



The influence of masseter and temporalis sarcomere length operating ranges as determined by laser diffraction on architectural estimates of muscle force and excursion in macaques (*Macaca fascicularis* and *Macaca mulatta*)

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ARTICLE INFO

Keywords:

Masseter
Temporalis
Sarcomere length
Fiber length
Macaque

ABSTRACT

Objective: Determine sarcomere length (L_s) operating ranges of the superficial masseter and temporalis *in vitro* in a macaque model and examine the impact of position-dependent variation on L_s and architectural estimates of muscle function (i.e., fiber length, PCSA) before and after L_s -normalization.

Design: Heads of adult *Macaca fascicularis* ($n = 4$) and *M. mulatta* ($n = 3$) were bisected postmortem. One side of the jaw was fixed in occlusion, the other in maximum gape. L_s was measured bilaterally using laser diffraction and these measurements were used to estimate sarcomere-length operating ranges. Differences in fiber length and PCSA between sides were tested for significance prior to and following L_s -normalization.

Results: Sarcomere-length operating ranges were widest for the anterior superficial masseter and narrowest for the posterior temporalis. Compared with other mammals, macaque operating ranges were wider and shifted to the right of the descending limb of a representative length-tension curve. Fibers were significantly stretched by as much as 100%, and PCSAs reduced by as much as 43%, on the maximally gaped compared with occluded sides. L_s -normalization substantially reduced position-dependent variance.

Conclusions: The superficial masseter ranges between 87–143% and the temporalis between 88–130% of optimal L_s from maximum gape to occlusion, indicating maximum relative L_s for these macaque muscles exceeds the upper end range previously reported for the jaw muscles of smaller mammals. The wider macaque operating ranges may be functionally linked to the propensity for facially prognathic primates to engage in agonistic canine display behaviors that require jaw-muscle stretch to facilitate production of wide jaw gapes.

1. Introduction

A theoretical tradeoff exists between force production and excursion in muscle based on the inverse relationship between a muscle's ability to generate force and the length of its fibers (Gans, 1982). In prior work, we have examined this potential tradeoff in several comparisons of primate jaw muscles, finding that some species exhibit this tradeoff (e.g., tree-gouging common marmosets; Taylor, Eng, Anapol, & Vinyard, 2009) while others do not (e.g., crab-eating macaques; Taylor & Vinyard, 2009; Terhune, Hylander, Vinyard, & Taylor, 2015). Multiple factors can potentially intervene to moderate this tradeoff such as increasing muscle weight, which increases a muscle's physiologic cross-sectional area (PCSA) and thus its force-generating capacity.

Another factor that impacts muscle force production is the lengths of constituent sarcomeres during contraction. Sarcomeres have the

capacity to shorten (concentric) and lengthen (eccentric) during muscle contraction; the range over which sarcomeres actively shorten and are lengthened within a muscle fiber characterizes the sarcomere-length operating range (L_s OR). It is well appreciated that changes in sarcomere length (L_s) impact the amount of force that a muscle can generate (Gordon, Huxley, & Julian, 1966; Podolsky & Shoenberg, 1983; Williams & Goldspink, 1978). The structural basis for the relationship between L_s and muscle force is described by the sarcomere length-tension (L-T) curve (Fig. 1). Every sarcomere has a length at which the magnitude of overlap between myosin and actin is optimal for producing force – the plateau region of the L-T curve (Fig. 1). When sarcomeres are lengthened beyond their optimal length during muscle stretch (the descending limb of the L-T curve), the overlap between actin and myosin filaments is decreased and muscle force diminishes (Fig. 1). If a muscle is sufficiently stretched to the point where no

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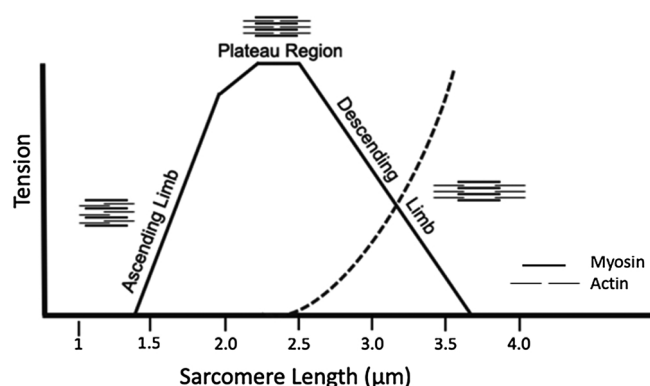


