

Published in final edited form as:

J Anat. 2009 January ; 214(1): 36–44. doi:10.1111/j.1469-7580.2008.01004.x.

Comparative Micro-Anatomy of the Orbicularis Oris Muscle between Chimpanzees and Humans: Evolutionary Divergence of Lip Function

Carolyn R. Rogers¹, Mark P. Mooney^{2,3,4}, Timothy D. Smith^{4,5}, Seth M. Weinberg⁶, Bridget M. Waller⁷, Lisa A. Parr^{8,9}, Beth A. Docherty¹⁰, Christopher J. Bonar¹¹, Lauren E. Reinholt⁵, Frederic W.-B. Deleyiannis¹², Michael I. Siegel^{3,4}, Mary L. Marazita^{2,6}, and Anne M. Burrows^{4,10}

¹ Division of Plastic Surgery, Department of Surgery, School of Medicine, University of Wisconsin Hospital and Clinics, USA

² Department of Oral Biology, School of Dental Medicine, University of Pittsburgh, USA

³ Department of Orthodontics, School of Dental Medicine, University of Pittsburgh, USA

⁴ Department of Anthropology, University of Pittsburgh, USA

⁵ School of Physical Therapy, Slippery Rock University, USA

⁶ Center for Craniofacial and Dental Genetics, School of Dental Medicine, University of Pittsburgh, USA

⁷ Centre for the Study of Emotion, Department of Psychology, University of Portsmouth, UK

⁸ Yerkes National Primate Research Center, USA

⁹ Department of Psychiatry and Behavior, Emory University, USA

¹⁰ Department of Physical Therapy, Duquesne University, USA

¹¹ Cleveland Metroparks Zoo, USA

¹² Division of Plastic Surgery, Department of Surgery, School of Medicine, University of Pittsburgh, USA

Abstract

The orbicularis oris muscle (OOM) plays a role in the production of primate facial expressions and vocalizations, nutrient intake, and in some non-human primates it is used as a prehensile, manipulative tool. Since the chimpanzee (*Pan troglodytes*) is the closest living relative of humans, a comparison of the OOM between these species may increase our understanding of the morphological specializations related to differing functional demands of their lips and the factors responsible for their divergent evolution. To these ends, this study compares the microanatomy of the mid-line upper fibers of the OOM between chimpanzees and humans. A mid-line portion of the OOM was harvested from upper lips of three chimpanzee and five human cadavers. The sampled blocks included the area between the lateral borders of the nasal alar cartilages in both species. Each sample was processed for paraffin histology, sectioned, and stained with a variety of protocols. Sections were examined for fiber direction and relative thickness of muscle layers. Ratios of cross-sectional connective tissue area vs. cross-sectional muscle tissue area, muscle fiber diameter, and relative dermal thickness were calculated for each species. In both species, a clear pars marginalis

layer was recognized, contrary to previous reports that only humans possess this layer. In chimpanzees, relative fiber diameter and the relative amount of muscle tissue (i.e., based on connective tissue area: muscle tissue area ratio) were significantly ($p < 0.05$) greater than in humans. In contrast, measurements of relative dermal thickness showed that humans have a greater average dermal thickness of the upper lip than chimpanzees. Taken together, these results suggest that both human and chimpanzee OOM upper fibers meet the specific functional demands associated with their divergent vocal and facial display repertoires, the development of human speech, and the use of the upper lip as a prehensile tool in chimpanzees.

Keywords

chimpanzee; lips; orbicularis oris; histomorphometrics; wadging; speech; evolution

Introduction

The orbicularis oris muscle (OOM) is one of the mimetic, or facial expression, muscles which are found in all mammals (Young, 1957; Gibbs et al., 2002). In humans it is a complex, multi-layered muscle that attaches via a thin, superficial musculoaponeurotic system (SMAS) to the dermis of the upper and lower lips and serves as an attachment site for many other muscles around the oral region (Thaller et al., 1990; Larrabee & Mikielski, 1993; Ghassemi et al., 2003). Like all mimetic muscles, the OOM is branchiomeric in origin, derived from the 2nd (hyoid) branchial arch and is innervated by the facial nerve (Young, 1957; O’Rahilly & Müller, 2007). While most human mimetic muscles develop from only one of the multiple embryonic laminae, the OOM develops from two separate embryonic laminae, the mandibular lamina (which differentiates partially into the lower fibers of the OOM) and the infraorbital lamina (which develops into the upper fibers of the OOM) (Gasser, 1967; Burrows, 2008).

The exact anatomical nature of this muscle in humans remains poorly understood relative to other muscles (Standring, 2004). Our most complete understanding comes from Lightoller (1925) who examined five postnatal and three fetal specimens. This nearly 100-year old description of the human OOM continues to be widely cited (Latham & Deaton, 1976; Standring, 2004; Hwang et al., 2007a, b). The human OOM consists of upper fibers and lower fibers. These in turn are each described as consisting of left and right “pars peripheralis” and “pars marginalis” segments, creating eight separate parts. The pars marginalis and pars peripheralis components are described as meeting at the vermilion border of the lips (Fig. 1). Both Lightoller (1925) and Standring (2004) describe each of the eight muscle parts as resembling a fan having its stem attached to the modiolar region of the lips, with the pars peripheralis segments as open and the pars marginalis segments as closed (see Fig. 1). In the human upper lip the peripheralis segments are the largest and are attached to other muscles near the lips. In humans, the upper fibers of the OOM may decussate in the median plane and create the unique human structure known as the philtrum as they pass into their dermal insertions (Latham & Deaton, 1976). However, not all authors support this view of philtral formation (e.g., Briedis & Jackson, 1980; Namnoum et al., 1997).

The pars marginalis segments are described as being smaller in area and unique to humans (Lightoller, 1925; Pellatt, 1979; Standring, 2004). These fibers are a single, narrow-diameter band lodged within the tissues of each vermilion zone of the lip (see Fig. 1), lying anterior to the pars peripheralis segments. In the median plane, these fibers may meet with and attach into the fibers from the other side, then attach into the dermis of the vermilion zone. Laterally, the pars marginalis segments attach into the modiolus (Latham & Deaton, 1976; Standring, 2004). The posteriorly located pars peripheralis segment is described as consisting of horizontal, oblique, and incisal (longitudinal) fiber bands while the anteriorly located pars

marginalis segment is described as only having horizontal fibers (Kraus et al., 1966; Delaire & Precious, 1986; Mooney et al., 1988).

Contraction of the pars peripheralis fibers in humans positions the lip in labial elevation, an action involved in both facial expression and speech. The pars marginalis fibers act primarily on the portion of the lip covered by the vermilion. These fibers act to press the lip to the maxillary teeth or invert it closer to the oral cavity, wrapping the lip around the incisal and occlusal borders of the teeth. Additionally, action of the pars marginalis fibers is heavily implicated in human speech by “gently” moving the upper lip in production of labial sounds (Standring, 2004).

In general, contraction of both the pars marginalis and pars peripheralis fibers in humans produces change in the shape of the lips and the size of the opening of the oral cavity, actions used in feeding (Tamura et al., 1998; Jacinto-Gonçalves et al., 2004), communication via facial expressions (Ekman & Oster, 1979), and in the production of human speech (Rastatter & DeJarnette, 1984; Rastatter et al., 1987; Standring, 2004; Regalo et al., 2005; Raphael et al., 2007).

