Social variables exert selective pressures in the evolution and form of primate facial musculature

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Summary: Mammals use their faces in social interactions more so than any other vertebrates. Primates are an extreme among most mammals in their complex, direct, life-long social interactions and their frequent use of facial displays is a means of proximate visual communication with conspecifics. The available repertoire of facial displays is primarily controlled by mimetic musculature, the muscles that move the face. The form of these muscles is, in turn, limited by and influenced by phylogenetic inertia but here we use examples, both morphological and physiological, to illustrate the influence that social variables may exert on the evolution and form of mimetic musculature among primates.

Ecomorphology is concerned with the adaptive responses of morphology to various ecological variables such as diet, foliage density, predation pressures, and time of day activity. We present evidence that social variables also exert selective pressures on morphology, specifically using mimetic muscles among primates as an example. Social variables include group size, dominance "style", and mating systems. We present two case studies to illustrate the potential influence of social behavior on adaptive morphology of mimetic musculature in primates: 1) gross morphology of the mimetic muscles around the external ear in closely related species of macaque (*Macaca mulatta* and *M. nigra*) characterized by varying dominance styles and 2) comparative physiology of the orbicularis oris muscle among select ape species. This muscle is used in both facial displays/expressions and in vocalizations/human speech. We present qualitative observations of myosin fiber-type distribution in this muscle of siamang (*Symphalangus syndactylus*), chimpanzee (*Pan troglodytes*), and human to demonstrate the potential influence of visual and auditory communication on muscle physiology. In sum, ecomorphologists should be aware of social selective pressures as well as ecological ones, and that observed morphology might reflect a compromise between the demands of the physical and social environments.

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INTRODUCTION

Vertebrate faces are complex structures that have evolved to simultaneously satisfy multiple functional demands including, but not limited to, dietary functions (procuring and processing nutrients), vision, breathing, and social communication such as olfaction and hearing (Gregory, 1929; Young, 1957; Janvier, 1996). Faces may be conceptualized as consisting of structurally and functionally integrated units based upon these demands but evolution of these units and the face as a whole are constrained by phylogeny and developmental pathways. The evolution of the vertebrate face provided a location where most of the sensory organs and the innovation of dentition could be clustered together, greatly increasing foraging and hunting efficiency relative to invertebrates (Gregory, 1929; Dupret et al., 2014).

Mammals evolved features including heterodonty (teeth of different shapes), mammary glands and suckling, an external nose, mobile vibrissae, and mobile external ears, all of which are related to the face (Young, 1957, 1962; Lieberman, 2011). These evolutionary innovations are associated with a shift away from communication centered primarily around chemical senses toward the greater inclusion of auditory and visual communication modes. Increased reliance on auditory and visual communication was also accompanied by reorganizations within the auditory, visual, and olfactory regions of the brain (Northcutt, 2002; Rowe et al., 2011; Kaas, 2013). While most mammals still use olfaction as a social communication tool (with the probable exception of cetaceans), the production of sometimes elaborate vocalizations/calls, the mammalian cochlea and three-ossicle middle ear, and the development of patterned, brightly colored fur and skin point to the importance of auditory and visual communication among mammals (Young, 1957; Vater et al., 2004; Merritt, 2010; Kermack & Kermack, 2014).

The advent of mammalian apomorphies related to the face is associated with the most mobile and ornamentally patterned faces among all vertebrates. Mammals have the ability to deform the facial mask (including movement of the vibrissae) and the external ears via contraction of the mimetic muscles (Young, 1957; Burrows, 2008). These muscles exist in various forms among all vertebrate classes and they are derived from the second (hyoid) branchial arch with innervation from the 7th cranial nerve, the facial nerve (e.g., Larsen, 2001; Sperber, 2010). Mammalian mimetic musculature is unique among other vertebrates in their attachments directly into the soft, mobile dermis of the face, including the cartilages of the external ears and external nose (Noden, 1984; Gibbs et al., 2002; Burrows, 2008; Diogo et al., 2008). Non-mammalian vertebrates use these muscles in breathing and feeding functions but in mammals they also take on new roles in assistance with gathering sensory information, making facial displays or expressions during social interactions, moving the external ears, and changing the size of the openings for the external nose, eyes, and mouth (Burrows, 2008; Diogo et al., 2008).

Primates, especially anthropoids, are dependent upon visual communication more so than most other mammalian orders and it often occurs via facial displays (Dominy & Lucas, 2001; Regan et al., 2001; Jacobs, 2009; Liebal et al., 2013). Indeed, the evolution of trichromatic vision and the high visual acuity within Old World primates have been linked at least in part to their elaborate use of visual communication, including skin and fur pigmentation and facial displays (e.g., Dominy & Lucas, 2001; Gilad et al., 2004; Veillieux & Kirk, 2004; Setchell et al., 2006; Kamilar et al., 2013).

