interactions) is a significant

302   predictor of facial nerve nuclei volumes in catarrhines (Old World monkeys and apes).

303   These studies demonstrate that there is a strong co-evolution between social group size and

304   neurobiological components of facial musculature, at least in the catarrhines. Overall, it

305   appears that as group size increases, primate species have more brain area dedicated to the

306   production of facial displays/expressions. Facial expressions thus seem to play a role in

307   facilitating group cohesion.

308   Given the various morphological and physiological links to ecology and especially to

309   social variables in primate mimetic musculature, it should be possible to understand how

310   variation in the social environment influences variation in mimetic muscle morphology. As

311   part of a larger investigation into these relationships and their roles in the evolution of

312   primate mimetic musculature, we present two case studies at both the gross and

313   microanatomical levels. These are illustrative examples only and do not represent fully

314   developed analyses.   These cases show the potential role that social behaviour can play in

315   exerting a clear selective pressure on morphology of mimetic muscles.

316

317   **Case Study 1**: Closely related macaques have differing mimetic muscles, or "Phylogeny

318   Does Not Always Dictate Morphology"

319   It is well known that phylogeny does not always reflect ecological preferences, social

320   behaviour, or morphology of a species and macaques are an outstanding illustration of this

321   point.   Macaques are one of the most ubiquitous and successful of living primates, living in

322   highly varied climate zones from snow-covered mountains in Japan (*Macaca fuscata*) to

323   semi-desert zones in northern Africa (*M. sylvanus*). Macaques are one of the few primates

324   that thrive alongside humans in urban settings and some macaque populations are even

325   provisioned by humans in these settings (Thierry, 2007). All species share some common

326   demographical and basic behavioral patterns. They all primarily consume fruits and live in

327   multi-male/multi-female groups organized along a linear hierarchy and group size in

328   macaques may reach up to 100 individuals (Thierry, 2007). In contrast to these similarities in

329   basic socio-demographic characteristics, macaques differ widely in their pattern of

330   aggression, affiliation, and dominance (Thierry, 2007). Because of the close phylogenetic

331   relationships and basic socio-demographic similarities, but differences in social behavior,

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332   macaques provide a good model to test hypotheses that ecological and social characteristics

333   can play a role in the evolution of interspecific variation in mimetic morphology.

334   Rhesus macaques (*Macaca mulatta*) inhabit widely fragmented environments

335   throughout the Indian subcontinent up to Afghanistan and Indochina, co-existing in some

336   instances with humans (Thierry et al., 2004). They consume leaves and fruits but have

337   adapted to consume a wide variety of foods. Habitats are diverse and include urban

338   settings, evergreen forests, semi-deserts, *etc*. Group sizes also vary but outside of semi-

339   provisioned, urban settings, *M. mulatta* typically occur in groups of around 50-90

340   individuals. Rigid, linear dominance hierarchies characterize *M. mulatta*. Outcomes of

341   social interactions are almost always certain, being determined by the ranks of the

342   participants in what is termed a "despotic" social style, where some individuals have more

343   power than others (Flack & de Waal, 2004; Thierry, 2007). Facial displays are important and

344   are frequently used as part of the social maintenance system for these hierarchies.

345   Movements of the external ear are particularly noted in *M. mulatta* facial display

346   repertoires (Partan, 2002; Parr et al., 2010) and the anatomy of the muscles around the

347   external ear is well known (e.g., Huber, 1933; Burrows et al., 2009).

348   Sulawesi crested macaques (*M. nigra*) are closely related to rhesus macaques but

349   behave very differently. They inhabit a much more restricted range, being found only in a

350   small part of Indonesia and they live in densely foliated tropical forests. Their diet is similar

351   to that of *M. mulatta* (Thierry, 2007). *M. nigra* is characterized by practicing a more

352   "tolerant" social system with a greater repertoire of facial displays, but fewer displays that

353   focus on movement of the external ears (Thierry, 2000; Dobson, 2012b). Descriptions of

354   facial displays include far fewer movements of the external ear – in fact, only one

355   movement (ears flattened against the back of skull) is documented in their behavioural

356   repertoire (Thierry et al. 2000). Fights are frequent but often of low intensity and the

357   outcomes of social interactions are far more uncertain than in the despotic species such as

358   *M. mulatta* (i.e. power asymmetries are weaker in *M. nigra*) (Petit & Thierry, 1994; Thierry

359   et al., 2008).