Fig. 1. Schematic of a representative sarcomere length-tension curve for skeletal muscle. Myosin (thick) and actin (thin) filaments show varying amounts of overlap in different regions of the length-tension curve. Tension diminishes as myofilament overlap increases (Ascending Limb) or decreases (Descending Limb) relative to the Plateau Region. Dotted line represents passive tension.

myosin cross-bridges can interact with actin filaments, no force can be generated. Stretch beyond the sarcomere operating range, whether via trauma or fatigue, can disrupt myofibril architecture (Fridén & Lieber, 1992; Lieber & Fridén, 1993). As sarcomeres shorten during muscle contraction, more cross-bridges are formed and active force increases until the plateau region is reached. With continued shortening (the ascending limb of the L-T curve), the actin filaments begin overlapping one another. This overlap impedes the formation of additional cross bridges, again diminishing muscle force production (Fig. 1). At sufficiently short lengths, the myosin filament reaches the z-disk, which prohibits any further shortening of the sarcomere. At this point, no more force can be generated. Thus, where sarcomeres (and by extension, muscle fibers) operate on the length-tension (L-T) curve has important implications for muscle function.

The influence of sarcomere length changes on muscle function during contraction leads to consideration of a problem frequently encountered in studies of muscle fiber architecture; namely, the variance that is introduced into architectural estimates of muscle force when joints are fixed in different positions. It is widely appreciated that joint position contributes significantly to variation in sarcomere and, by extension, fiber length in limb (Felder, Ward, & Lieber, 2005; Sacks & Roy, 1982; Williams & Goldspink, 1978) and jaw-closing (Nordstrom &

Yemm, 1972; Nordstrom, Bishop, & Yemm, 1974) muscles. Fixation of limbs in either flexed or extended positions results in shortened or lengthened muscles, depending on the muscle's position, and subsequent changes in fiber lengths (Felder et al., 2005; Nordstrom & Yemm, 1972; Williams & Goldspink, 1978). Because fiber length (L_f) is used in the equation to estimate muscle PCSA (Gans, 1982; Powell, Roy, Kanim, Bello, & Edgerton, 1984; Weber, 1851), and PCSA is proportional to a muscle's maximum force-generating capacity (Powell et al., 1984), positional variation impacting L_f necessarily impacts architectural estimates of muscle force. Moreover, stretch-related changes in fiber architecture have physiological consequences as they result in muscles operating on different portions of the L-T curve (e.g., Williams & Goldspink, 1978).

One way to minimize positional variation in fiber length within a given muscle across individuals is to select a similar joint position of interest either experimentally at the time of fixation (Anapol & Jungers, 1986; Felder et al., 2005; Sacks & Roy, 1982) or opportunistically in a comparative sample (Perry & Wall, 2008; Taylor & Vinyard, 2004). However, in practice, cadaveric specimens are often obtained from museums, zoological institutions and research centers, where fixation of cadavers in desired joint positions is generally not possible. In such instances, it is common practice to normalize fiber length estimates using a standard sarcomere length (L_s) to facilitate comparisons among individuals and species (Anapol & Barry, 1996; Anapol & Gray, 2003; Anapol, Shahnoor, & Gray, 2004; Anapol, Shahnoor, & Ross, 2008; Eng, Ward, Vinyard, & Taylor, 2009; Huq, Wall, & Taylor, 2015; Lieber & Blevins, 1989; Lieber & Fridén, 2001; Organ, Teaford, & Taylor, 2009; Taylor et al., 2009; Ward et al., 2006).