Primate Facial Displays as Visual Communication

Visual communication among conspecifics within Primates is part of maintaining social groups, social bonds, reproduction, and many aspects of daily life, especially so among the diurnal species (Liebal et al., 2013). Primates generate visual communication signals in the face and these signals include skin coloration/patterning and facial expressions/displays (Santana et al., 2012, 2014; Liebal et al., 2013). Skin coloration and patterning make up the "external morphology" of the face (Santana et al., 2012). External morphology provides cues on identity, both at the species and individual levels, and is important in assigning identity for recognition of kin, individuals, and mate recognition (Gauthier & Logothetis, 2000; Higham et al., 2012; Santana et al., 2012). Regarding facial coloration, a recent study revealed the influence of ecological factors on facial pigmentation, showing that species living in tropical, dense and humid forest of Africa tend to have darker faces than species living elsewhere (Santana et al. 2013).

"Internal facial morphology" consists of the mimetic musculature and its motor supply, branches of the facial nerve (Santana et al., 2012). Mimetic musculature is responsible for generating facial displays or facial expressions (Burrows & Cohn, 2014). These displays assist in regulating and maintaining social bonds and the social group by cuing conspecifics on the emotional and behavioral intentions of the sender (Morimoto & Fujita, 2011; Liebal et al., 2013). Facial displays/expressions are achieved by deforming the facial mask to reveal the emotional state or behavioral intent of the sender (Schmidt & Cohn, 2001; Burrows, 2008; Burrows & Cohn, 2014). Meanings of these displays are usually inferred from both the accompanying behaviors within the sender (such as loud vocalizations) or the behavioral responses of the receiver (such as fleeing).

Comparing facial display repertoires among primate species (and non-primate, mammalian species) can be useful for conceptualizing the evolution of facial displays/expressions, social behaviour, and the evolution of human social behavior. Development of the Facial Action Coding System (FACS) for a variety of mammalian species allows for objective comparisons of facial displays. FACS is an anatomically based observational coding system (Ekman et al., 2002, Ekman and Friesen, 1978) that was first developed for use in human facial expression analysis. FACS uses numbers to refer to specific units of movement (Action Units: AUs), each based on a specific mimetic muscle contraction or combination of muscle contractions. As it is anatomically based, FACS lends itself well to modification across species as any commonalities between the faces of different species can be used as a starting point. FACS has now been modified for use with chimpanzees (ChimpFACS: Vick et al., 2007), rhesus macaques (MaqFACS: Parr et al., 2010), gibbons and siamangs (GibbonFACS: Waller et al., 2012), orangutans (OrangFACS: Caeiro et al., 2013), domestic dogs (DogFACS: Waller et al., 2013), domestic cats (CatFACS: Caiero et al., in prep) and horses (EquiFACS: Wathan et al., 2015). Development of similar systems across a wider range of species (both primates and non-primates) is essential to make large scale, multi-species comparisons. Thus, an understanding of the mimetic musculature can inform our understanding of social behavior among species.

Primate Social Systems

Most primates are highly social (e.g., Schultz, 1969). They interact frequently and regularly with other group members beyond the family unit. However, different taxa within the order Primates use social behaviour in highly contrasting ways (Schultz, 1969; Burrows, 2008).

Prosimians (the lorises, galagos, lemurs, and tarsiers) are typically understood as being the least gregarious of all primate species. They are mostly nocturnal, arboreal, relatively small-bodied (with small faces), and have a relatively low brain size to body size ratio compared to anthropoids (Hill, 1953, 1955; Schultz, 1969; Martin, 1990; Sussman, 1999). Some of these species live as individual adults that have overlapping ranges, such as in mouse lemurs (*Microcebus*), dwarf lemurs (*Cheirogaleus*), tarsiers (*Tarsius*), lorises (*Loris*, *Nycticebus*),and some galagos (*Galago*, *Otolemur*). In this type of social system direct, proximate encounters occur that may be either affiliative or agonistic (friendly or aggressive) and it is known that some of these encounters involve facial displays (Bearder & Doyle, 1974; Charles-Dominique, 1977; Martin, 1990; Andrès et al., 2003; Nash, 2003; Kessler et al., 2012; Eichmueller et al., 2013). These prosimian species may form small groups that consist of a mother, her infant, and an adult daughter, taxa such as the mouse lemurs. While these primate species do not form large social groups they still typically come together in mixed sex sleeping groups, a behavior that has been linked to both temperature regulation and safety against predators (Radespiel et al., 2003; Rasoloharijaona et al., 2008; Biebouw et al., 2009). While facial displays have been documented in some of these taxa (e.g., Charles-Dominique, 1977), auditory communication (via elaborate long- and short-distance calls) and olfactory communication figure prominently in these species (Martin, 1990; Sussman, 1999; Liebal et al., 2013).

The diurnal lemurs can be strikingly different from lorises, galagos, nocturnal lemurs (mouse lemurs and dwarf lemurs), and tarsiers. Taxa such as the large-bodied sifakas (*Propithecus* spp.) and ring-tailed lemurs (*Lemur catta*) are diurnal, more often terrestrial, and can form relatively large multi-male/multi-female groups (up to 16 individuals) in a polygamous setting (Richard, 1985; Gould, 1997). Polygamy, the ability of one individual to control reproductive access to multiple individuals of the opposite sex, typically takes the form of polygyny within primates, the ability of one male to control access to multiple females (Fleagle, 2013). However, within some of the diurnal lemurs it takes the form of polyandry, one female controlling reproductive access to multiple males (Sussman, 1999). *L. catta* has a complex dominance hierarchical system along the matriline (a system where social rank is determined based upon kinship to the dominant female). Facial displays of submission and aggression have been documented in *Propithecus* and *L. catta* in the wild (Jolly, 1965; Richard & Heimbuch, 1975).