360   In an effort to explore the potential ecomorphological relationships among social

361   behaviour and mimetic musculature in the despotic *M. mulatta* vs. the tolerant *M. nigra*,

362   the present case study describes mimetic muscles around the external ear in both species.

363   As part of a larger study into the mimetic musculature of *M. nigra*, five cadaveric specimens

364   were dissected at the Royal Museums of Scotland (four adult and one juvenile). While the

365   entire faces were dissected on each cadaver, we only report in this case study on the

366   muscles surrounding the external ear. Burrows et al. (2009, in review) presented detailed

367   descriptions of mimetic musculature around the entire faces in *M. mulatta* and *M. nigra*.

368   Seiler (1970, 1971, 1973, 1974, 1977) also presented reports of external ear musculature of

369   a variety of *Macaca* species. Here, we describe musculature from the present study but a

370   more full and detailed account of the entire set of mimetic musculature of *M. nigra* vs. *M.

371   mulatta* is presented in Burrows et al. (in review), including evidence from the previous

372   work of Seiler (1970, 1971, 1973, 1974, 1977).

373   Figure 1 is an abstract representation of the musculature surrounding the external

374   ears in both *M. nigra* and *M. mulatta*. *M. mulatta* mimetic musculature is shown here only

375   for comparison to *M. nigra*. Table 1 describes musculature presence and form in both

376   species of macaque. Seiler (1971) reported on a dissection of a specimen of *M. nigra*

377   (referred to therein as *Cynopithecus niger*) but did not specifically focus on the musculature

378   surrounding the external ear.

379   Overall, *M. nigra* has fewer muscles associated with the external ear than *M.*

380 *mulatta*: six in *M. mulatta* (two of those being variably present) and four in *M. nigra* (three

381 of those being variably present). The posterior auricularis muscle in *M. nigra* typically had a

382 single belly while this muscle in *M. mulatta* had two bellies (Burrows et al., 2009). Despite

383 the close phylogenetic relationship between *M. mulatta* and *M. nigra*, the external ear

384 muscles of *M. nigra* appear to be more similar to those in the distantly related

385 gibbons/siamangs (the hylobatids), which are lesser apes (Burrows et al. 2011). Both

386 hylobatids and *M. nigra* have poorly developed external ear muscles relative to *M. mulatta*.

387 Movements of the external ears are minimal in hylobatid facial displays (Waller et al,

388 gibbonFACS), similar to the facial display repertoire of *M. nigra* (Thierry et al., 2000).   If

389 phylogeny were the main driving force behind form of macaque mimetic musculature, we

390 would expect 1). *M. mulatta* and *M. nigra* to have more similar musculature of the external

391 ear and 2). that they would both have more similar musculature to one another than either

392 does to hylobatids. Mimetic musculature around the external ear in these two species of

393 macques may be partially influenced by social behaviour differences.

394   *M. mulatta* employs a wide range of facial displays that are routinely used in social

395 encounters (Parr et al., 2010). Movements of the external ear in *M. mulatta* are frequent

396 and varied in these encounters, moving in both submissive and aggressive contexts. These

397 movements have been described in Parr et al. (2010). Despite the fact that *M. mulatta* has

398 more robust development of the external ear muscles, *M. nigra* has a greater facial display

399 repertoire overall (Dobson, 2012b).

400   According to the *Power Asymmetry Hypothesis of Motivational Emancipation*

401 (Preuschoft and van Hooff, 1995), the flexibility in the use and appearance of

402 communicative signals is partly determined by characteristics of the social environment. In

403 species such as *M. mulatta*, which are characterized by high power asymmetries, the

17

404   outcome of social interactions is highly predictable and mainly determined by the relative

405   dominance status of the individuals. In this context, individuals benefit from clear,

406   unambiguous communication signals, which will reduce the likelihood of confusion

407   regarding future behaviour. For example, rhesus macaques use the silent bared-teeth face

408   to formally indicate their subordinate status when approached by higher-ranking

409   individuals. *M. nigra* on the other hand, live in a more relaxed social system where the

410   outcome of social interactions is less predictable and more uncertain. Facial expressions

411   such as the silent bared-teeth are more graded and blended and are used across context

412   (Thierry et al. 1989; Thierry et al. 2000). These differences in how facial expressions are used

413   might be reflected in the anatomy, with rhesus macaques having more developed ear

414   muscles allowing for more numerous movements and sustained activation to produce

415   unambiguous signals, thereby reducing uncertainty in the outcome of social interactions.