As part of our efforts to understand the evolutionary factors involved in shaping human communication, human societies, and cognitive processes, a comparative understanding of the mimetic musculature is required (Darwin, 1872; Schmidt & Cohn, 2001; Gibbs et al., 2002; Burrows & Smith, 2003; Diogo, 2004; Burrows et al., 2006; Vick et al., 2007; Burrows, 2008; Waller et al., 2008). The OOM may be an especially important piece of evidence because of its multi-functional nature in nutrient intake, vocal and non-vocal communication, tool use, and the unique vocal communication mode of human speech (Ekman & Oster, 1979; Rastatter et al., 1987; Gibbs et al., 2002; Oster, 2004; Regalo et al., 2005; Waller & Dunbar, 2005).

As the chimpanzee is widely held to be our closest living relative (Chen & Li, 2001; Groves, 2001; The Chimpanzee Sequencing & Analysis Consortium, 2005; Patterson et al., 2006), its anatomy and behavior are often a focus in efforts to reveal the processual and mechanistic events in human evolution (Hopkins et al., 1993; Bard, 2003; Nishimura et al., 2006; Waller et al., 2006; Sanz & Morgan, 2007; Tomasello et al., 2007; Burrows, 2008). An understanding of the chimpanzee OOM may help not only to further our understanding of the evolutionary relationship between chimpanzees and humans, but may assist in our understanding of how the OOM functions in both species in terms of their unique social behaviors, communication mechanisms, and feeding behavior.

While our knowledge of the human OOM is not itself complete, our understanding of the OOM in the chimpanzee is especially lacking. The chimpanzee OOM has been described as being “primitive” relative to that of humans. It is also described as lacking the separation into pars marginalis and pars peripheralis layers seen in humans (Sonntag, 1923; Lightoller, 1925; Pellatt, 1979). More recently, Burrows et al. (2006) described the chimpanzee OOM at the gross anatomical level as resembling that of humans. While this study found minimal differences between the chimpanzee and human OOM it was limited by using only gross descriptions and did not provide any microanatomical descriptions or histomorphometrics. The purpose of this study is to provide microanatomical data from the chimpanzee and human OOM upper fibers in order to establish comparative and evolutionary frameworks for understanding the structure and function of this muscle and the lips.

Materials & Methods

Three chimpanzees (*Pan troglodytes*) were used in the present study. After death, heads were disarticulated from the cervical portion of the spine by the facility veterinary staff and immersed in 10% buffered formalin solution. These samples were not previously frozen. Two (one adult

male and one adult female) were obtained from the Yerkes National Primate Research Center (Atlanta, GA) and the third (a juvenile male) was obtained from the Southwest Foundation for BioMedical Research (San Antonio, TX). The upper lips were excised as single, intact blocks approximately 1cm lateral to each of the nares. The upper lip was released from the face by cutting along the gum line and placed in 10% buffered formalin solution. All specimens were from previous studies which had met IACUC requirements at the respective institutions.

Fresh upper lips from two male and three female adult human cadavers were also used. These specimens were obtained from a facial plastic surgery training course held at the University of Washington (Seattle, WA) in October 2005. Material for the training course consisted of previously frozen intact dismembered heads. This research protocol was approved by the University of Pittsburgh's Committee for Oversight of Research Involving the Dead (CORID).

Immediately following the plastic surgery course, the upper lips of both cadavers were excised as single, intact blocks of tissue extending horizontally between the oral commissures and vertically between the oral fissure and the base of the columella. This region included the philtrum plus tissue extending laterally to the lateral border of the nasal alae. The upper lip was then released from the face by cutting along the gum line. The tissue specimens were immediately placed in 10% buffered formalin solution and labeled numerically for anonymity.

The mid-line portion of the upper OOM was specifically chosen in both species because this is the only area of the muscle that is free of other muscular attachments (Standring, 2004; Burrows et al., 2006). Lateral to the nasal alar cartilages in both species, other mimetic muscles attach into the upper OOM (Standring, 2004; Burrows et al., 2006). Thus, isolating the OOM from these other muscles would be unlikely. While the human philtral region has been cited by some authors as being depauperate of muscle fibers (Latham & Deaton, 1976), others have described it as having full representation of fibers (Breidis & Jackson, 1980; Namnoum et al., 1997). In either case, the sampled sections in humans included a full representation of the upper OOM from the region between the lateral borders of the nasal alar cartilages. This area would provide both a sampling of the philtral region and regions that have been cited as having full fiber representation (Latham & Deaton, 1976; Namnoum et al., 1997).

All specimens were processed for paraffin-based histology and each block was cut transversely at 12 micrometers with cuts perpendicular to the epidermis. Approximately every fifth section was mounted and stained with either hematoxylin and eosin, or with Gomori trichrome.

The force that any given skeletal muscle may generate is dependent in part upon muscle volume and in part upon the length of sarcomeres. This length in turn is typically characterized by the physiological cross-sectional area (PCSA) and fiber length of the muscle (Gans, 1982; Otten, 1988). While PCSA and fiber length are considered to be "gold standard" estimates of potential contractile force of a muscle previous studies utilizing these methods have focused on limb muscles and masticatory muscles (e.g., Anapol & Barry, 1996; Antón, 2000; Anapol & Gray, 2003; Taylor & Vinyard, 2004; Taylor et al., 2006). Limb and masticatory muscles are relatively simple to separate from their bony attachments and from one another so that the muscle can be reliably isolated and examined. Mimetic muscles, by their very nature, cannot reliably be separated from their dermal attachments (Huber, 1931; Standring, 2004; Burrows et al., 2006; Burrows, 2008). Additionally, most of these muscles, especially the OOM, are 7 attached intimately to one another so that they cannot be isolated for examination (Larrabee & Makielski, 1993; Standring, 2004). Thus, estimates of PCSA and fiber length in mimetic muscles would be unreliable. Other methods of estimating potential contractile force in mimetic muscles are called for. We outline here alternative methodologies for providing such estimates while fully recognizing that these methods do not provide the ultimate information on potential contractile force that would be gleaned from measuring PCSA and fiber length.

The higher the volume of muscle fibers in a given muscle, the greater the potential contractile force of that muscle (Gans, 1982; Herring et al., 1984; Otten, 1988; van Eijden et al., 1996). While information from PCSA and fiber length would provide the best estimate of potential contractile force, we may gain an estimate by calculating cross-sectional connective tissue area vs. cross-sectional muscle tissue area. Fiber diameter is an additional way of estimating potential contractile force of any given muscle (Goodmurphy & Ovalle, 1999; Rowleson et al., 2005; van Wassenbergh et al., 2007). The greater the fiber diameter, the greater the number of myofibrils packaged into that fiber, which may be used as a morphological estimate of potential contractile force. Additionally, an assessment of the proportions of the pars peripheralis (posterior) fibers and the pars marginalis (anterior) fibers may provide us with a more complete understanding of how these layers function in both species.