Anthropoids consist of the New World monkeys (platyrrhines), Old World monkeys (catarrhines), and apes. They are the best understood in terms of visual communication by way of facial displays. Anthropoids are typically larger-bodied (with larger faces) than prosimians, are almost all diurnal and more often terrestrial, and often form big social groups (Sussman, 2000; Ankel-Simons, 2001; Fleagle, 2013).

Social group sizes within anthropoids can be quite large from 40 individuals up to groups that consist of over 300 individuals (Dunbar, 1991; Rowe, 1996). These species usually form multi-male/multi-female polygynous groups with one dominant male and agonistic (aggressive) encounters can be frequent. Anthropoids use olfactory communication but the olfactory structures, as well as olfactory regions of the brain, are reduced relative to prosimians (Martin, 1990). Vocalizations (both short- and long-distance varieties) are also used in anthropoids but there is strong evidence that visual communication via facial displays is the primary means of proximate, social communication (Liebal et al., 2013).

In polygamous (both polyandrous and polygynous) societies, social interactions are more frequent and proximate than in the nocturnal prosimians (Liebal et al., 2013). Due in part to the more complex and frequent social interactions that typify anthropoids relative to prosimians, anthropoids have a higher brain size to body size ratio than prosimians and part of the relatively increased brain size is located in regions associated with the neurobiology of facial processing (Dunbar, 1989; Burrows, 2008; Parr, 2011; Fleagle, 2013).

Apes (the lesser apes: gibbons and siamangs; and the greater apes: orangutans, gorillas, bonobos, and chimpanzees, along with humans) are all diurnal, large-bodied species that mostly live in big groups that are mostly characterized by polygynous systems (Goodall, 1986; Bartlett, 2008; Fleagle, 2013). While social relationships may be more fluid than in Old World monkeys, social interactions in apes are typified by complex facial display repertoires (e.g., Ekman et al., 2002, Ekman and Friesen, 1978; Goodall, 1986; Vick et al., 2007; Waller et al., 2012; Caiero et al., 2013).

Monogamous relationships within primates are rare (Clutton-Brock, 1974; Fleagle, 2013; Liebal et al., 2013). Owl monkeys (the New World *Aotus* spp.), the sole nocturnal anthropoid, are typically monogamous but our best understanding of primate monogamy may be the gibbons (*Hylobates* spp.) and siamangs (*Symphalangus* spp). Due in part to their frequent use of monogamy, opportunities for proximate social interactions with a high number of individuals are lower in lesser apes than in the polygamous greater ape species (Waller et al., 2012; Fleagle, 2013). Along those lines, recent studies demonstrated that gibbons and siamangs have fewer mimetic muscles than their close relatives the chimpanzees (Burrows et al., 2011; Diogo et al., 2012b) and fewer facial displays (Waller et al., 2012).

Orangutans (*Pongo* spp.) are a special case among apes. These are large-bodied, arboreal primates and they live relatively solitary lifestyles compared to the other great apes (e.g., Galdikas, 1988). However, like all primates, they exploit the social group throughout their life histories. Orangutans may form travel bands (where individuals feed and travel together when fruit is abundant), temporary aggregations (where individuals feed together but travel separately when fruit, their main food source, is scarce), and consortships (where a sexually receptive female travels in coordination with a male for a defined period of time). Typically, mothers and immature offspring travel together and may include an older daughter and her offspring in the group. It is especially noteworthy that orangutans may form larger groups depending upon the specific study site and fruit availability (Knott, 1998; van Schaik, 1999; Knott & Kahlenberg, 2010). Despite the large cheek flanges that some mature males form and the relatively low frequencies of social interactions with multiple individuals, orangutans have been documented to produce about the same number of facial displays as chimpanzees, but fewer than humans (Waller et al., 2013).

Ecomorphological Relationships in Primate Mimetic Musculature

Primates present a wide range of facial morphology, skin and fur coloration, and use of facial displays (Schultz, 1969; Liebal et al., 2013). Santana and colleagues (2014) demonstrated that interspecific variation in facial coloration is associated with degree of facial mobility within diurnal anthropoids. Species with multi-colored faces tended to have the lowest range of facial displays and species with more "plain" faces tended to have the highest range of facial displays. Body size and face size also influence facial display repertoire. Dobson (2009a) found that anthropoids with small faces tended to have fewer facial displays than anthropoids with larger faces, most likely due to improved visual acuity in large-bodied (and large-faced) anthropoids.