416   These subtle differences in social behaviour, facial displays, and mimetic musculature

417   morphology are a good example of how social variables can be part of the ecomorphological

418   relationships found among primates at the gross level.

419

420   **Case Study 2** – Myosin Fiber Type Distribution in the Orbicularis Oris Muscle, or "Phylogeny

421   Does Not Always Dictate Muscle Physiology"

422   All skeletal muscle, including mimetic musculature, works by getting shorter or

423   contracting (Gans, 1982). Each muscle is made up of smaller units that work together to

424   contract. Muscles consist of packaged units called "fascicles", collections of muscle fibers

425   enveloped by connective tissue. Each muscle fiber (or myofiber) in turn consists of bundles

426   of myofibrils, which are made up of many filaments of contractile proteins. One of those

427   contractile proteins is myosin. All mammalian skeletal muscle includes myosin, which

18

428 interacts with other muscle proteins to produce shortening of the overall muscle (Lieber,

429 2010).

430   There are several types of myosin proteins but the most abundant and best

431 understood for mammalian skeletal muscle physiology are type I (slow-twitch) and type II

432 (fast-twitch) myosin (Barany, 1967; Staron, 1997). Type I fibers take more time and more

433 energy to contract. As a trade-off, they are slow to fatigue and hold the contraction longer.

434 In humans, these types of fibers tend to dominate in muscles of the limbs (except for the

435 hand) and spine. Type II fibers consist of a number of isoforms (different sub-types) but

436 overall they are able to contract more quickly than type I fibers but use less energy. As a

437 trade-off, they are quick to fatigue and cannot hold the contraction as long as type I fibers.

438 In humans, these types of fibers tend to dominate in muscles of the face and in the human

439 hand (Stål et al., 1987, 1990; Stål, 1994; Lieber, 2010). Furthermore, the potential

440 instantaneous force that each fiber-type can generate differs, with slow-twitch myosin

441 fibers generating a lower instantaneous force than fast-twitch.

442   As an example, standing in a long line at a check-out may be aggravating but our

443 lower limb and spine musculature, dominated by fatigue-resistant type I myosin fibers,

444 typically don't fail us and we're able to wait for our turn. Imagine, though, holding a smile

445 that long. The mimetic muscles that control smiling, dominated by quick-to-fatigue type II

446 myosin fibers, typically fire that smile quickly but we tire after just a minute or so of holding

447 that smile for family photos.

448   All mammalian skeletal muscle consists of mixtures of slow-twitch and fast-twitch

449 myosin fibers distributed throughout the muscle. Each muscle has a different percentage of

450 slow-twitch and fast-twitch fibers depending upon the work that the particular muscle does.

451 It is well established that human mimetic musculature is dominated by fast-twitch myosin

452   fibers (e.g., Stål et al., 1987, 1990; Stål, 1994). Our facial muscles are able to contract

453   quickly and spontaneously (think of how quickly and automatically we smile at the sight of a

454   familiar friend or a funny joke) but it is difficult to hold that contraction longer than a few

455   seconds before fatigue sets in. These differences in the ratio of slow-twitch to fast-twitch

456   myosin fibers can inform our understanding of muscle function and preceding evolutionary

457   pressures.

458   Our understanding of the gross and comparative anatomy of primate mimetic

459   musculature is improving all the time due to a wealth of recent studies (Burrows & Smith,

460   2003; Burrows, 2008; Burrows et al., 2006, 2009, 2011; Diogo et al., 2012, 2013a, b).

461   However, we are only beginning to understand the comparative physiology of primate

462   mimetic musculature and what implications this may have for our conceptualization of the

463   evolution of social behaviour and visual communication. A recent study by Sanders et al.