Variation in masseter and temporalis sarcomere lengths from occlusion to maximum mouth opening (jaw gape) has been documented in a handful of species (Table 1). However, we currently do not know the impact of this variation on jaw-adductor fiber architecture (e.g., fiber length, PCSA). To better understand this system, we report on estimates of L_s measured *in vitro* for the masseter and temporalis muscles in a moderately large-bodied, facially prognathic Old World monkey (*Macaca*) that generates relatively wide jaw gapes as a component of their social display behavior (Deputte, 1994). We then use these data to experimentally test the extent to which maximum jaw gape impacts sarcomere and fiber lengths and how these changes influence muscle force production. Finally, we quantitatively test the ability of L_s -normalization to effectively eliminate joint-angle dependent variation in fiber length in jaw adductors.

Table 1

Sarcomere length ranges reported for the masseter and temporalis muscles in various species.^a

Species	Muscle	L_s Min (μm)	L_s Max (μm)	Reference
Human	Masseter	1.90	4.80	van Eijden & Raadsheer, (1992)
Human	Temporalis	2.20	3.80	van Eijden & Raadsheer (1992)
Rabbit	Masseter	2.13	3.27	Weijts & Wielen-Drent (1983)
Rabbit	Temporalis	2.10	2.80	Weijts & van der Wielen-Drent (1982)
Rat	Anterior masseter	1.94	2.98	Nordstrom et al. (1974)
Rat	Posterior masseter	2.09	2.45	Nordstrom et al. (1974)
Rat	Temporalis	1.77	2.29	Nordstrom et al. (1974)
Common marmoset	Anterior superficial masseter	1.63	2.87	Eng et al. (2009)
Common marmoset	Posterior superficial masseter	1.63	1.73	Eng et al. (2009)
Common marmoset	Anterior temporalis	1.59	2.47	Eng et al. (2009)
Common marmoset	Middle temporalis	1.59	2.44	Eng et al. (2009)
Common marmoset	Posterior temporalis	1.59	2.29	Eng et al. (2009)
Cotton-top tamarin	Anterior superficial masseter	1.51	3.39	Eng et al. (2009)
Cotton-top tamarin	Posterior superficial masseter	1.51	1.92	Eng et al. (2009)
Cotton-top tamarin	Anterior temporalis	1.77	3.47	Eng et al. (2009)
Cotton-top tamarin	Middle temporalis	1.77	3.44	Eng et al. (2009)
Cotton-top tamarin	Posterior temporalis	1.77	2.67	Eng et al. (2009)

^a L_s minimum (Min) and maximum (Max) is measured at occlusion and a maximum linear jaw gape of 10.5 mm, respectively, in the rabbit, and at occlusion and a maximum linear jaw gape of 16.5 mm in the rat. L_s Min is measured at occlusion in the common marmoset and cotton-top tamarin and L_s Max is modeled in both species to a maximum active jaw gape of 24.2 mm. L_s Min in humans is measured from a Caucasian cadaveric sample with the jaws fixed in the mouth-closed position and an average interincisal distance of 4.2 mm; the L_s Max for human masseter and temporalis are modeled estimates.

2. Materials and methods

2.1. Samples

We took sarcomere and architectural measurements of the superficial masseter and temporalis muscles on four cadaveric adult female *Macaca fascicularis* (7.6–10.6 years; 3.0–4.4 kg) and three adult male *M. mulatta* (9.0–15.0 years; 9.1–12.0 kg). The heads were bisected post-mortem and one side of the jaw was fixed in centric occlusion while the other side was fixed in maximum jaw gape. All macaque cadavers were without obvious craniofacial or dental pathologies. No animals were sacrificed for purposes of this study.

2.2. Fiber architecture measurements

For each fixed specimen, the skin and overlying fascia were removed and the right and left masseter and temporalis muscles harvested en masse from the skull. Muscles were blotted dry, trimmed of fat and fascia and weighed to the nearest 1.0 g or 0.1 g depending on size. The deep and superficial portions of the masseter muscles were separated and the superficial masseter was used for analysis. Following previously published protocols (Anapol & Barry, 1996; Anapol & Jungers, 1986; Anapol et al., 2008; Taylor et al., 2009; Terhune et al., 2015) we separated the superficial masseter and temporalis muscles into anterior and posterior regions, and sectioned these muscle regions along their lengths, from superficial to deep (perpendicular to the plane of bony attachment), to prepare each region for *in situ* fiber length measurements (Fig. 2).