Ecomorphology is concerned with the relationships between morphological form of any individual and the environment of that individual. Skeletal and dental morphologies across primate species have been shown to be adaptive to environmental factors. For example, dentition within primates that are primarily seed-eaters, gum and sap-eaters and fruit feeders shows unique morphological features linked to acquiring and processing these particular foods (e.g., Hylander, 1975; Lambert et al., 2004; Burrows & Nash, 2010; Burrows et al., 2015). Mandibular morphology has similarly been linked to dietary niche across a range of primate taxa (e.g., Ross & Wall, 2000; Ravosa et al., 2007; Mork et al., 2010). These ecomorphological relationships have mainly been conceptualized as a focus on the functional interactions and adaptive responses between morphology and the physical/ecological environment (such as density of leaf cover, temperature, and dietary niche). However, physical and ecological features of environments are not the only factors that need to be considered in ecomophological relationships, especially within primates.

Ecomorphological pressures shaping primate mimetic musculature include dietary niche, foliage density, etc. (Liebal et al., 2013). However, mimetic musculature also adapts to ecomorphological pressures focusing on the social environment (Schmidt & Cohn, 2001). Social environments are crucial in imposing constraints, selective pressures, and adaptive niches for exploitation within primates (e.g., Dunbar, 1989, 1998, 2009). For example, diurnal anthropoids who live in large social groups have the highest range of facial displays relative to those that live in smaller groups (Dobson, 2009b). Linking broad social behaviors to specific morphologies might not always be straightforward, but for mimetic muscle morphology there is a clear and direct link between morphology and social communication with conspecifics since contraction of the musculature leads directly to the facial display. Whereas other social behaviors (such as approach and avoidance) might be hard to link to specific morphologies, facial displays/expressions are overtly linked to mimetic muscle anatomy (Burrows & Cohn, 2014). As such, variation in these muscles, both at the gross and microanatomical levels, is likely to result in differences in facial display/expression behavior.

Much of our previous understanding of mimetic musculature and its evolution in primates was rooted solely in phylogeny. Huber (1931) held that facial expression musculature was the simplest and least complex in prosimians (complexity here referring to number of individual muscles, relative sizes, interconnections, and attachment sites). Under this “phylogenetic” model, complexity of mimetic muscle morphology increased in a simple linear, step-wise fashion up the phylogenetic scale until humans, where the ultimate in complexity was achieved. This view has traditionally also been applied to facial display repertoire with the most simple, undifferentiated displays being rooted in the prosimians, ever increasing in a step-wise, linear fashion up to humans, where the most complex, subtle, and graded displays are found.

This "phylogenetic model" of morphology has recently been challenged. Work in wide phylogenetic, ecological, and social environment ranges of primates (and some non-primate mammals) has shown that social environment variables play a considerable role in the adaptive morphology of mimetic musculature (Burrows & Smith, 2003; Burrows et al., 2006, 2009, 2011; Burrows, 2008; Diogo et al., 2008, 2012a, b; Diogo & Wood, 2012; Rogers et al., 2009; Diogo et al., 2014). Clearly, a simple, linear phylogenetic model of primate mimetic musculature evolution is inaccurate and incomplete.

Neurobiological evidence also indicates that there are considerable socioecological variables involved in the evolution of facial displays among primate species. Sherwood (2005) examined facial nerve neuron number across a wide phylogenetic range of primates, including social group size as a variable and correcting for body size difference. This study demonstrated that species that live in large, complex social groups had more facial nerve neurons than species that live in small social groups, indicating more potential control over mimetic musculature. Additionally, Sherwood et al. (2005) found relatively greater volume of facial nerve nuclei in the great apes and humans compared to all other Old World primates, suggesting increased differentiation of the facial muscles and greater utilization of the visual channel in social communication. Lastly, Dobson (2012a) showed that neocortex size (the area of the brain that includes regions devoted to social interactions) is a significant predictor of facial nerve nuclei volumes in catarrhines (Old World monkeys and apes). These studies demonstrate that there is a strong co-evolution between social group size and neurobiological components of facial musculature, at least in the catarrhines. Overall, it appears that as group size increases, primate species have more brain area dedicated to the production of facial displays/expressions. Facial expressions thus seem to play a role in facilitating group cohesion.

Given the various morphological and physiological links to ecology and especially to social variables in primate mimetic musculature, it should be possible to understand how variation in the social environment influences variation in mimetic muscle morphology. As part of a larger investigation into these relationships and their roles in the evolution of primate mimetic musculature, we present two case studies at both the gross and microanatomical levels. These are illustrative examples only and do not represent fully developed analyses. These cases show the potential role that social behaviour can play in exerting a clear selective pressure on morphology of mimetic muscles.

Case Study 1: Closely related macaques have differing mimetic muscles, or "Phylogeny Does Not Always Dictate Morphology"

It is well known that phylogeny does not always reflect ecological preferences, social behaviour, or morphology of a species and macaques are an outstanding illustration of this point. Macaques are one of the most ubiquitous and successful of living primates, living in highly varied climate zones from snow-covered mountains in Japan (*Macaca fuscata*) to semi-desert zones in northern Africa (*M. sylvanus*). Macaques are one of the few primates that thrive alongside humans in urban settings and some macaque populations are even provisioned by humans in these settings (Thierry, 2007). All species share some common demographical and basic behavioral patterns. They all primarily consume fruits and live in multi-male/multi-female groups organized along a linear hierarchy and group size in macaques may reach up to 100 individuals (Thierry, 2007). In contrast to these similarities in basic socio-demographic characteristics, macaques differ widely in their pattern of aggression, affiliation, and dominance (Thierry, 2007). Because of the close phylogenetic relationships and basic socio-demographic similarities, but differences in social behavior, macaques provide a good model to test hypotheses that ecological and social characteristics can play a role in the evolution of interspecific variation in mimetic morphology.