All mounted sections were viewed under a Leica MZ-12 light microscope and representative images were taken at 8x and 100x for assessing muscle fiber direction, relative (percentage) connective tissue cross-sectional area, relative (percentage) muscle tissue cross-sectional area, relative (percentage) areas of the section occupied by pars marginalis and pars peripheralis fibers, ratios of pars marginalis fiber area to pars peripheralis fiber area, and relative dermal thickness. In order to assess fiber diameter between species, representative images were taken at 400x. All images were stored on a PC as TIF files.

Connective tissue: muscle tissue area ratios were calculated using the 100x images of sections stained with Gomori trichrome. Using Adobe Photoshop (Adobe Systems, Inc.), muscle tissue in representative sections was selected based on color (variations of magenta) and converted to black in each image. The total "black" area in each image was calculated using Scion Image (Scion Corp.) and reported as a percentage of the total area of the image. This area was calculated in Scion Image. The reported areas are an average of all samples. Relative areas of pars peripheralis and pars marginalis fibers were calculated using the 8x images. Using Adobe Photoshop, the regions occupied by the pars marginalis fibers and the pars peripheralis fibers were outlined with a black line. The area within these boundaries was calculated using Scion Image and these areas were reported as percentages of the entire cross-section. A total of 17 individual sections from chimpanzees and 14 individual sections from humans were sampled for this procedure.

In order to calculate fiber diameter, representative images of the pars marginalis and pars peripheralis layers from sections cut in the transverse plane were viewed at 400x. In order to take the measurements, representative muscle fascicles were chosen that had a clear perimysium encasing all muscle fibers with care taken to avoid fragmented fascicles. Every fiber in each fascicle was measured for maximum diameter. For fibers that were oriented obliquely, minimum diameter was instead measured (Dubowitz, 1985). In humans, 26 fascicles were sampled from the five individuals. In chimpanzees, 18 fascicles were sampled from the three individual specimens. All diameters were obtained using Scion Image.

In order to measure dermal thickness, representative sections from each species were photographed at 8x, stored on a PC as TIF files, and were measured using Scion Image. Each photograph was measured at three different locations: the two lateral-most edges of the section and the mid-line. The maximum thickness of the dermis at each of these locations was measured as well as the maximum thickness of the muscle layers (see Fig. 3). These values were then used to create ratios of dermal thickness to muscle thickness and an average ratio was then calculated for each species. For this procedure, 33 sections were measured from chimpanzees and 17 sections from humans.

Means of pars peripheralis area to pars marginalis area, fiber diameters, total muscle fiber thickness, total dermal thickness, and dermis area to muscle tissue area were compared between

species using a Student's t-test for independent measures. Means of connective tissue:muscle fiber area ratios, pars peripheralis segment area percentage, and pars marginalis segment area percentage were compared between species using a Kolmogorov-Smirnov test as percentages are typically not normally distributed (Sokal & Rohlf, 1995). All differences were considered to be statistically significant if $p < 0.05$.

Results

Figure 2 shows representative transverse sections through the upper fibers of the OOM in humans and chimpanzees. In agreement with previous studies (Delaire & Precious, 1986; Mooney et al., 1988), the human OOM upper fibers clearly show transverse, oblique, and longitudinal fibers. Transverse fibers typically appeared to be most numerous in the pars peripheralis segment while the longitudinal fibers typically appeared to be more evenly distributed between the pars marginalis and pars peripheralis segments. In both species the pars peripheralis segment typically was more densely packed with muscle fibers than the pars marginalis segment and typically appeared to have roughly equal proportions of longitudinal and transverse fibers. Unlike a previous study by Latham & Deaton (1976), no human section in the present study appeared to show a paucity of any kind of muscle fiber in the mid-line region, near the location of the philtrum. This is in agreement, though, with results from Briedis & Jackson (1980) and Namnoun et al. (1997). No representation of the SMAS was found in either humans or chimpanzees from the sampled areas. This is in agreement with previous reports of the anterior limits of this structure in humans and other non-human primates (Thaller et al., 1990).

The chimpanzee upper OOM has a clear, anteriorly located set of fibers that resemble the pars marginalis segment described for humans (Fig. 2), contrary to descriptions from previous studies (Sonntag, 1923; Lightoller, 1925; Pellatt, 1979). This pars marginalis layer typically contained all three fiber-direction types as in humans. The transverse fibers appear to be common in the peripheralis segment as in humans, but these fibers were also typically heavily deposited in the marginalis segment. Both oblique and longitudinal fibers typically appeared to be most common in the pars peripheralis segment but the pars marginalis segment also had densely packed fascicles of longitudinal fibers. The pars peripheralis segment was typically characterized by densely-packed fascicles with roughly equal proportions of longitudinal and transverse fibers. Similar to the human, the chimpanzee pars marginalis segment had scant muscle fibers relative to the pars peripheralis segment, but the chimpanzee pars marginalis segment appeared to be far more densely packed than in humans.

Calculations of average relative cross-sectional muscle area are shown in Table 1. These calculations reveal that chimpanzees had significantly ($p < 0.05$) more average relative cross-sectional muscle area in the OOM (nearly 30% of the total area of the section) than humans (roughly 20%). While there was no significant difference ($p > 0.05$) between the species in relative area of the pars peripheralis or pars marginalis areas, the mean ratio of pars peripheralis to pars marginalis fiber area was significantly higher in chimpanzees (1.866) than in humans (1.438). Fiber diameter measurements in both species revealed that chimpanzees have significantly ($p < 0.05$) wider muscle fibers than humans in both pars peripheralis and pars marginalis segments (Table 1 and Figs. 2 and 3).

Calculations of total muscle fiber thickness revealed that chimpanzees have significantly greater muscle fiber thickness than humans (over 50% greater). However, humans have significantly greater dermal tissue thickness than chimpanzees and a significantly greater dermis area to muscle tissue area ratio than chimpanzees (Table 1, Fig. 2).

Discussion

A previous study (Burrows et al., 2006) demonstrated great similarity at the gross anatomical level in the OOM between chimpanzees and humans. In the present study there are also clear similarities at the microanatomical level. A distinct, separate pars marginalis layer was demonstrated in the present study, contrary to previous reports that it is present only in humans, being missing (Sonntag, 1923) or “incompletely formed” in chimpanzees (Lightoller, 1925).

The development of separate pars marginalis and pars peripheralis segments is well known in humans (e.g., Standring, 2004) but has not been described in non-human primates. Lightoller (1928) described incompletely separated pars marginalis and pars peripheralis segments in orangutans, a baboon, and a rhesus macaque (*Macaca mulatta*), similar to his description of a chimpanzee (1925). More recently, Docherty et al. (2008) described a similar arrangement of the upper OOM in a microanatomical study of *Macaca mulatta* upper lips. Pars marginalis and peripheralis layers were discernible but there was an irregular boundary between the layers. Yet these authors found no indication at all of distinct pars marginalis and pars peripheralis segments in the upper OOM of the greater bushbaby *Otolemur garnettii*. The evolutionary and adaptive importance of the development of two separate marginalis and peripheralis segments in primates is still unclear as we only have data from a few species. However, the absence of two separate layers in *O. garnettii*, the “incomplete” state in *M. mulatta* (Lightoller, 1928; Docherty et al., 2008) along with the appearance of distinct separate layers in chimpanzees and humans may indicate that the development of separate pars marginalis and pars peripheralis layers is a relatively recent development in the primate OOM and is a derived character of the OOM in certain primate taxa (e.g., hominoids).

