Comparative microanatomy of the orbicularis oris muscle between chimpanzees and humans: evolutionary divergence of lip function

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Abstract

The orbicularis oris muscle 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. As the chimpanzee (*Pan troglodytes*) is the closest living relative of humans, a comparison of the orbicularis oris muscle between these species may increase our understanding of the morphological specializations related to the differing functional demands of their lips and the factors responsible for their divergent evolution. To this end, this study compares the microanatomy of the mid-line upper fibers of the orbicularis oris muscle between chimpanzees and humans. A mid-line portion of the orbicularis oris muscle was harvested from the 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, the relative fiber diameter and relative amount of muscle tissue (i.e. based on ratio of connective tissue area : muscle tissue area) 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 orbicularis oris muscle 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.

Key words chimpanzee; evolution; histomorphometrics; lips; orbicularis oris; speech; wadging.

Introduction

The orbicularis oris muscle (OOM) is one of the mimetic, or facial expression, muscles that 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 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 & Makielski, 1993; Ghassemi et al. 2003). Like all mimetic muscles, the OOM is branchiomeric in origin, derived from the second (hyoid) branchial arch and is innervated by the facial nerve (Young, 1957; O'Rahilly & Müller, 2007). Although 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) described 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, whereas the anteriorly located pars marginalis segment is described as only having horizontal fibers (Kraus et al. 1966; Delaire & Precious, 1986; Mooney et al. 1988).

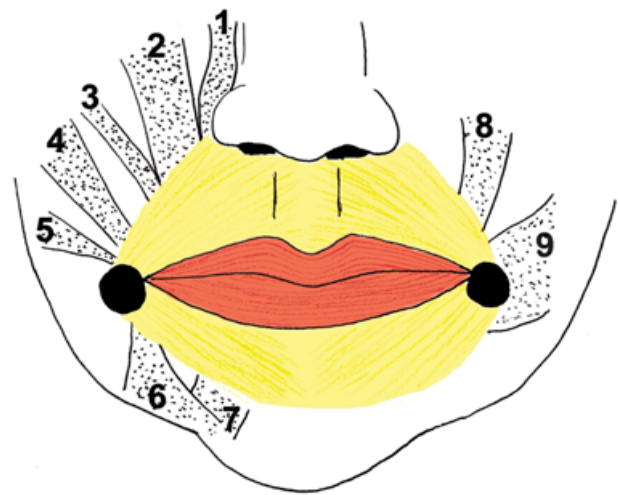Contraction of the pars peripheralis fibers in humans positions the lip in labial elevation, an action involved in

Fig. 1 Schematic representation of the OOM fibers in humans with their attachments (Lightoller, 1925; Standring, 2004). Yellow fibers represent the pars peripheralis (posteriorly located) and red fibers represent the 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 the stippled area represent superficially located mimetic muscles that attach to the peripheral fibers of the OOM. On the left side, muscles in the stippled area represent deeply located muscles that attach similarly to the OOM. 1, levator labii alaeque nasi muscle; 2, levator labii superioris muscle; 3, zygomaticus minor muscle; 4, zygomaticus major muscle; 5, risorius muscle; 6, depressor anguli oris muscle; 7, depressor labii inferioris muscle; 8, levator anguli oris muscle; 9, buccinator muscle. Note that, although the buccinator muscle 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; Namnoum 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).

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 also assist in our understanding of how the OOM functions in both species in terms of their unique social behaviors, communication mechanisms and feeding behavior.

Although our knowledge of the human OOM is not 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 the 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. Although 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 was 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 and 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, USA) and the third (a juvenile male) was obtained from the Southwest Foundation for BioMedical Research (San Antonio, TX, USA). The upper lips were excised as single, intact blocks approximately 1 cm 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 that 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, USA) 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.