Rhesus macaques (*Macaca mulatta*) inhabit widely fragmented environments throughout the Indian subcontinent up to Afghanistan and Indochina, co-existing in some instances with humans (Thierry et al., 2004). They consume leaves and fruits but have adapted to consume a wide variety of foods. Habitats are diverse and include urban settings, evergreen forests, semi-deserts, *etc*. Group sizes also vary but outside of semi-provisioned, urban settings, *M. mulatta* typically occur in groups of around 50-90 individuals. Rigid, linear dominance hierarchies characterize *M. mulatta*. Outcomes of social interactions are almost always certain, being determined by the ranks of the participants in what is termed a “despotic” social style, where some individuals have more power than others (Flack & de Waal, 2004; Thierry, 2007). Facial displays are important and are frequently used as part of the social maintenance system for these hierarchies. Movements of the external ear are particularly noted in *M. mulatta* facial display repertoires (Partan, 2002; Parr et al., 2010) and the anatomy of the muscles around the external ear is well known (e.g., Huber, 1933; Burrows et al., 2009).

Sulawesi crested macaques (*M. nigra*) are closely related to rhesus macaques but behave very differently. They inhabit a much more restricted range, being found only in a small part of Indonesia and they live in densely foliated tropical forests. Their diet is similar to that of *M. mulatta* (Thierry, 2007). *M. nigra* is characterized by practicing a more “tolerant” social system with a greater repertoire of facial displays, but fewer displays that focus on movement of the external ears (Thierry, 2000; Dobson, 2012b). Descriptions of facial displays include far fewer movements of the external ear – in fact, only one movement (ears flattened against the back of skull) is documented in their behavioural repertoire (Thierry et al. 2000). Fights are frequent but often of low intensity and the outcomes of social interactions are far more uncertain than in the despotic species such as *M. mulatta* (i.e. power asymmetries are weaker in *M. nigra*) (Petit & Thierry, 1994; Thierry et al., 2008).

In an effort to explore the potential ecomorphological relationships among social behaviour and mimetic musculature in the despotic *M. mulatta* vs. the tolerant *M. nigra*, the present case study describes mimetic muscles around the external ear in both species. As part of a larger study into the mimetic musculature of *M. nigra*, five cadaveric specimens were dissected at the Royal Museums of Scotland (four adult and one juvenile). While the entire faces were dissected on each cadaver, we only report in this case study on the muscles surrounding the external ear. Burrows et al. (2009, in review) presented detailed descriptions of mimetic musculature around the entire faces in *M. mulatta* and *M. nigra*. Seiler (1970, 1971, 1973, 1974, 1977) also presented reports of external ear musculature of a variety of *Macaca* species. Here, we describe musculature from the present study but a more full and detailed account of the entire set of mimetic musculature of *M. nigra* vs. *M. mulatta* is presented in Burrows et al. (in review), including evidence from the previous work of Seiler (1970, 1971, 1973, 1974, 1977).

Figure 1 is an abstract representation of the musculature surrounding the external ears in both *M. nigra* and *M. mulatta*. *M. mulatta* mimetic musculature is shown here only for comparison to *M. nigra*. Table 1 describes musculature presence and form in both species of macaque. Seiler (1971) reported on a dissection of a specimen of *M. nigra* (referred to therein as *Cynopithecus niger*) but did not specifically focus on the musculature surrounding the external ear.

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

mulatta: six in *M. mulatta* (two of those being variably present) and four in *M. nigra* (three of those being variably present). The posterior auricularis muscle in *M. nigra* typically had a single belly while this muscle in *M. mulatta* had two bellies (Burrows et al., 2009). Despite the close phylogenetic relationship between *M. mulatta* and *M. nigra*, the external ear muscles of *M. nigra* appear to be more similar to those in the distantly related gibbons/siamangs (the hylobatids), which are lesser apes (Burrows et al. 2011). Both hylobatids and *M. nigra* have poorly developed external ear muscles relative to *M. mulatta*. Movements of the external ears are minimal in hylobatid facial displays (Waller et al, gibbonFACS), similar to the facial display repertoire of *M. nigra* (Thierry et al., 2000). If phylogeny were the main driving force behind form of macaque mimetic musculature, we would expect 1). *M. mulatta* and *M. nigra* to have more similar musculature of the external ear and 2). that they would both have more similar musculature to one another than either does to hylobatids. Mimetic musculature around the external ear in these two species of macques may be partially influenced by social behaviour differences.

M. mulatta employs a wide range of facial displays that are routinely used in social encounters (Parr et al., 2010). Movements of the external ear in *M. mulatta* are frequent and varied in these encounters, moving in both submissive and aggressive contexts. These movements have been described in Parr et al. (2010). Despite the fact that *M. mulatta* has more robust development of the external ear muscles, *M. nigra* has a greater facial display repertoire overall (Dobson, 2012b).