For each muscle region, we measured fiber length (L_f) as the distance between the proximal and distal myotendinous junctions (IMT to the superficial tendon; Fig. 2). We measured six adjacent fibers from each of two locations for a total of 12 fibers per muscle region and a maximum of 24 fibers per muscle. For each fiber, we measured the perpendicular distance (a) from the distal myotendinous junction (superficial tendon) to the central tendon (IMT; Fig. 2) and used this measurement to estimate pinnation angle. Care was taken to measure only intact, uncut fibers running from tendon attachment to tendon attachment and to ensure that L_f measurements were sampled from comparable sites from right and left sides of the skull and across specimens.

Upon completion of fiber length measurements, a small chunk of muscle was removed from each L_f sampling site and digested at room temperature in 30% HNO_3 to facilitate isolation of fiber bundles. Small fiber bundles then were manually separated under a dissecting stereomicroscope (Nikon SMZ 1500), mounted on glass slides and cover-slipped. We measured *in situ* sarcomere lengths ($\pm 0.01 \mu\text{m}$) directly from these measured fibers using laser diffraction (Lieber, Yeh, & Baskin, 1984) and normalized L_f of the measured fibers to a standardized L_s of $2.41 \mu\text{m}$.¹ Normalized L_f (NL_f) was computed as:

$$NL_f = L_f (2.41 \mu\text{m}/L_s).$$

We calculated average L_f and NL_f for the anterior and posterior superficial masseter and temporalis. We computed pinnation angle for both raw (L_f) and normalized (NL_f) fibers as the arcsine of $a/\text{fiber length}$. We estimated physiologic cross-sectional area (PCSA) for the

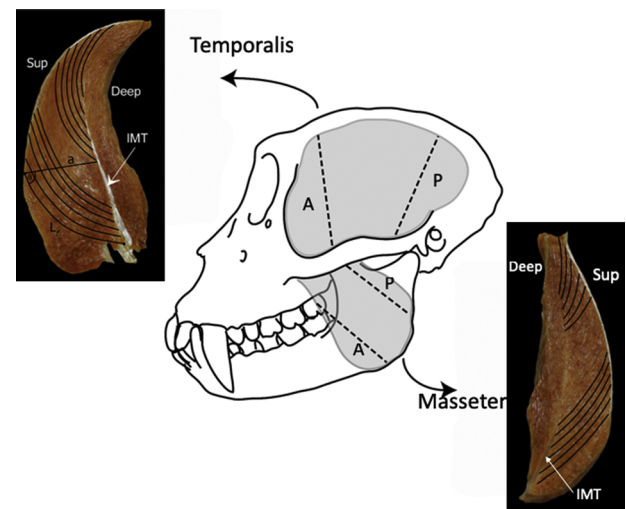


Fig. 2. Schematic of a male macaque skull (*M. fascicularis*). The gray-shaded areas represent the temporalis and masseter muscles *in situ*. Once removed en masse from the skull, each muscle was sectioned along its length into anterior and posterior regions (black hatched lines) for fiber length measurements. Cross sections of each muscle depict measurements taken at each section: L_f , fiber length; a , perpendicular distance from the intramuscular tendon [IMT] to the superficial tendon. Pinnation angle $[\theta]$ was computed as the arcsine of a/L_f .

superficial masseter and temporalis following Gans and Bock (1965) and Powell et al. (1984):

$$\text{PCSA} (\text{mm}^2) = \text{muscle mass} \times \cos(\theta) / L_f \times 1.0564 (\text{gm}/\text{cm}^3),$$

where 1.0564 is muscle-specific density (Murphy & Beardsley, 1974). We employed the same equation using NL_f to estimate normalized PCSA (NPCSA).