464   (2013) showed that human tongue musculature has a greater percentage of slow-twitch

465   fibers than tongue musculature from chimpanzees. Authors of that study correlated this

466   evolutionary innovation in muscle physiology of the human tongue with the ability of the

467   human tongue to slow down and produce more specific and longer contractions during

468   speech, relative to how the tongue behaves in chimpanzees during vocalizations.

469   Some mimetic musculature in humans is also used during speech (Lieberman, 2007;

470   Raphael et al., 2007; Taylor et al., 2012; Popat et al., 2013). Human lips act in part as

471   "articulators" during speech, refining the sounds that come from the larynx into specific,

472   meaningful speech units (e.g., McGurk & MacDonald, 1976; Raphael et al., 2007). For

473   example, differential articulating action of the lips can help the listener differentiate a hard

474   "c" sound (as in "cat") from a softer "b" sound (as in "bat"). The orbicularis oris muscle is

475   one of the mimetic muscles that moves the lips, during facial displays/expressions,

476   eating/suckling, and during speech (or vocalizations in non-human primates) (e.g., Rastatter

477   & DeJarnette, 1984; Burrows & Cohn, 2014). The orbicularis oris muscle encircles and

478   attaches to the lips in a sphincter-like fashion (Standring, 2010). Burrows et al. (2014)

479   sampled mimetic musculature, including the orbicularis oris muscle, from humans,

480   chimpanzees, and rhesus macaques. These species present a range of phylogenetic

481   relationships: chimpanzees and humans are closely related while both are relatively

482   distantly related to rhesus macaques (Groves, 2001). Humans vocalize primarily through

483   speech while chimpanzees and rhesus macaques use a variety of vocalizations, but not

484   speech. Burrows et al. (2014) demonstrated that, while humans have a greater percentage

485   of fast-twitch fibers than slow-twitch fibers, the relationship holds true for both the closely

486   related chimpanzees and the distantly related rhesus macaques. However, humans had a

487   significantly higher percentage of slow-twitch myosin fibers than both chimpanzees and

488   rhesus macaques. In other words, our minority of slow-twitch fibers was far greater than

489   the minority of slow-twitch fibers in chimpanzees and macaques. Humans had slow-twitch

490   fiber distribution of roughly between 15-20% while chimpanzees and macaques had only 2-

491   7% distribution of slow-twitch fibers.

492   As part of a larger effort to expand the phylogenetic sampling of myosin fiber type

493   distribution in primate mimetic muscles, the present case study shows preliminary findings

494   from sampling the orbicularis oris muscle from a siamang (*Symphalangus syndactulus*),

495   which is a lesser ape, a chimpanzee (*Pan troglodytes*), which is a greater ape, and a human.

496   Figure 2 shows select microimages of representative sections, highlighting fast-twitch and

497   slow-twitch myosin fibers and their distributions. Clearly, all species show strong reactivity

498   for fast-twitch (type II) myosin but humans show stronger reactivity for slow-twitch myosin

499   (type I) than both siamang and chimpanzee.

500   These data do not represent fiber counts and statistical analyses. These are merely

501   preliminary data used to illustrate the qualitative differences in myosin fiber distribution

502   and are part of a larger, qualitative study. Keeping this in mind, qualitative observational

503   results at this early stage consistently show that siamangs tend to have a slow-twitch fiber

504   distribution between humans and chimpanzees. While quantitative analyses are needed it

505   is worth noting at this early stage that siamangs (and the other lesser apes, the gibbons) are

506   noted in part for their intensive use of "songs" and "duets", a type of sustained, long-

507   distance vocalization used to maintain social bonds and territorial boundaries. These

508   vocalizations can be heard for at least two kilometres and can last for many minutes

509   (Bartlett, 2008). They have been cited as maintaining pair & family bonds, territorial

510   boundaries, individual identity, and mate attraction (Raemaekers et al., 1984; Geissmann,

511   1999, 2002; Terleph et al., 2015) and are associated with specific morphological

512   specializations such as an enlarged laryngeal air sac (Fitch, 2000). Siamangs and gibbons

513   produce these songs by forming the lips into a funnel-shape and holding that lip posture

514   while the song is produced. It is possible that the qualitatively observed differential

515   distribution of slow-twitch myosin fibers from the orbicularis oris muscle noted in the

516   present case study, humans > siamangs > chimpanzees, is reflective of an evolutionary

517   divergence in the adaptive physiology of the orbicularis oris muscle. Without question,

518   quantitative counts of fiber-type distribution will provide more definitive evidence for (or

519   against) this potential physiological adaptation.

