

Development of rhesus macaque (*Macaca mulatta*) facial musculature: implications for
macaque social behavior ontogeny

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Abstract

Rhesus macaques (*Macaca mulatta*) have long been used as a model for the evolution of some aspects of human social behavior and they are among the most completely understood species of the macaque genus. Rhesus macaques have a despotic dominance hierarchy with a well-documented facial display repertoire. However, we know little about the ontogenetic changes in gross facial musculature and how this might relate to corresponding facial display behavior. In an effort to illuminate our understanding, we dissected facial masks from 13 *M. mulatta* cadavers that died naturally, shortly after birth or were stillborn, and we compared these results to those from adult rhesus macaques. Results reveal that, unlike the adults in the present study, infant rhesus macaques have extrinsic external ear muscles and muscles associated with the lower lip that are very gracile and poorly developed. Musculature associated with the upper lip and nares are well developed, individually distinct, and robust, like those of the adults in our sample and adult *M. mulatta*. However, we were unable to locate the zygomaticus major muscle in any fetal/infant sample. These results may reflect simple variation in mimetic muscle ontogeny, differences related to facial allometry, or they could reflect a behaviorally meaningful adaptation to different life stages of macaque ontogeny.

Introduction

Facial expressions are adaptations for forming and maintaining social bonds. They are one of the most frequently used modes of non-vocal communication among primates, including humans (Schmidt & Cohn, 2001; Burrows, 2008; Waller *et al.*, 2017). Among humans, facial expressions are adaptive, used in all cultures, and some are universally recognized (Schmidt & Cohn, 2001; Waller *et al.*, 2008; Burrows & Cohn, 2014; Klingner & Guntinas-Lichias, 2023). Facial expressions are mechanisms to transmit information on the intentions, motivations and/or emotional state of the signaler and are achieved via contraction of facial musculature. They also offer important insights on the evolutionary neurobiology (Barton, 1996; Dunbar, 1998; Burrows, 2008; Waller *et al.*, 2008; Albohn & Adams, 2022; Kavanagh *et al.*, 2022). The use of clear facial expressions allows the signaler to communicate his or her intentions to a receiver, which functions in part to regulate the social group (Spoor & Kelly, 2004).

Facial expressions are produced by facial, or mimetic, musculature (Ekman & Friesen, 1979; Schmidt & Cohn, 2001; Burrows, 2008). These muscles are attached into the dermis of the face and produce facial movement when they contract. Due to this relationship, we can assign specific facial movements to specific muscles and create objective facial movement systems that help us understand how humans and other animals use their faces in social communication, as well as how the face and its movement may have evolved (Ekman & Friesen, 1978; Vick *et al.*, 2007; Parr *et al.*, 2010; Waller *et al.*, 2012).

Facial, or mimetic, muscles develop from the 2nd branchial arch and are all innervated by the facial nerve (Cranial Nerve 7). They generally attach to periosteum and/or hyaline cartilage of the nose and ears and to the dermis of the face, scalp, and neck. In most mammals, they

deform the facial mask into expressions of social communication, but they also move the external ear and vibrissae, and change the shape and size of the openings for the eye, nares, and oral cavity. Facial muscles begin to develop in humans during the 3rd-8th weeks of intrauterine life and coalesce from thickened mesenchyme surrounding the 2nd branchial arch, forming five sheets or “laminae” on each side of the face. Individual facial muscles form from these laminae (except for the platysma muscle). During further embryonic and fetal development, these muscles increase their structural independence from one another (see Huber [1933], Gasser [1967], and Warmbrunn *et al.* [2018] for a more in-depth discussion).