Results of comparing relative cross-sectional area of muscle versus cross-sectional area of connective tissue and fiber diameters between the species may reflect the divergent function of the upper lip in chimpanzees and humans. Chimpanzees had a significantly lower ratio of cross-sectional connective tissue area vs. cross-sectional muscle area in the sampled section of the upper OOM than humans. Similarly, chimpanzees had average fiber diameters that were roughly three times greater than humans. While the “gold standard” in determining potential contractile force of any given muscle is physiological cross-sectional area (PCSA) and muscle fiber length (e.g., Anapol & Jungers, 1986; Antón, 1999; Anapol & Gray, 2003; Taylor & Vinyard, 2004), the methodologies for gathering these measurements are not possible with primate mimetic muscles due to their attachments into one another. Connective tissue:muscle tissue area ratio gives information on the percentage of a sampled section that is occupied by muscle tissue vs. connective tissue. Fiber diameter gives a morphological indicator of the relative number of myofibrils packaged in any given muscle fiber (Gans, 1982; Otten, 1988; van Wassenbergh et al., 2007). Thus, we can make some very cautious and preliminary inferences on how these muscles may be used in each species. While critical data on potential contractile force, such as PCSA and muscle fiber length, are not available, the findings here suggest that chimpanzees have an upper OOM that can generate greater muscle force in the mid-line aspect relative to humans.

Both chimpanzees and humans use movements of the upper lip in their facial display repertoires and in modification of vocalizations (van Hooff, 1973; Abbs et al., 1984; Goodall, 1986; Parr et al., 1998; Parr & de Waal, 1999; Schmidt & Cohn, 2001; Parr, 2003; Ito et al., 2004; Vick et al., 2007) with an obvious difference being the development of human speech. Chimpanzees use their lips in a variety of vocalizations such as “lip smacking”, “sputtering”, and in the “pant-hoot” (Goodall, 1986; Nishida et al., 1999, 2004). However, the movements of the upper lip accompanying production of these sounds are described as being large-scale in nature, not subtle, fine, and discrete movement that often characterizes movement of the upper lip in human speech (e.g., Standring, 2004; Raphael et al., 2007). Humans use the lips as part of the

supralaryngeal vocal tract (along with the tongue and soft palate) in modifying speech sounds and in aiding the visual perception of speech (Titze, 1994; Lieberman, 2007; Raphael et al., 2007). Human speech involves both vowel and consonant production. While most of the ability to generate vowel sounds involves movement of the tongue, movements of the upper lip are necessary for generating labial consonant sounds (Titze, 1994; Raphael, 2007). Additionally, the ability to change the shape of the upper lip provides not only some of the visual impacts associated with accurate perception of speech but it also affects the resonance properties of the supralaryngeal vocal tract and provides articulation of speech sounds (McGurk & MacDonald, 1976; Rastatter & DeJarnette, 1984; Titze, 1994; Regalo et al., 2005; Caviness et al., 2006; Raphael et al., 2007). The movements of the human upper lip involved in these speech activities do not involve a great contractile force from the upper OOM but use only a small fraction of the force available (Rastatter & DeJarnette, 1984; Barlow & Muller, 1991; Hinton & Arokiasamy, 1997; Regalo et al., 2005). Clearly position of the tongue and larynx is of prime importance to the evolution of human speech (e.g., Lieberman et al., 2000; Nishimura et al., 2003) but movements of the lip are important in modification of human speech sounds.

While the human upper lip seems to be specialized for activities that involve fine and discrete movements used in speech, chimpanzees differ markedly in their use of the upper lip as a prehensile tool in a number of activities. In grooming the lips are used to pluck objects from the hair/skin of the individual being groomed, which may occur many times throughout the day (Goodall, 1986; Nakamura, 2003). Chimpanzees use their prehensile lips in tool use/modification, where it can be used to fracture sticks, strip leaves, etc. (Whiten et al., 1999; Whiten & Boesch, 2001; Sanz & Morgan, 2007) and they use them in feeding contexts. While percentages vary among populations, fruit-feeding generally makes up a large percentage of chimpanzee diets (Wrangham et al., 1993, 1994). In order to consume the fruit pulp individuals must treat the seed(s) in some fashion. Individual chimpanzees may remove the seed from the pulp via a behavior known as “wadging”. Here, the entire fruit is put into the mouth and manipulated with the lips against the lower incisors to extract fruit juice and pulp. The seed is then extracted from the mouth using the lips and spat out (Goodall, 1986; Lambert, 1999). Such an activity of pressing the lips against the dentition is characteristic of the function of the human *pars marginalis* and may be accomplished in the chimpanzee similarly.

While chimpanzees had relatively more muscle per cross-sectional area and greater muscle fiber diameter, humans had a significantly thicker dermis. In the uniquely everted human lips, the dermis gives the lips a structurally plump, “full” appearance (Standring, 2004). As such, the relatively greater thickness of the dermal layer in humans relative to chimpanzees may be a mechanism for drawing attention to the lips, both during facial displays and in speech where the lips are used in audio-visual speech recognition (McGurk & MacDonald, 1976; Calvert & Campbell, 2003; Schwartz et al., 2004; Burrows, 2008). Moreover, the plump, everted appearance of the human lips has been associated with both male and female evaluations of physical attractiveness of the opposite sex (Jones 1999; Gangstead & Scheyd, 2005). The increased thickness of the dermis associated with the upper lip in humans may, then, be associated with the need to quickly locate the lips and attend to them in facial display contexts, during speaking bouts and in evaluation of potential mate quality.

Conclusions

Human and chimpanzee lips have diverged evolutionarily from one another. Human lips seem to be specialized for functions associated with the unique vocal communication mode of speech as well as for attracting visual attention. Chimpanzee lips seem to be specialized for functions associated with a prehensile structure such as tool modification and feeding via “wadging”. A more complete understanding of how the OOM functions in these species and the factors involved in evolutionary divergence of the OOM and the upper lip will necessitate examination

of a much broader phylogenetic range of species as well as studies that focus on characteristics of the facial nerve and on the histochemical characteristics of the OOM.

Acknowledgements

This study was supported by NIH grants RO1-DE016148 and P50-DE016215. We wish to thank Seth Dobson, Iain Matthews, and Karen Schmidt for helpful comments on various stages of this manuscript. We also wish to thank the anonymous reviewers and the receiving editor, Prof. Dan Lieberman, whose comments greatly improved the quality of this manuscript.