According to the *Power Asymmetry Hypothesis of Motivational Emancipation* (Preuschoft and van Hooff, 1995), the flexibility in the use and appearance of communicative signals is partly determined by characteristics of the social environment. In species such as *M. mulatta*, which are characterized by high power asymmetries, the outcome of social interactions is highly predictable and mainly determined by the relative dominance status of the individuals. In this context, individuals benefit from clear, unambiguous communication signals, which will reduce the likelihood of confusion regarding future behaviour. For example, rhesus macaques use the silent bared-teeth face to formally indicate their subordinate status when approached by higher-ranking individuals. *M. nigra* on the other hand, live in a more relaxed social system where the outcome of social interactions is less predictable and more uncertain. Facial expressions such as the silent bared-teeth are more graded and blended and are used across context (Thierry et al. 1989; Thierry et al. 2000). These differences in how facial expressions are used might be reflected in the anatomy, with rhesus macaques having more developed ear muscles allowing for more numerous movements and sustained activation to produce unambiguous signals, thereby reducing uncertainty in the outcome of social interactions. These subtle differences in social behaviour, facial displays, and mimetic musculature morphology are a good example of how social variables can be part of the ecomorphological relationships found among primates at the gross level.

Case Study 2 – Myosin Fiber Type Distribution in the Orbicularis Oris Muscle, or "Phylogeny Does Not Always Dictate Muscle Physiology"

All skeletal muscle, including mimetic musculature, works by getting shorter or contracting (Gans, 1982). Each muscle is made up of smaller units that work together to contract. Muscles consist of packaged units called "fascicles", collections of muscle fibers enveloped by connective tissue. Each muscle fiber (or myofiber) in turn consists of bundles of myofibrils, which are made up of many filaments of contractile proteins. One of those contractile proteins is myosin. All mammalian skeletal muscle includes myosin, which interacts with other muscle proteins to produce shortening of the overall muscle (Lieber, 2010).

There are several types of myosin proteins but the most abundant and best understood for mammalian skeletal muscle physiology are type I (slow-twitch) and type II (fast-twitch) myosin (Barany, 1967; Staron, 1997). Type I fibers take more time and more energy to contract. As a trade-off, they are slow to fatigue and hold the contraction longer. In humans, these types of fibers tend to dominate in muscles of the limbs (except for the hand) and spine. Type II fibers consist of a number of isoforms (different sub-types) but overall they are able to contract more quickly than type I fibers but use less energy. As a trade-off, they are quick to fatigue and cannot hold the contraction as long as type I fibers. In humans, these types of fibers tend to dominate in muscles of the face and in the human hand (Stål et al., 1987, 1990; Stål, 1994; Lieber, 2010). Furthermore, the potential instantaneous force that each fiber-type can generate differs, with slow-twitch myosin fibers generating a lower instantaneous force than fast-twitch.

As an example, standing in a long line at a check-out may be aggravating but our lower limb and spine musculature, dominated by fatigue-resistant type I myosin fibers, typically don’t fail us and we’re able to wait for our turn. Imagine, though, holding a smile that long. The mimetic muscles that control smiling, dominated by quick-to-fatigue type II myosin fibers, typically fire that smile quickly but we tire after just a minute or so of holding that smile for family photos.

All mammalian skeletal muscle consists of mixtures of slow-twitch and fast-twitch myosin fibers distributed throughout the muscle. Each muscle has a different percentage of slow-twitch and fast-twitch fibers depending upon the work that the particular muscle does. It is well established that human mimetic musculature is dominated by fast-twitch myosin fibers (e.g., Stål et al., 1987, 1990; Stål, 1994). Our facial muscles are able to contract quickly and spontaneously (think of how quickly and automatically we smile at the sight of a familiar friend or a funny joke) but it is difficult to hold that contraction longer than a few seconds before fatigue sets in. These differences in the ratio of slow-twitch to fast-twitch myosin fibers can inform our understanding of muscle function and preceding evolutionary pressures.

Our understanding of the gross and comparative anatomy of primate mimetic musculature is improving all the time due to a wealth of recent studies (Burrows & Smith, 2003; Burrows, 2008; Burrows et al., 2006, 2009, 2011; Diogo et al., 2012, 2013a, b). However, we are only beginning to understand the comparative physiology of primate mimetic musculature and what implications this may have for our conceptualization of the evolution of social behaviour and visual communication. A recent study by Sanders et al. (2013) showed that human tongue musculature has a greater percentage of slow-twitch fibers than tongue musculature from chimpanzees. Authors of that study correlated this evolutionary innovation in muscle physiology of the human tongue with the ability of the human tongue to slow down and produce more specific and longer contractions during speech, relative to how the tongue behaves in chimpanzees during vocalizations.