Macaques are a commonly used model organism for testing hypotheses related to the evolution of social behavior in humans because they present a wide range of social systems from despotic to relatively tolerant (Capitanio, 2010; Thierry *et al.*, 2010; Maestripieri & Hoffman, 2012). Rhesus macaques (*Macaca mulatta*) are found throughout India, Nepal, and parts of China and, in some areas, live in close contact with humans. Rhesus macaques exhibit a despotic social system in which females inherit their rank from their mother and participants employ stereotyped facial displays as part of rank management (Thierry *et al.*, 2010, 2022; Adams *et al.*, 2015; Robinson *et al.*, 2018). Adults have well understood facial musculature and a clear, discrete facial display repertoire which can be measured using the macaque facial action coding system (MaqFACS) (Burrows *et al.*, 2009; Parr *et al.*, 2010), which allows us to make direct comparisons of facial movement among individuals.

The growing body of literature on facial muscle anatomy (both gross and microanatomy), biomechanics, and physiology has improved our understanding of the evolution of primate social behavior, non-verbal communication, and evolutionary

neurobiology (Burrows & Smith, 2003; Burrows *et al.*, 2006, 2016; Burrows, 2008; Diogo *et al.*, 2008, 2009; Burrows & Cohn, 2014; Dickinson *et al.*, 2020; Rotenstreich & Marom, 2023). Yet, despite this growing understanding of facial musculature morphology and physiology, especially within *M. mulatta*, we have a poor understanding of the ontogeny of both facial muscles and facial movement among primates, including humans. Glasser (1967) made careful and detailed observations of human facial muscle embryology but we know little about how facial muscle morphology (and physiology) might change postnatally and over an individual's lifetime, or how facial muscles might be used differently in infant primates. Given this gap in the literature, information documenting the correlation between facial muscle morphology and growth during ontogeny with facial expressions within and among primate species is needed.

We don't know if facial muscle ontogeny is merely growth in size of the infant musculature, or if infant facial muscles have their own morphology that changes through ontogeny. There is great debate over whether human facial expressions change in response to environmental and cultural influence or are fixed and universal from birth (Russell, 1994; Negrão *et al.*, 2021). Thus, improving our understanding of facial muscle morphology at and around birth is relevant across disciplines.

To these ends, the present study was designed to investigate whether fetal/infant *M. mulatta* facial muscles are, in essence, miniatures of the adult configuration that merely get larger during ontogeny or exhibit differences potentially subject to ontogenetic change.

Materials & Methods

The present study used 13 specimens of both fetal and stillborn/infant *M. mulatta*. All specimens were obtained from Yerkes National Primate Research Center (YNPRC) in Atlanta, GA, and were preserved in 10% buffered formalin after the heads were disarticulated from the cervical spine at YNPRC by veterinary staff. All research in the present study conforms to ethical research and treatment of non-human primates as outlined in the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates.

All fetal specimens were spontaneously aborted while all infant specimens died from natural causes or due to abandonment by the mother. Stillborn specimens were obtained when animal care staff found them in the enclosure. Some specimens were labeled as “stillborn” or “infant”, but most specimens were not labeled. There were no gross abnormalities in the heads of any of the specimens used in the present study.

Midline incisions were made on each head to create two separate face masks. Incisions were started at the nuchal region and continued over the scalp, down the midline of the face, and ending at the lower border of the mandible. The left side of the face mask was removed from the skull while the right side was left intact for any future analysis (see Burrows & Smith, 2003; Burrows *et al.*, 2006, 2009). Attachments of muscles to the skull were noted at this time.

To view the facial muscles on the mask, we used both gross observation and the aid of a dissection scope. We used Burrows *et al.* (2009) as a guide to adult *M. mulatta* facial musculature in assessing musculature in the fetal/infant sample. Muscle presence, attachments, and form were noted in each specimen that we examined in the present study. Facial muscles are typically responsible for moving specific areas, or regions, of the face so we

break the face up into regions for the present study: orbital region (typically moved by the orbicularis oculi, frontalis, corrugator supercilli, depressor supercilli, and procerus muscles), nasal region (nasalis, depressor septi nasi, and levator labii superioris alaeque nasi muscles), oral region (orbicularis oris, levator labii superioris, depressor anguli oris, depressor labii inferioris, zygomaticus major, zygomaticus minor, and mentalis muscles), and ear region (occipitalis, orbitoauricularis, posterior auricularis, superior auricularis, anterior auricularis, depressor helicis, and platysma muscles). While we recognize that placing these muscles into discrete regions is a slight oversimplification, we place them in areas that move when the muscles contract (see Standring, 2006; Burrows et al., 2009). Duquesne University Institutional Animal Care and Use Committee does not review work associated with deceased animals.