References

- Abbs JH, Gracco VL, Blair C. Functional muscle partitioning during voluntary movement: facial muscle activity for speech. *Exp Neurol* 1984;85:469–479. [PubMed: 6468573]
- Anapol F, Barry K. Fiber architecture of the extensors of the hindlimb in semiterrestrial and arboreal guenons. *Am J Phys Anthropol* 1996;99:429–447. [PubMed: 8850183]
- Anapol FC, Gray JP. Fiber architecture of the intrinsic muscles of the shoulder and arm in semiterrestrial and arboreal guenons. *Am J Phys Anthropol* 2003;122:51–65. [PubMed: 12923904]
- Anapol FC, Jungers WL. Architectural and histochemical diversity within the quadriceps femoris of the brown lemur (*Lemur fulvus*). *Am J Phys Anthropol* 1986;69:355–375. [PubMed: 3706515]
- Antón SC. Macaque masseter muscle: internal architecture, fiber length and cross-sectional area. *Int J Primatol* 1999;20:441–462.
- Antón SC. Macaque pterygoid muscle: internal architecture, fiber length and cross-sectional area. *Int J Primatol* 2000;21:131–156.
- Bard KA. Development of emotion expressions in chimpanzees (*Pan troglodytes*). *Ann NY Acad Sci* 2003;1000:88–90. [PubMed: 14766622]
- Barlow SM, Muller EM. The relationship between interangle span and in vivo resultant force in the perioral musculature. *J Speech Lang Hear Res* 1991;34:252–259.
- Briedis J, Jackson IT. The anatomy of the philtrum: observations made on dissections in the normal lip. *Br J Plast Surg* 1980;34:128–132. [PubMed: 7236966]
- Burrows AM. The facial expression musculature in primates and its evolutionary significance. *BioEssays* 2008;30:212–225. [PubMed: 18293360]
- Burrows AM, Smith TD. Muscles of facial expression in *Otolemur*, with a comparison to Lemuroidea. *Anat Rec* 2003;274A:827–836.
- Burrows AM, Waller BM, Parr LA, Bonar CJ. Muscles of facial expression in the chimpanzee (*Pan troglodytes*): descriptive, comparative and phylogenetic contexts. *J Anat* 2006;208:153–167. [PubMed: 16441560]
- Calvert GA, Campbell R. Reading speech from still and moving faces: the neural substrates of visible speech. *J Cogn Neurosci* 2003;15:57–70. [PubMed: 12590843]
- Caviness JN, Liss JM, Adler C, Evidente V. Analysis of high-frequency electroencephalographic-electromyographic coherence elicited by speech and oral nonspeech tasks in Parkinson's disease. *J Speech Lang Hear Res* 2006;49:424–438. [PubMed: 16671854]
- Chen FC, Li WH. Genomic divergences between humans and other hominoids and the effective population size of the common ancestor of humans and chimpanzees. *Am J Hum Genet* 2001;68:444–456. [PubMed: 11170892]
- Darwin, CR. *The Expression of Emotions in Man and Animals*. London: J Murray; 1872.
- Delaire J, Precious D. Influence of the nasal septum on maxillonasal growth in patients with congenital labiomaxillary cleft. *Cleft Pal J* 1986;23:270–277.
- Diogo R. Muscles versus bones: catfishes as a case study for an analysis on the contribution of mycological and osteological structures in phylogenetic reconstructions. *Anim Biol* 2004;54:373–391.
- Docherty BA, Cray JJ Jr, Smith TD, Reinholt LE, Burrows AM. Comparative microanatomy of primate facial musculature: facing up to function. *Am J Phys Anthropol Suppl* 2008;46:91.
- Dubowitz, V. *Muscle Biopsy: A Practical Approach*. 2. London: Bailliere Tindall Press; 1985.

- van Eijden TMGJ, Koolstra JH, Brugman P. Three-dimensional structure of the human temporalis muscle. *Anat Rec* 1996;246:565–572. [PubMed: 8955797]
- Ekman P, Oster H. Facial expression of emotion. *Ann Rev Psych* 1979;20:527–554.
- Gangstead SW, Scheyd GJ. The evolution of human physical attractiveness. *Annu Rev Anthropol* 2005;34:523–548.
- Gans C. Fiber architecture and muscle function. *Exercise Sport Sci Rev* 1982;10:160–207.
- Gasser RF. The development of the facial muscles in man. *Am J Anat* 1967;120:357–376.
- Ghassemi A, Prescher A, Riediger D, Axer H. Anatomy of the SMAS revisited. *Aesth Plast Surg* 2003;27:258–264.
- Gibbs S, Collard M, Wood B. Soft-tissue anatomy of the extant hominoids: a review and phylogenetic analysis. *J Anat* 2002;200:3–49. [PubMed: 11833653]
- Goodall, J. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge: Harvard University Press; 1986.
- Goodmurphy CW, Ovalle WK. Morphological study of two human facial muscles: orbicularis oculi and corrugator supercilii. *Clin Anat* 1999;12:1–11. [PubMed: 9890723]
- Groves, C. *Primate Taxonomy*. Washington, DC: Smithsonian Institution; 2001.
- Herring SW, Grimm AF, Grimm BR. Regulation of sarcomere number in skeletal muscle: a comparison of hypotheses. *Muscle Nerve* 1984;7:161–173. [PubMed: 6717493]
- Hinton VA, Arokiasamy WMC. Maximum interlabial pressures in normal speakers. *J Speech Lang Hear Res* 1997;40:400–404. [PubMed: 9130207]
- van Hooff, JARAM. A structural analysis of the social behaviour in a semi-captive group of chimpanzees. In: Hinde, RA., editor. *Nonverbal Communication*. Cambridge: Cambridge University Press; 1973. p. 209-241.
- Hopkins WD, Bard KA, Jones A, Bales S. Chimpanzee hand preference for throwing and infant cradling: implications for the origin of human handedness. *Curr Anthropol* 1993;34:786–790.
- Huber, E. *Evolution of Facial Musculature and Expression*. Baltimore: The Johns Hopkins University Press; 1931.
- Hwang K, Kim DJ, Hwang SH. Immunohistochemical study of differences between the muscle fiber types in the pars peripheralis and marginalis. *J Craniofac Surg* 2007a;18:591–593. [PubMed: 17538323]
- Hwang K, Kim DJ, Hwang SH. Musculature of the pars marginalis of the upper orbicularis oris muscle. *J Craniofac Surg* 2007b;18:151–154. [PubMed: 17251855]
- Ito T, Murano EZ, Gomi H. Fast force-generation dynamics of human articular muscles. *J Appl Physiol* 2004;96:2318–2324. [PubMed: 14990556]
- Jacinto-Gonçalves SR, Gavio MB, de Oliveira AS, Semeguini TA. Electromyographic activity of perioral muscle in breastfed and non-breastfed children. *J Clin Pediatr Dent* 2004;29:57–62. [PubMed: 15554405]
- Jones D. An evolutionary perspective on physical attractiveness. *Evol Anthropol* 1999;5:97–109.
- Kraus, BS.; Kitamura, H.; Latham, RA. *Atlas of Developmental Anatomy of the Face*. New York: Harper & Row, Publishers; 1966.
- Lambert JE. Seed handling in chimpanzees (*Pan troglodytes*) and redtail monkeys (*Cercopithecus ascanius*): Implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. *Am J Phys Anthropol* 1999;109:365–386. [PubMed: 10407465]
- Larrabee, WF., Jr; Makielski, KH. *Surgical Anatomy of the Face*. New York: Raven Press; 1993.
- Latham RA, Deaton TG. The structural basis of the philtrum and the contour of the vermilion border: a study of the musculature of the upper lip. *J Anat* 1976;121:151–160. [PubMed: 1254526]
- Lieberman P. The evolution of human speech. *Curr Anthropol* 2007;48:39–66.
- Lightoller GS. Facial muscles: The modiolus and muscles surrounding the rima oris with some remarks about the panniculus adiposus. *J Anat* 1925;60(part 1):1–85. [PubMed: 17104082]
- Lightoller GS. The facial muscles of three orang utans and two cercopithecidae. *J Anat* 1928;63:19–81. [PubMed: 17104211]