Some mimetic musculature in humans is also used during speech (Lieberman, 2007; Raphael et al., 2007; Taylor et al., 2012; Popat et al., 2013). Human lips act in part as "articulators" during speech, refining the sounds that come from the larynx into specific, meaningful speech units (e.g., McGurk & MacDonald, 1976; Raphael et al., 2007). For example, differential articulating action of the lips can help the listener differentiate a hard "c" sound (as in "cat") from a softer "b" sound (as in "bat"). The orbicularis oris muscle is one of the mimetic muscles that moves the lips, during facial displays/expressions, eating/suckling, and during speech (or vocalizations in non-human primates) (e.g., Rastatter & DeJarnette, 1984; Burrows & Cohn, 2014). The orbicularis oris muscle encircles and attaches to the lips in a sphincter-like fashion (Standring, 2010). Burrows et al. (2014) sampled mimetic musculature, including the orbicularis oris muscle, from humans, chimpanzees, and rhesus macaques. These species present a range of phylogenetic relationships: chimpanzees and humans are closely related while both are relatively distantly related to rhesus macaques (Groves, 2001). Humans vocalize primarily through speech while chimpanzees and rhesus macaques use a variety of vocalizations, but not speech. Burrows et al. (2014) demonstrated that, while humans have a greater percentage of fast-twitch fibers than slow-twitch fibers, the relationship holds true for both the closely related chimpanzees and the distantly related rhesus macaques. However, humans had a significantly higher percentage of slow-twitch myosin fibers than both chimpanzees and rhesus macaques. In other words, our minority of slow-twitch fibers was far greater than the minority of slow-twitch fibers in chimpanzees and macaques. Humans had slow-twitch fiber distribution of roughly between 15-20% while chimpanzees and macaques had only 2-7% distribution of slow-twitch fibers.

As part of a larger effort to expand the phylogenetic sampling of myosin fiber type distribution in primate mimetic muscles, the present case study shows preliminary findings from sampling the orbicularis oris muscle from a siamang (*Symphalangus syndactulus*), which is a lesser ape, a chimpanzee (*Pan troglodytes*), which is a greater ape, and a human. Figure 2 shows select microimages of representative sections, highlighting fast-twitch and slow-twitch myosin fibers and their distributions. Clearly, all species show strong reactivity for fast-twitch (type II) myosin but humans show stronger reactivity for slow-twitch myosin (type I) than both siamang and chimpanzee.

These data do not represent fiber counts and statistical analyses. These are merely preliminary data used to illustrate the qualitative differences in myosin fiber distribution and are part of a larger, qualitative study. Keeping this in mind, qualitative observational results at this early stage consistently show that siamangs tend to have a slow-twitch fiber distribution between humans and chimpanzees. While quantitative analyses are needed it is worth noting at this early stage that siamangs (and the other lesser apes, the gibbons) are noted in part for their intensive use of “songs” and “duets”, a type of sustained, long-distance vocalization used to maintain social bonds and territorial boundaries. These vocalizations can be heard for at least two kilometres and can last for many minutes (Bartlett, 2008). They have been cited as maintaining pair & family bonds, territorial boundaries, individual identity, and mate attraction (Raemaekers et al., 1984; Geissmann, 1999, 2002; Terleph et al., 2015) and are associated with specific morphological specializations such as an enlarged laryngeal air sac (Fitch, 2000). Siamangs and gibbons produce these songs by forming the lips into a funnel-shape and holding that lip posture while the song is produced. It is possible that the qualitatively observed differential distribution of slow-twitch myosin fibers from the orbicularis oris muscle noted in the present case study, humans > siamangs > chimpanzees, is reflective of an evolutionary divergence in the adaptive physiology of the orbicularis oris muscle. Without question, quantitative counts of fiber-type distribution will provide more definitive evidence for (or against) this potential physiological adaptation.

As the only monogamous ape, siamangs (and gibbons) are noted for having fewer facial displays than chimpanzees and humans (Waller et al., 2012; Scheider et al., 2014). The development of an elaborated and structurally complex set of vocalizations in these primates may be a “trade-off” for the less frequent use of facial displays. Further quantitative analyses on specific percentages of slow-twitch vs. fast-twitch myosin fiber distribution among these species will provide better and definitive evidence. Further studies on how the oribicularis oris muscle behaves in vocalizations across a wide phylogenetic, ecological, and social range of primates would aid our understanding.

At this juncture it is worth noting that physiological cross-sectional area (PCSA) of muscle fibers is the preferred variable for estimating potential contractile force of any given muscle (e.g., Gans & Bock, 1965; Gans, 1982). In combination with fiber-type distribution, it can provide a more complete picture of how much force a muscle can generate when it contracts. One component of determining PCSA involves harvesting the entire muscle. However, since mimetic muscles attach into one another and, like the orbicularis oris muscle, may be a sphincter (or circle), it is not yet practical to pursue this method of estimating force-generating potential in mimetic muscles.

Discussion

Understanding the links among morphology, ecology, and the social environment is not always straightforward. Neither is it always possible to link specific aspects of morphology directly to ecology and social behaviours. However, for facial expressions/displays there is a clear and direct link among the morphology of the face, the behavioural expression of facial movement, and social interaction with conspecifics.

Ecomorphological considerations in primate facial displays and mimetic musculature have been strengthened in recent years by examinations not only of phylogenetic relationships but the inclusion of ecological variables (such as density of foliation, diet, communication modes) and social group variables (such as size of group, dominance relationships). This multifactorial methodology is continually improving our understanding of how facial musculature, facial displays, and primate sociality have co-evolved. Much work remains, especially on the relatively under-studied nocturnal prosimians and the platyrrhines (or New World monkeys).