2.3. Data analysis

We measured *in situ* sarcomere lengths bilaterally for each specimen from muscles fixed in occlusion on one side and from muscles fixed in maximum gape on the other side. These values provide estimates of minimum and maximum sarcomere lengths, respectively, to yield estimates of L_s OR for each muscle region. We superimposed the L_s ORs on a representative L-T curve derived from rhesus macaque myofibril lengths (Walker & Schrodt, 1974). We estimated L_f and NL_f for each muscle region (*i.e.*, anterior and posterior) and PCSA and NPCSA for each muscle (*i.e.*, superficial masseter and temporalis) for the occluded and maximally gaped sides.

Macaca fascicularis are smaller in body (Smith & Jungers, 1997) and jaw (Hylander, 2013) size compared with *M. mulatta* and both species are sexually dimorphic. Although each individual served as its own control, males and females differed in maximum gape and, thus, in their L_s ORs. Maximum gape at time of fixation ranged between 56.0–58.8 mm for female *M. fascicularis* and between 87.4–103.2 mm for male *M. mulatta*. Given this, we treated the female *M. fascicularis* and male *M. mulatta* separately in all statistical analyses.

We used one-tailed paired Student's *t*-tests to evaluate differences in L_s , L_f , and PCSA between the occluded and gaped sides. We predicted significantly longer sarcomeres, longer fibers, and smaller PCSAs for the muscles fixed in maximum jaw gape. The majority of the heads fixed in centric occlusion showed a nominal amount of variation in incisor gape (between 0–4.0 mm for *M. fascicularis* and 0–4.5 mm for *M. mulatta*). However, one male *M. mulatta* had a linear gape on the occluded side of 8.9 mm ($\sim 10\%$ of maximum gape). Thus, we normalized the muscles from both the occluded and gaped sides and tested for significant side-to-side differences. We predicted no significant differences between the occluded and maximally gaped sides in fiber length or PCSA following

¹ Various standards have been used to normalize raw muscle fibers to a standard sarcomere length to minimize positional variation in architectural estimates of L_f in limb (Powell et al., 1984; Felder et al., 2005) and jaw (Anapol et al., 2008) muscles. As optimal L_s has not been empirically determined for any jaw adductor in any primate species, we use a standard of $2.41 \mu\text{m}$, which falls within the range of optimal L_s for mammalian striated muscle (Huxley, 1957, 1972) and is the empirically determined optimal L_s for macaque hindlimb muscle (Walker & Schrodt, 1974). The use of this standard should not be construed to indicate fibers are being restored to their optimal L_s .

Table 2

Sarcomere length operating ranges for the anterior and posterior superficial masseter and temporalis muscles in *Macaca fascicularis* and *M. mulatta* and results of tests for significant differences in L_s Min and L_s Max.^a

Muscle	Species	L_s Min (μ m)	L_s Max (μ m)	% Increase	p-value
Anterior superficial masseter (ASM)	<i>M. fascicularis</i>	2.22	3.85	73.4	0.0006
	<i>M. mulatta</i>	1.99	3.45	73.4	0.0012
Posterior superficial masseter (PSM)	<i>M. fascicularis</i>	2.26	3.55	57.1	0.0015
	<i>M. mulatta</i>	1.96	2.92	49.0	0.0155
Anterior temporalis (AT)	<i>M. fascicularis</i>	2.08	3.40	63.5	0.0005
	<i>M. mulatta</i>	2.08	2.93	40.9	0.0064
Posterior temporalis (PT)	<i>M. fascicularis</i>	2.04	3.18	55.9	0.0002
	<i>M. mulatta</i>	2.28	2.98	30.7	0.0074

^a L_s Min and L_s Max are based on species means.

sarcomere-length normalization of the muscles. We used an *a priori* $\alpha = 0.05$.