- McGurk H, MacDonald J. Hearing lips and seeing voices. *Nature* 1976;264:746–748. [PubMed: 1012311]
- Mooney MP, Siegel MI, Kimes KR, Todhunter J. Development of the orbicularis oris muscle in normal and cleft lip and palate human fetuses using three-dimensional computer reconstruction. *Plast Reconstr Surg* 1988;81:336–345. [PubMed: 3277211]
- Nakamura M. ‘Gatherings’ of social grooming among wild chimpanzees: implications for evolution of sociality. *J Hum Evol* 2003;44:59–71. [PubMed: 12604304]
- Namnoum JD, Hisley KC, Graepel S, Hutchins GN, Vander Kolk CA. Three-dimensional reconstruction of the human fetal philtrum. *Ann Plast Surg* 1997;38:202–208. [PubMed: 9088454]
- Nishida T, Kano T, Goodall J, McGrew W, Nakamura M. The ethogram and ethnography of Mahale chimpanzees. *Anthropol Sci* 1999;107:141–188.
- Nishida T, Mitani JC, Watts DP. Variable grooming behaviours in wild chimpanzees. *Folia Primatol* 2004;75:31–36. [PubMed: 14716152]
- Nishimura T, Mikami A, Suzuki J, Matsuzawa T. Descent of the larynx in chimpanzee infants. *Proc Natl Acad Sci USA* 2003;100:6930–6933.
- Nishimura T, Mikami A, Suzuki J, Matsuzawa T. Descent of the hyoid in chimpanzees: evolution of face flattening and speech. *J Hum Evol* 2006;51:244–254. [PubMed: 16730049]
- O’Rahilly R, Müller F. The development of the neural crest in the human. *J Anat* 2007;211:335–351. [PubMed: 17848161]
- Oster, H. The repertoire of infant facial expressions: an ontogenetic perspective. In: Nadel, J.; Muir, D., editors. *Emotional Development: Recent Research Advances*. New York: Oxford University Press; 2004. p. 261–292.
- Otten E. Concepts and models of functional architecture in skeletal muscle. *Exercise Sport Sci Rev* 1988;16:89–137.
- Parr LA, Hopkins SD, de Waal FBM. The perception of facial expressions by chimpanzees, *Pan troglodytes*. *Evol Comm* 1998;2:1–23.
- Parr LA, de Waal FBM. Visual kin recognition in chimpanzees. *Nature* 1999;399:147–148.
- Parr LA. The discrimination of faces and their emotional content by chimpanzees (*Pan troglodytes*). *Ann NY Acad Sci* 2003;1000:56–78. [PubMed: 14766620]
- Patterson N, Richter DJ, Gnerre S, Lander ES, Reich D. Genetic evidence for complex speciation of humans and chimpanzees. *Nature* 2006;441:1103–1108. [PubMed: 16710306]
- Pellatt A. The facial muscles of three African primates, contrasted with those of *Papio ursinus*. *S Afr J Sci* 1979;75:436–440.
- Raphael, L.J.; Borden, G.J.; Harris, K.S. *Speech Science Primer: Physiology, Acoustics, and Perception of Speech*. 5. Philadelphia: Lippincott, Williams & Wilkins; 2007.
- Rastatter M, DeJarnette G. EMG activity with jaw fixed of orbicularis oris superior, orbicularis oris inferior and masseter muscles of articulatory disordered children. *Percept Motor Skills* 1984;58:191–196.
- Rastatter M, McGuire R, Blair B. EMG activity of orbicularis oris superior, orbicularis oris inferior, and masseter muscles of mild and moderate articulatory disordered children. *Percept Mot Skills* 1987;64:725–726. [PubMed: 3601595]
- Regalo SCH, Vitti M, Moraes MTB, et al. Electromyographic analysis of the orbicularis oris muscle in oralized deaf individuals. *Braz Dent J* 2005;16:237–242. [PubMed: 16429191]
- Rowlerson A, Raoul G, Daniel Y, et al. Fiber-type differences in masseter muscle associated with different morphologies. *Am J Orthod Dentofacial Orthop* 2005;127:37–46. [PubMed: 15643413]
- Sanz CM, Morgan DB. Chimpanzee tool technology in the Goulougo Triangle, Republic of Congo. *J Hum Evol* 2007;52:420–433. [PubMed: 17194468]
- Schmidt KL, Cohn JF. Human facial expressions as adaptations: evolutionary questions in facial expression research. *Yearb Phys Anthropol* 2001;44:3–24.
- Schwartz JL, Berthommier F, Savariaux C. Seeing to hear better: evidence for early audio-visual interactions in speech identification. *Cognition* 2004;93:B69–78. [PubMed: 15147940]
- Sokal, R.R.; Rohlf, F.J. *Biometry*. 3. New York: W.H. Freeman and Company; 1995.

- Sonntag CF. On the anatomy, physiology, and pathology of the chimpanzee. *Proc Zool Soc London* 1923;23:323–429.
- Standring, S. *Gray's Anatomy: The Anatomical Basis of Clinical Practice*. 39. London: Churchill Livingstone.; 2004.
- Tamura Y, Matsushita S, Shinoda K, Yoshida S. Development of perioral muscle activity during suckling in infants: a cross-sectional and follow-up study. *Dev Med Child Neurol* 1998;40:344–348. [PubMed: 9630263]
- Taylor AB, Jones KE, Kunwar R, Ravosa MJ. Dietary consistency and plasticity of masseter fiber architecture in postweaning rabbits. *Anat Rec* 2006;288:1105–1111.
- Taylor AB, Vinyard CJ. Comparative analysis of masseter fiber architecture in tree-gouging (*Callithrix jacchus*) and nongouging (*Saguinus oedipus*) callitrichids. *J Morphol* 2004;261:276–285. [PubMed: 15281057]
- Thaller SR, Kim S, Patterson H, Widman M, Daniller A. The submuscular aponeurotic system (SMAS): a histologic and comparative anatomy evaluation. *Plast Reconstr Surg* 1990;86:690–696. [PubMed: 2217583]
- The Chimpanzee Sequencing and Analysis Consortium. Initial sequence of the chimpanzee genome and comparison with the human genome. *Nature* 2005;437:69–87. [PubMed: 16136131]
- Titze, IR. *Principles of Voice Production*. Englewood Cliffs, NJ: Prentice-Hall; 1994.
- Tomasello M, Hare B, Lehmann H, Call J. Reliance on head versus eyes in the gaze following of great apes and human infants: the cooperative eye hypothesis. *J Hum Evol* 2007;52:314–320. [PubMed: 17140637]
- Vick SJ, Waller BM, Parr LA, Smith Pasqualini MC, Bard KA. A cross-species comparison of facial morphology and movement in humans and chimpanzees using the facial action coding system (FACS). *J Nonverb Behav* 2007;31:1–20.
- Waller BM, Dunbar RIM. Differential behavioural effects of silent bared teeth display and relaxed open mouth display in chimpanzees (*Pan troglodytes*). *Ethology* 2005;111:129–42.
- Waller BM, Parr LA, Gothard KM, Burrows AM, Vick SJ, Fuglevand AJ. Intramuscular electrical stimulation of facial muscles in the rhesus macaque. *Phys Beh* 2008;95:93–100.
- Waller BM, Vick SJ, Parr LA, et al. Intramuscular electrical stimulation of facial muscles in humans and chimpanzees: Duchenne revisited and extended. *Emotion* 2006;6:367–382. [PubMed: 16938079]
- van Wassenbergh S, Herrel A, Adriaens D, Aerts P. Interspecific variation in sternohyoideus muscle morphology in clariid catfishes: functional implications for suction feeding. *J Morphol* 2007;268:232–242. [PubMed: 17265443]
- Whiten A, Goodall J, McGrew WC, et al. Cultures in chimpanzees. *Nature* 1999;399:682–685. [PubMed: 10385119]
- Whiten A, Boesch C. The cultures of chimpanzees. *Sci Am* 2001;284:60–67. [PubMed: 11132425]
- Wrangham RW, Conklin NL, Etot G, et al. The value of figs to chimpanzees. *Int J Primatol* 1993;14:243–256.
- Wrangham RW, Chapman CA, Chapman LJ. Seed dispersal by forest chimpanzees in Uganda. *J Trop Ecol* 1994;10:355–368.
- Young, JZ. *The Life of Mammals*. Oxford: Clarendon Press; 1957.