520   As the only monogamous ape, siamangs (and gibbons) are noted for having fewer

521   facial displays than chimpanzees and humans (Waller et al., 2012; Scheider et al., 2014).

522   The development of an elaborated and structurally complex set of vocalizations in these

523   primates may be a "trade-off" for the less frequent use of facial displays. Further

524   quantitative analyses on specific percentages of slow-twitch vs. fast-twitch myosin fiber

525   distribution among these species will provide better and definitive evidence. Further

526   studies on how the oribicularis oris muscle behaves in vocalizations across a wide

527   phylogenetic, ecological, and social range of primates would aid our understanding.

528   At this juncture it is worth noting that physiological cross-sectional area (PCSA) of

529   muscle fibers is the preferred variable for estimating potential contractile force of any given

530   muscle (e.g., Gans & Bock, 1965; Gans, 1982). In combination with fiber-type distribution, it

531   can provide a more complete picture of how much force a muscle can generate when it

532   contracts. One component of determining PCSA involves harvesting the entire muscle.

533   However, since mimetic muscles attach into one another and, like the orbicularis oris

534   muscle, may be a sphincter (or circle), it is not yet practical to pursue this method of

535   estimating force-generating potential in mimetic muscles.

536

537   **Discussion**

538   Understanding the links among morphology, ecology, and the social environment is

539   not always straightforward. Neither is it always possible to link specific aspects of

540   morphology directly to ecology and social behaviours. However, for facial

541   expressions/displays there is a clear and direct link among the morphology of the face, the

542   behavioural expression of facial movement, and social interaction with conspecifics.

543   Ecomorphological considerations in primate facial displays and mimetic musculature

544   have been strengthened in recent years by examinations not only of phylogenetic

545   relationships but the inclusion of ecological variables (such as density of foliation, diet,

546   communication modes) and social group variables (such as size of group, dominance

547   relationships). This multifactorial methodology is continually improving our understanding

23

548   of how facial musculature, facial displays, and primate sociality have co-evolved. Much

549   work remains, especially on the relatively under-studied nocturnal prosimians and the

550   platyrrhines (or New World monkeys).

551   While examinations of gross morphology of the mimetic muscles will continue to be

552   illuminating, our best efforts may be aimed at neurological and physiological investigations

553   into this musculature. Our understanding of many physiological basics, myosin fiber-types

554   notwithstanding, such as physiologic cross-sectional area and fiber lengths, remains poor.

555   Neurobiological research into prosimian facial displays and its link to social behavior is

556   especially lacking. These species represent our closest extant representatives of the first

557   primates so research aimed here may be helpful in efforts to reconstruct the lifestyles of

558   stem primates.

559   Overall, these qualitative case studies add to the growing body of evidence that

560   primate mimetic musculature form and evolution are adaptive to social, communicative

561   pressures. While we know that mimetic musculature in extant species is adaptive to social

562   variables (such as group size and dominance "style"), future studies may be able to

563   extrapolate our current knowledge to taxa represented only in the fossil record.

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901 **Table 1** External ear muscles in *Macaca mulatta* vs. *M. nigra* (see Figure 1, also)

902

Muscle	*Macaca mulatta*	*Macaca nigra*
superior auricularis m.	P	V (2/3)
	robust, flat band	thin, scant fibers
posterior auricularis m.	P	V (2/3)
	robust, two heads	thin, single head
anterior auricularis m.	V (2/5)	V (1/3)
	flat, thin muscle	as in *M. mulatta*
inferior auricularis m.	V (2/6)	A
orbitoauricularis m.	P	P
tragicus m.	P	P
antitragicus m.	P	A