Immediately after 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). Other mimetic muscles attach into the upper OOM lateral to the nasal alar cartilages in both species (Standring, 2004; Burrows et al. 2006). Thus, isolation of the OOM from these other muscles would be unlikely. Although 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 a full representation of fibers (Briedis & 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 a sampling of both 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 μm with cuts perpendicular to the epidermis. Approximately every fifth section was mounted and stained with either hematoxylin and eosin or 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 the 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). Although the PCSA and fiber length are considered to be 'gold standard' estimates of the 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 be reliably separated from their dermal attachments (Huber, 1931; Standring, 2004; Burrows et al. 2006; Burrows, 2008). Additionally, most of these muscles, especially the OOM, are attached intimately to one another so that they cannot be isolated for examination (Larrabee & Makielski, 1993; Standring, 2004). Thus, estimates of the 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 the PCSA and fiber length.

The greater 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). Although information from the PCSA and fiber length would provide the best estimate of potential contractile force, we may gain an estimate by calculating the cross-sectional connective tissue area vs. cross-sectional muscle tissue area. Fiber diameter is an additional way of estimating the potential contractile force of any given muscle (Goodmurphy & Ovalle, 1999; Rowlerson 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 light microscope (MZ-12, Leica) and representative images were taken at 8× and 100× to assess the 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. Representative images were taken at 400× in order to assess fiber diameter between species. All images were stored on a PC as TIF files.

The connective tissue : muscle tissue area ratios were calculated using the 100× 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. The relative areas of pars peripheralis and pars marginalis fibers were calculated using the 8× images. Using Adobe Photoshop, the regions occupied by the pars marginalis fibers and 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 the fiber diameter, representative images of the pars marginalis and pars peripheralis layers from sections cut in the transverse plane were viewed at 400×. In order to take the measurements, representative muscle fascicles that had a clear perimysium encasing all muscle fibers were chosen 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 measured instead (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 the dermal thickness, representative sections from each species were photographed at 8×, stored on a PC as TIF files and measured using Scion Image. Each photograph was measured at three different locations, i.e. 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 : 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.

Ratio of pars peripheralis area : pars marginalis area, fiber diameters, total muscle fiber thickness, total dermal thickness and ratio of dermis area : 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

Fig. 2 Representative images of the upper fibers of the OOM (transverse sections) in (a and b) a human and (c and d) a chimpanzee. (a and c) Images taken at 10×. (b and d) Images taken at 20×. Scale bars, 1 mm. M, pars marginalis layer; P, pars peripheralis layer. Note that the chimpanzee has a distinct marginalis layer, contrary to previous reports (Lightoller, 1925; Standring, 2004). T, transversely oriented fibers; o, obliquely oriented fibers; l, 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.
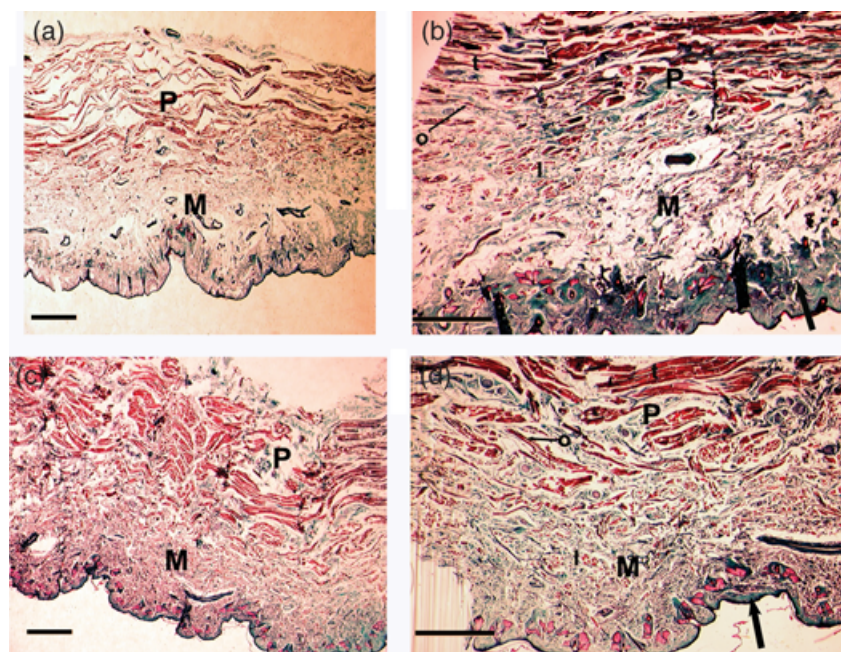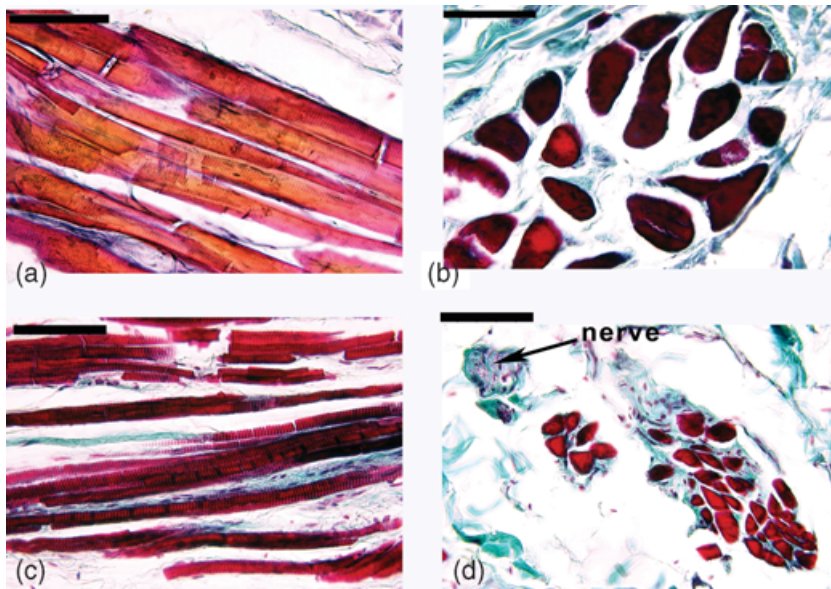
Fig. 3 Representative images of fiber diameters from the upper fibers of the OOM in (a and b) chimpanzees and (c and d) humans. (a and c) Longitudinally oriented fibers. (b and d) Transversely oriented fibers (from which fiber diameter measurements were taken). Scale bar, 5 μm.