3. Results and discussion

3.1. Macaque masseter and temporalis sarcomere length operating ranges

Sarcomere length operating ranges varied by individual, species, muscle and muscle region but all fell within the theoretical physiological range of 1.3–4.1 μ m (Walker & Schrodt, 1974; Table 2 and Supplementary Table S1). On the occluded side, minimum L_s ranged between 1.96–2.26 μ m for the superficial masseter and between 2.04–2.28 μ m for the temporalis (Table 2 and Fig. 3). Maximum L_s for the gaped side ranged between 2.92–3.85 μ m for the superficial masseter and 2.93–3.40 μ m for the temporalis (Table 2 and Fig. 3). These values represent percentage increases (*i.e.*, from minimum L_s to maximum L_s) of between 49–73% for the superficial masseter and 31–63% for the temporalis. The anterior superficial masseter operated over the widest L_s OR in both species/sexes, while the posterior temporalis operated over the narrowest range (Table 2 and Fig. 3). These results are consistent with previous findings for similar muscle regions in other mammals (Table 1). However, in *M. fascicularis*, there was a clear

antero-posterior gradient with L_s Max being greatest in the anterior superficial masseter, followed by the posterior superficial masseter, anterior temporalis and posterior temporalis (Table 2 and Fig. 3a). No such gradient was observed for *M. mulatta* (Fig. 3b).

3.2. Position-dependent variation and sarcomere-length normalization

Fibers from the gaped side of the jaws were significantly longer compared with the occluded side for both sexes/species (Table 3 and Fig. 5). Fibers were stretched by as much as 100% for the superficial masseter and by as much as 75% for the temporalis (Table 3). PCSAs were also significantly reduced in the gaped compared with the occluded sides, by as much as 43% for the masseter and 37% for the temporalis (Table 3 and Fig. 5). The reduction in PCSAs is the result of significantly elongated fibers (Table 3) combined with decreased pin-nation angles in comparison with the occluded side (Supplementary Table S2). Following L_s -normalization of fibers, there were no significant differences between the occluded and gaped sides in L_f or PCSA (Table 4 and Fig. 6), indicating that L_s -normalization effectively eliminated the joint-dependent variation in L_f and PCSA.

3.3. Comparison of L_s ORs between female *M. fascicularis* and male *M. mulatta*

For all muscle regions, smaller-bodied female *M. fascicularis* showed wider L_s ORs compared with larger-bodied male *M. mulatta* (Table 2; Figs. 3 and 4). *Macaca fascicularis* also displayed absolutely shorter fibers compared with *M. mulatta* (Table 3). When we statistically evaluated these differences in fiber length with the jaws in occlusion (using one-tailed Mann-Whitney U-tests), we found that *M. fascicularis* had significantly shorter fibers for the anterior ($p = 0.017$) and posterior ($p = 0.039$) masseter and the anterior ($p = 0.017$) and posterior ($p = 0.017$) temporalis, compared with *M. mulatta*. The wider L_s ORs observed for *M. fascicularis* can be explained by their significantly shorter fibers. Shorter fibers indicate fewer sarcomeres in series, resulting in a greater amount of stretch per sarcomere. The wider L_s OR of *M. fascicularis* were also shifted further to the right of the L-T curve such that they operated over a greater portion of the descending limb