Results

Facial masks from all infant/fetal specimens were exceptionally thin compared to adult *M. mulatta* and the other adult specimens from the present study (Burrows, 2008; Burrows et al., 2009; see Figure 1). No differences in gross morphology or attachments of facial muscles between the pre-term and infant specimens of *M. mulatta* were noted. Gross appearance of the facial musculature in the fetal/infant sample varied by region (Figure 1). Muscles in the ear and orbital regions were relatively thin and gracile compared to muscles from the oral region (especially the upper lip), which were robust and well-developed. Cheek pouches were relatively under-developed as well, compared to adult *M. mulatta*, but were present. As in adults, fetal/infant cheek pouches were enveloped by fibers of the platysma muscle (Burrows et

al., 2009). Additionally, there was little connective tissue in the infant/fetal sample compared to adults.

Facial muscle attachments in adult *M. mulatta* are described in Burrows *et al.* (2009) and in Diogo *et al.* (2009). Attachments of muscles in specimens from the present study did not differ in specific bony and dermal attachments from adults (Burrows *et al.*, 2009). Table 1 shows facial muscles located in the present study, along with comparisons to adult *M. mulatta* in Table 2 (Burrows *et al.*, 2009).

Ear Region Musculature

Presence of infant/fetal *M. mulatta* muscles in the ear region closely matched those from adults. However, infant/fetal specimens lacked both an observable superior auricularis muscle and an orbitoauricularis muscle (Table 1).

Orbital Region Musculature

Presence of musculature in the orbital region in the infant/fetal sample varied among specimens (Table 1). The corrugator supercilli muscle was found in 77% (10/13) of the specimens while the depressor supercilli muscle was only found in 23% (3/13) of specimens. The procerus muscle, very small and gracile even in adults (Burrows *et al.*, 2009), was in 38% (5/13) of the fetal/infant specimens. The zygomaticus minor muscle was not located in any fetal/infant specimen. In contrast, adult *M. mulatta* zygomaticus minor muscles were present in 40% (Table 2; Burrows *et al.*, 2009).

Oral Region Musculature

Of all regions, muscles in the oral region were the most robust, well- developed and resembling adult form, especially those associated with the upper lip. (Table 1). The levator labii superioris muscle was in 69% (9/13) of the specimens while the nasalis was located in 61.5% (8/13). The very small depressor septi nasi muscle and the depressor anguli oris muscle were in 38% of the specimens (5/13), and the depressor labii inferioris muscle was found in only 1 of the 13 specimens. These muscles, when present, were robust and easy to distinguish from surrounding tissues. Adult *M. mulatta* showed variation, also, in presence of oral region muscles with the depressor septi muscle found in less than half of the specimens (Table 2; Burrows *et al.*, 2009).

The zygomaticus major muscle was absent from the fetal/infant *M. mulatta* specimens. We were unable to locate any portion of this muscle using magnifying loupes or the dissecting microscope. Additionally, we dropped small volumes of alizarin blue dye onto the region of the mask where the muscle is typically located in adult primates, but no muscle fibers were picked up.

Discussion

Results of the present study demonstrate that infant/fetal *M. mulatta* facial musculature is not like “miniature” adult musculature. The infant/fetal sample had some similarities in facial muscle presence, form, and attachments to adults but there were many differences. Musculature of the orbital and ear regions was relatively gracile, compared to adult *M. mulatta*. Additionally, fetal/infant specimens were largely missing the procerus, zygomaticus

minor, and depressor supercilli muscles in the orbital region, and most of the ear region muscles that adults show (Table 1). However, musculature of the oral region/upper lip was typically robust and most muscles from adult *M. mulatta* were also present in the fetal/infant sample, except for the zygomaticus major muscle.