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, whereas 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 was typically 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. However, this is in agreement with results from Briedis & Jackson (1980) and Namnoum et al. (1997). No representation of the superficial musculoaponeurotic system 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 had 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 appeared 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 revealed 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 (approx. 20%). Although 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 : 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 had 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 had significantly greater muscle fiber thickness than humans (> 50% greater). However, humans had significantly greater dermal tissue thickness than chimpanzees and a significantly greater dermis area : muscle tissue area ratio than chimpanzees (Table 1, Fig. 2).

Table 1 Microanatomical characteristics of the OOM in chimpanzees and humans*

Measure	Species	
	Human (+ SEM)	Chimpanzee (+ SEM)
Muscle area (%)†	21.51	29.39
Peripheralis area (%)	31.61	46.65
Marginalis area (%)	18.17	27.07
Peripheralis area : marginalis area ratio†	1.438	1.866
Fiber diameter: peripheralis segment†	14.178 (0.664)	45.116 (1.144)
Fiber diameter: marginalis segment†	15.767 (0.665)	42.341 (0.761)
Fiber diameter: peripheralis 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)

*Average fiber diameter (μm); total muscle fiber thickness and total dermal thickness (mm); percentages tested with Kolmogorov-Smirnov goodness-of-fit test. All other measurements tested with Student's t-test for independent measures.
†Statistical significance ($P < 0.05$).

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 (Lightoller, 1925). More recently, Docherty et al. (2008) described a similar arrangement of the upper OOM in a microanatomical study of *M. mulatta* upper lips. Pars marginalis and pars peripheralis layers were discernible but there was an irregular boundary between the layers. However, 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) and 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).

The results of comparing the relative cross-sectional area of muscle with the 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 : 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. Although the 'gold standard' in determining the potential contractile force of any given muscle is the 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. The 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. Although critical data on the potential contractile force, such as the 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 the 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. Although 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 et al. 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 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, the 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.

Although 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 they 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. Although 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 the 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 similarly accomplished in the chimpanzee.

Although 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 therefore 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 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.

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