918 Note: "P": present; "V": variably present; "A": absent

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921 **Figures**
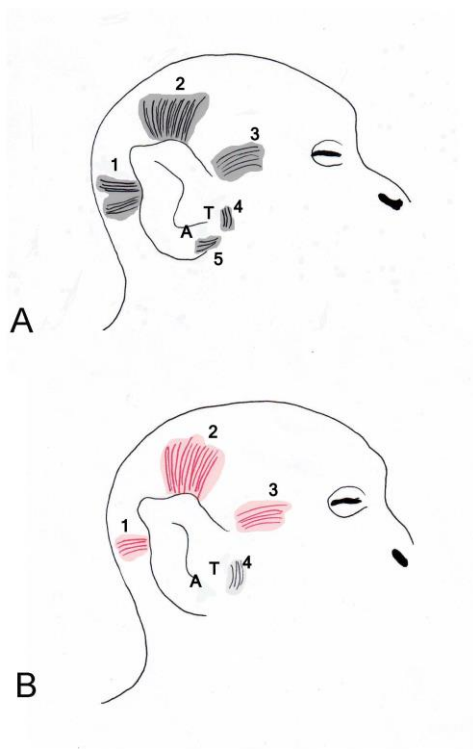
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923 <u>Figure 1</u> Abstract representations of the mimetic muscles surrounding the external ears in

924 A) rhesus macaque (*Macaca mulatta*) and B) Sulawesi macaque (*M. nigra*). 1: posterior

925 auricularis muscle; 2: superior auricularis muscle; 3: anterior auricularis muscle; 4: tragicus

926 muscle; 5: antitragicus muscle; T: tragus; A: antitragus. Red coloration of select muscles in

927 *M. nigra* indicates that these muscles varied, relative to those of *M. mulatta*.
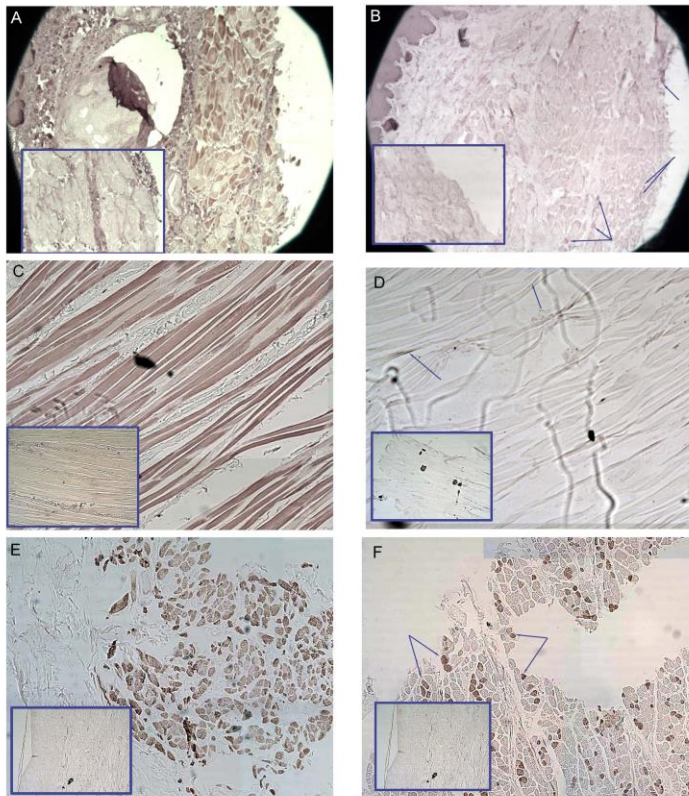
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929 <u>Figure 2</u> Micronatomical image of A) & B) siamang, *Symphalangus syndactylus*; C) & D)

930 chimpanzee, *Pan troglodytes*, and E) & F) human, *Homo sapiens* highlighting fast twitch and

931 slow-twitch myosin fibers. All images on the left are fast-twitch reactivity, all images on the

932 right are slow-twitch reactivity. Inset images offset by blue are control images. Note that all

933 three species show strong reactivity for fast-twitch (type II) myosin (images on the right).

934 Human (panel F) slow-twitch reactivity is strong while chimpanzee (panel D) shows almost

935 no slow-twitch reactivity. Siamang (panel B) shows intermediate slow-twitch reactivity.

936 Arrows indicate fibers in slow-twitch panels that are reactive.