The robust development of muscles in the oral region from the fetal/infant sample is expected. Newborn infants need to be able to suckle, and movement of the lips plays a role in this process. Ear movement and movement of the orbital region may not be as critical for the infant to thrive, and these muscles may become more robust over time.

It is possible that the diminutive size of the fetal/infant specimens caused us to miss the zygomaticus major muscle, but this is unlikely because we found much smaller muscles, such as the depressor septi and corrugator supercilli muscles. Thus, it may be most parsimonious to conclude that the zygomaticus major muscle is not yet fully developed in the ontogenetic sample.

While it is not completely clear, the zygomaticus major muscle in humans seems to develop from the infraorbital lamina between the 6th and 8th week of intrauterine life (see Gasser, 1967; Som & Naidich, 2014) for a more complete discussion of the embryology of the human face). In addition to the zygomaticus major muscle, the infraorbital lamina develops into most of the muscles of the midface (Gasser, 1967; Som & Naidich, 2014). While the infraorbital lamina develops into multiple muscles, it does not help answer the question of why we were unable to locate a zygomaticus major.

Ontogenetic growth of the midface in rhesus macaques is rapid and results in an elongated midface, unlike the slower growth rate and resulting abbreviated midface in humans

(Enlow, 1966). During midfacial growth, the external surface of the human midfacial skeleton is entirely resorptive in nature, while the same area in rhesus macaques is depositional in nature. While the exact mechanisms are unclear, this action in ontogeny of the rhesus macaque midface may influence the "missing" zygomaticus major muscle in our sample.

The zygomaticus major muscle in adult *M. mulatta*, as well as many other anthropoids, is robust and part of facial displays, including the bared teeth display and the play face (Burrows *et al.*, 2009; Diogo *et al.*, 2009; Parr *et al.*, 2010; Clark *et al.*, 2020). We know little about facial displays in infant and juvenile *M. mulatta*, so it is possible that this muscle is not critically important during early ontogeny of rhesus macaques. The zygomaticus major muscle is used to draw the corners of the mouth caudally and superiorly, closer to the external ear (Parr *et al.*, 2010). This action is part of many facial displays in adult rhesus macaques (Partan, 2002; Parr *et al.*, 2010), but this action would be unlikely to be useful during suckling.

Interestingly, in humans, zygomaticus major underpins the facial expression 'smiling' which, although appearing early on in infancy during sleep and across alert contexts, does not fully link to social contexts until one month of age or later (Messinger & Fogel, 2007). Instead, early human infancy is characterized by patterns of increasingly strong and bilateral zygomaticus major contraction suggesting a developmental process of neuromuscular coordination (Messinger & Fogel, 2007).

We suggest that future studies with an increased sample size would help definitively answer the questions surrounding ontogeny of both facial musculature and facial display behavior in rhesus macaques. The present study suggests that infant rhesus macaques are born with robust and well-developed facial muscles in the oral region/upper lip, which may be an

adaptation for feeding behavior, but that musculature in the ear and orbital regions lag. Studies focused on the ontogeny of facial displays are needed to probe these questions more fully.

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Conflict of Interest Statement

The authors have no conflicts to declare.

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Figure Legends

Figure 1 – Top: Left facial mask of an infant rhesus macaque, *Macaca mulatta*. Colored shapes indicate regions of the face that are shown in close-up below. Bottom left: Focus on muscles associated with the auricular region; bottom middle: focus on muscles associated with the orbital region; bottom right: focus on muscles associated with the oral region. Abbreviations: CS – corrugator supercilli muscle; OOcM – orbicularis oculi muscle; LLS – levator labii superioris muscle; DS – depressor septi muscle; DAO – depressor anguli oris muscle; DLI – depressor labii inferioris muscle; OOM – orbicularis oris muscle. Note that not all muscles that were located are labelled in this image because some muscles photographed poorly.