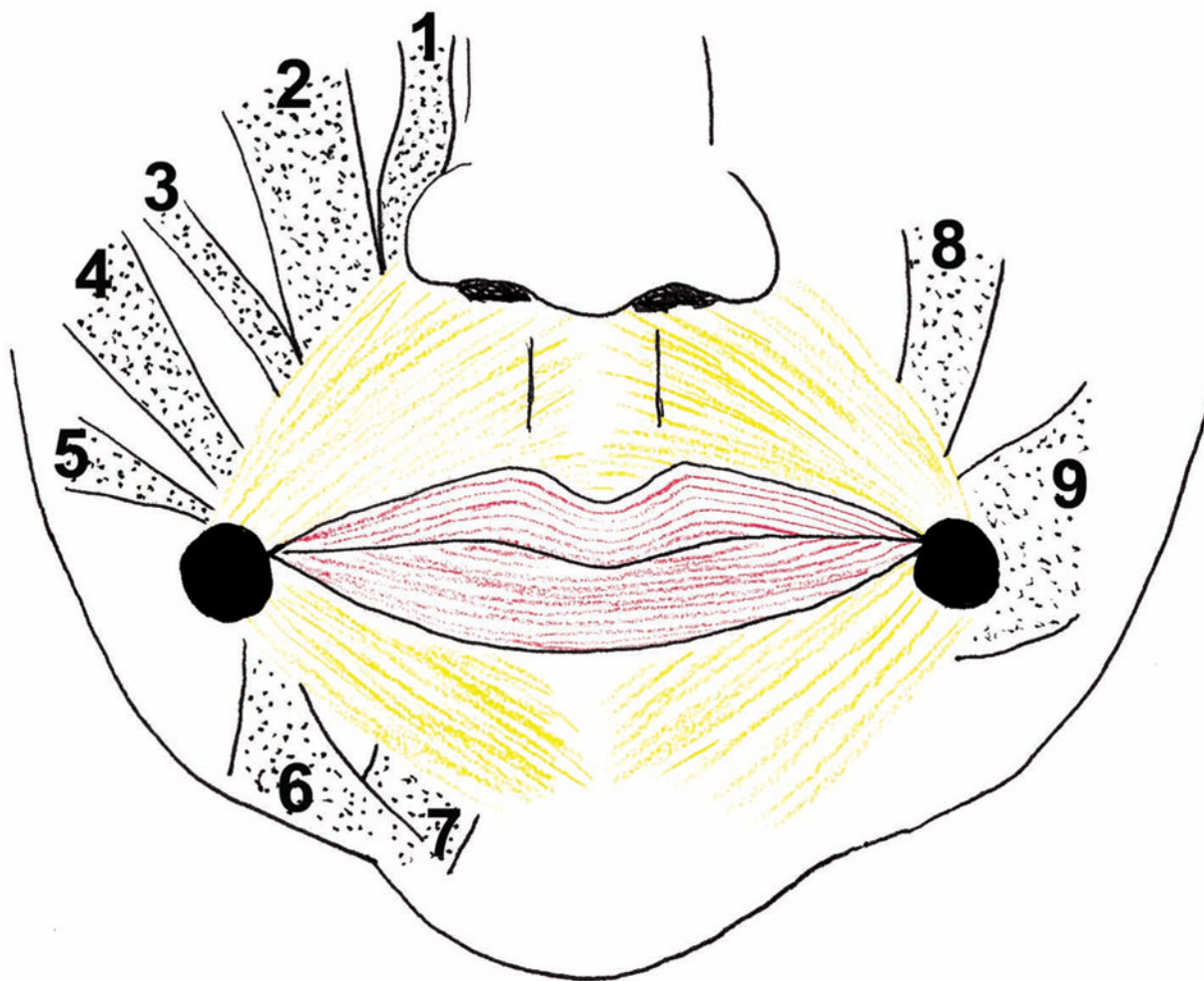


Figure 1. Schematic representation of the orbicularis oris muscle fibers in humans with their attachments (Lightoller, 1925; Standring, 2005). Fibers in yellow represent pars peripheralis (posteriorly located) and fibers in red represent pars marginalis (anteriorly located). Black circles at the corners of the mouth represent the modiolar region, where all eight segments of the OOM attach. On the right side, muscles in stipple represent superficially located mimetic muscles that attach to the peripheral fibers of the OOM. On the left side, muscles in stipple represent deeply located muscles that attach similarly to the OOM. 1 - levator labii alaeque nasi m.; 2 - levator labii superioris m.; 3 - zygomaticus minor m.; 4 - zygomaticus major m.; 5 - risorius m.; 6 - depressor anguli oris m.; 7 - depressor labii inferioris m.; 8 - levator anguli oris m.; 9 - buccinator m. Note that while the buccinator m. is not considered to be a “mimetic” muscle it is nevertheless attached to the OOM. Note that this figure does not show muscle fiber decussation in the philtral region as described by Latham & Deaton (1976) because there is considerable debate about this issue (see Briedis & Jackson, 1980; Nammoun et al., 1997). In this figure, the area in the mid-line of the upper lip where yellow fibers are depauperate would represent the area of decussation in the view of Latham & Deaton (1976).