While examinations of gross morphology of the mimetic muscles will continue to be illuminating, our best efforts may be aimed at neurological and physiological investigations into this musculature. Our understanding of many physiological basics, myosin fiber-types notwithstanding, such as physiologic cross-sectional area and fiber lengths, remains poor. Neurobiological research into prosimian facial displays and its link to social behavior is especially lacking. These species represent our closest extant representatives of the first primates so research aimed here may be helpful in efforts to reconstruct the lifestyles of stem primates.

Overall, these qualitative case studies add to the growing body of evidence that primate mimetic musculature form and evolution are adaptive to social, communicative pressures. While we know that mimetic musculature in extant species is adaptive to social variables (such as group size and dominance "style"), future studies may be able to extrapolate our current knowledge to taxa represented only in the fossil record.

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

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

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

Figures

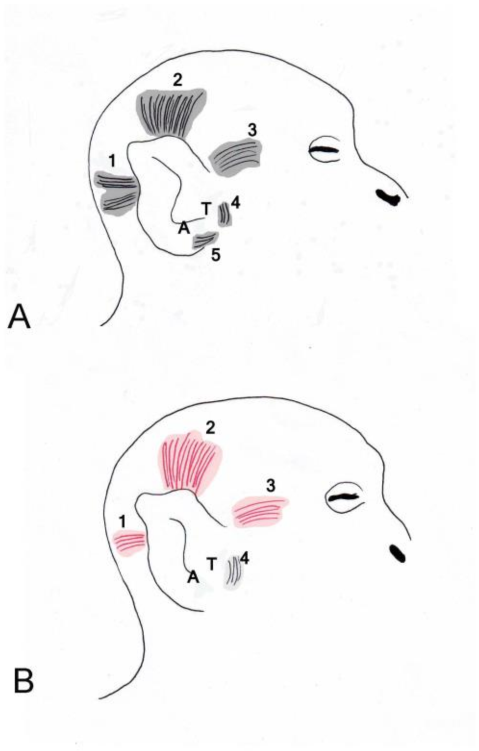

Figure 1 Abstract representations of the mimetic muscles surrounding the external ears in A) rhesus macaque (*Macaca mulatta*) and B) Sulawesi macaque (*M. nigra*). 1: posterior auricularis muscle; 2: superior auricularis muscle; 3: anterior auricularis muscle; 4: tragicus muscle; 5: antitragicus muscle; T: tragus; A: antitragus. Red coloration of select muscles in *M. nigra* indicates that these muscles varied, relative to those of *M. mulatta*.

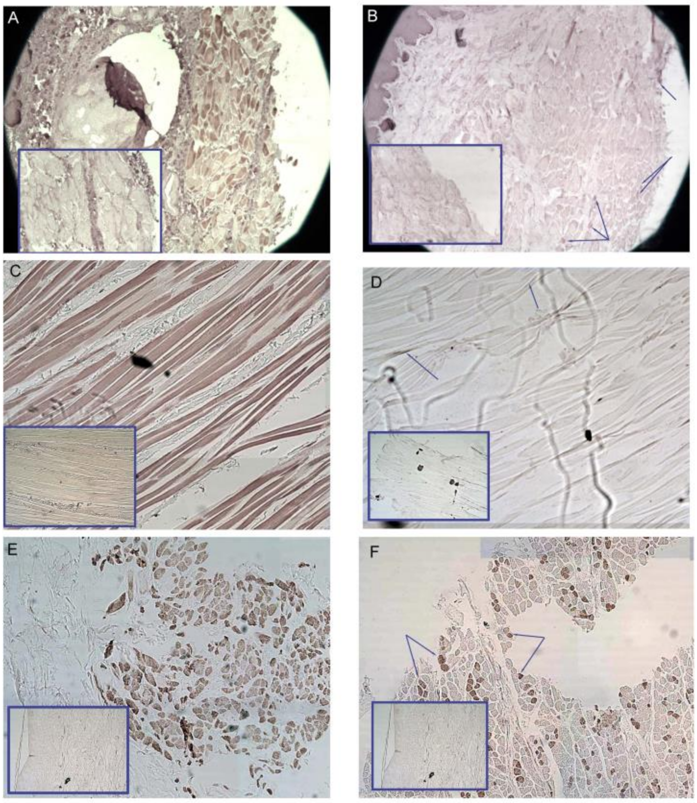

Figure 2 Micronatomical image of A) & B) siamang, *Symphalangus syndactylus*; C) & D) chimpanzee, *Pan troglodytes*, and E) & F) human, *Homo sapiens* highlighting fast twitch and slow-twitch myosin fibers. All images on the left are fast-twitch reactivity, all images on the right are slow-twitch reactivity. Inset images offset by blue are control images. Note that all three species show strong reactivity for fast-twitch (type II) myosin (images on the right). Human (panel F) slow-twitch reactivity is strong while chimpanzee (panel D) shows almost no slow-twitch reactivity. Siamang (panel B) shows intermediate slow-twitch reactivity. Arrows indicate fibers in slow-twitch panels that are reactive.