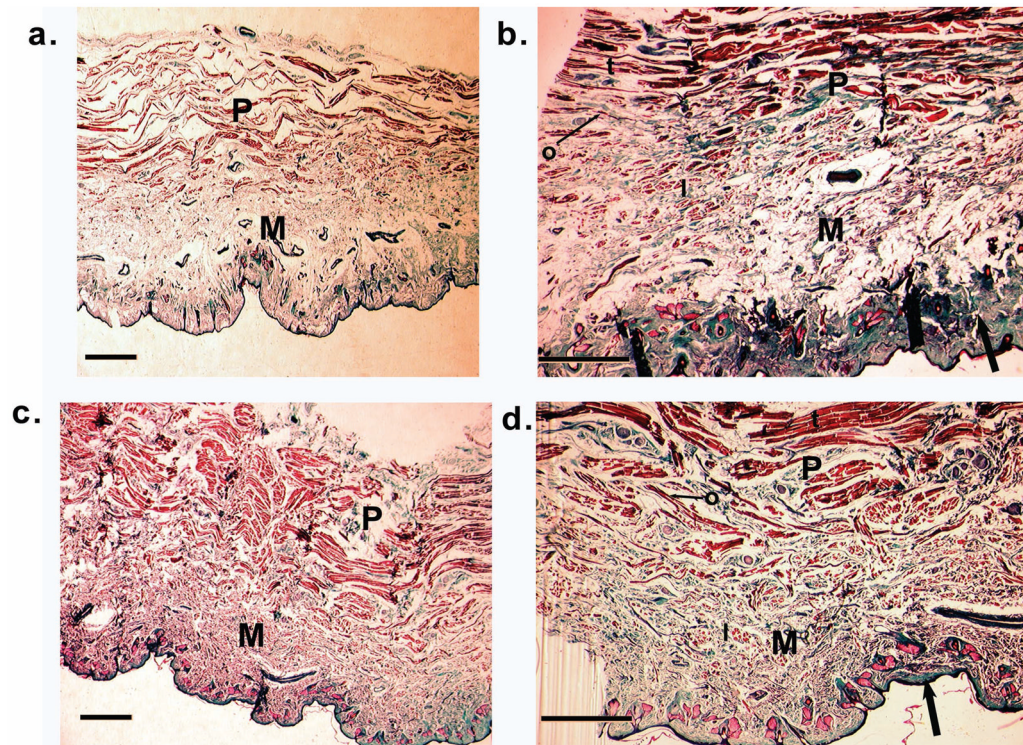


Figure 2. Representative images of the upper fibers of the OOM (transverse sections) in a.) and b.) a human and c.) and d.) a chimpanzee. Images from the left side of the figure were taken at 10x and images from the right were taken at 20x (scale bars represent 1mm). “M” stands for pars marginalis layer and “P” stands for pars peripheralis layer. Note that the chimpanzee has a distinct marginalis layer, contrary to previous reports (Lightoller, 1925; Standring, 2004). “t” stands for transversely oriented fibers, “o” stands for obliquely oriented fibers, and “l” stands for longitudinally oriented fibers. In b.) and d.) the arrow represents the dermal layer, stained teal. Note the thicker dermal area in humans and the denser populations of muscle fibers in the chimpanzee. In all images the epidermis/dermis is located at the bottom of the section.

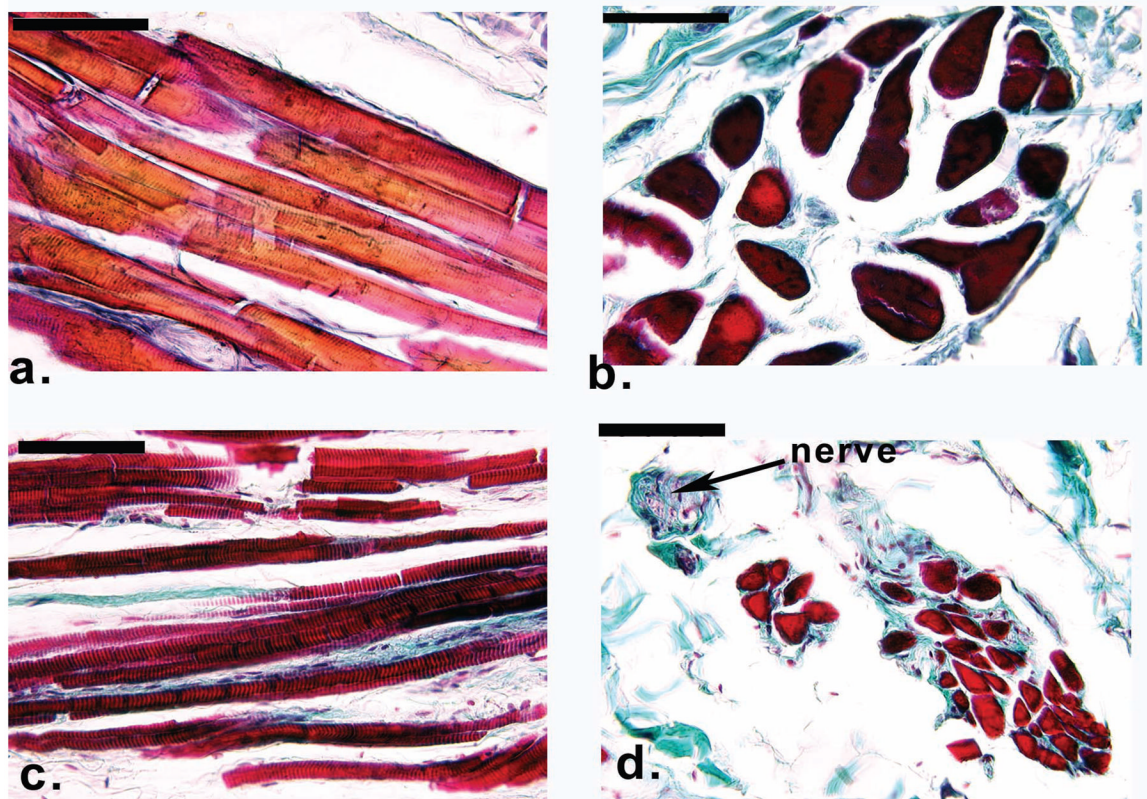


Figure 3. Representative images of fiber diameters from the upper fibers of the OOM in (top row) chimpanzees and (bottom row) humans. Images from the left side of the figure are longitudinally oriented fibers. Images from the right side of the figure are transversely oriented fibers (from which fiber diameter measurements were taken). Scale bars represent 5 microns.

Table 1
Microanatomical characteristics of the OOM in chimpanzees and humans[/]

Measure	Species	
	Human (+SEM)	Chimpanzee (+SEM)
Muscle Area (%) [*]	21.51	29.39
Periphalis Area (%)	31.61	46.65
Marginalis Area (%)	18.17	27.07
Periphalis Area:Marginalis Area [*]	1.438	1.866
Fiber Diameter Periphalis Segment [*]	14.178 (0.664)	45.116 (1.144)
Fiber Diameter Marginalis Segment [*]	15.767 (0.665)	42.341 (0.761)
Fiber Diameter Periphalis Segment (oblique fibers) [*]	13.843 (0.987)	27.427 (0.949)
Fiber Diameter Marginalis Segment (oblique fibers) [*]	17.480 (1.056)	30.583 (1.154)
Total Muscle Thickness [*]	3.270 (0.165)	5.848 (0.110)
Total Dermal Thickness [*]	2.672 (0.137)	1.535 (0.081)
Connective Tissue:Muscle Fiber Area Ratio [*]	0.8449 (0.055)	0.2649 (0.014)

[/] Avg. fiber diameters in μm ; total muscle fiber thickness and total dermal thickness in millimeters; percentages tested with Kolmogorov-Smirnov goodness of fit test; all other measurements tested with Student's t-test for independent measures;

* – denotes statistical significance at $p < 0.05$ level.