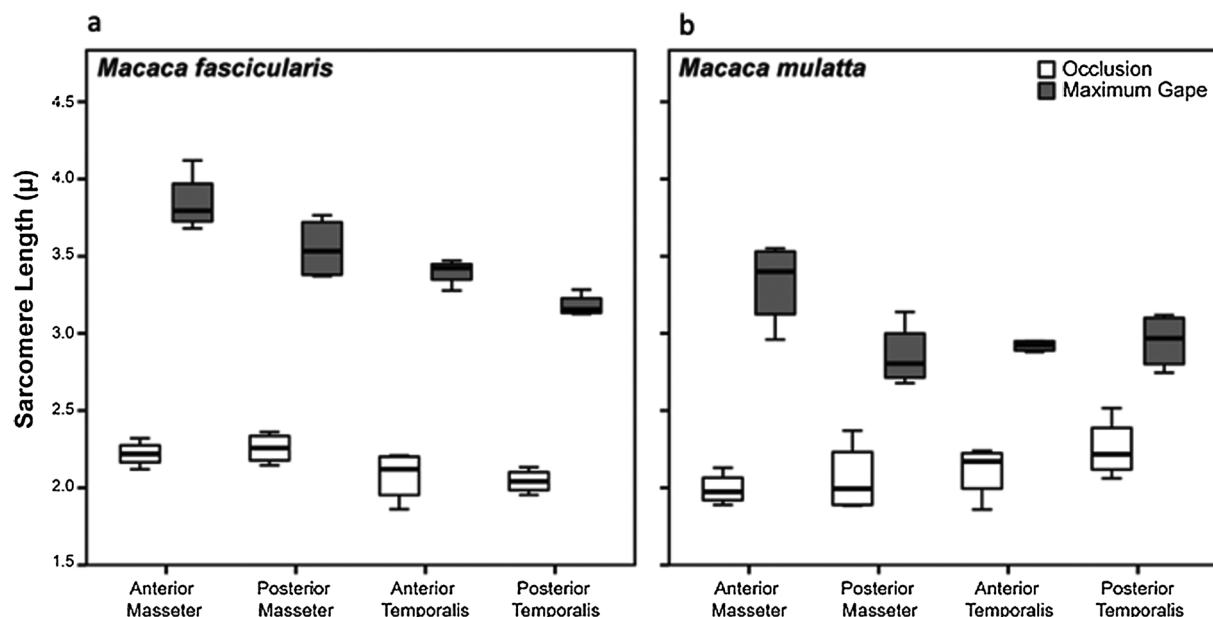


Fig. 3. Box plots of masseter and temporalis sarcomere length measurements taken at occlusion and maximum jaw gape for a) *M. fascicularis* and b) *M. mulatta*. Sarcomere lengths at maximum jaw gape were significantly ($p < 0.05$) greater compared with sarcomere lengths at occlusion in both species for all muscle regions (see Table 2). Sarcomere length operating range was greatest for the anterior superficial masseter in both species. In this and all subsequent box plots, line within box denotes median. Boundaries of the box represent 25th and 75th percentiles. Whiskers indicate 10th and 90th percentiles.

Table 3

Means (\pm standard deviations) and one-tailed significance tests for differences in superficial masseter and temporalis fiber lengths and PCSAs between occluded and gaped sides.^a

Measurements	<i>M. fascicularis</i>				<i>M. mulatta</i>			
	Occluded side	Gaped side	%Change	p-value	Occluded side	Gaped side	%Change	p-value
Superficial Masseter								
Anterior L_f (mm)	10.2 \pm 0.7	19.4 \pm 3.5	88.7	0.006	18.8 \pm 3.9	37.7 \pm 8.9	100.1	0.013
Posterior L_f (mm)	9.6 \pm 0.5	17.4 \pm 0.9	81.9	0.002	11.4 \pm 2.2	18.9 \pm 2.1	66.5	0.016
PCSA (cm ²)	3.6 \pm 0.9	2.0 \pm 0.4	42.8	0.016	7.3 \pm 1.8	4.2 \pm 0.6	43.0	0.027
Temporalis								
Anterior L_f (mm)	11.2 \pm 0.6	19.6 \pm 3.5	74.6	0.006	26.8 \pm 3.3	36.6 \pm 4.6	36.6	0.041
Posterior L_f (mm)	12.2 \pm 2.3	18.8 \pm 1.3	54.3	0.005	30.0 \pm 5.5	41.8 \pm 5.5	39.2	0.006
PCSA (cm ²)	9.9 \pm 0.7	6.3 \pm 1.0	36.7	0.004	15.6 \pm 2.1	11.4 \pm 1.8	27.2	0.012

^a %Change represents the % increase in fiber length, and the % decrease in PCSA, in the gaped compared with the occluded sides.

Table 4

Means (\pm standard deviations) and significance tests for differences in architectural estimates normalized for sarcomere length between occluded and gaped sides.^a

Measurements	<i>M. fascicularis</i>				<i>M. mulatta</i>			
	Occluded side	Gaped side	%Change	p-value	Occluded side	Gaped side	%Change	p-value
Superficial Masseter								
Anterior NL_f (mm)	11.2 \pm 0.9	12.2 \pm 2.3	9.0	0.340	22.8 \pm 3.9	26.3 \pm 5.3	15.3	0.052
Posterior NL_f (mm)	10.3 \pm 0.8	12.0 \pm 0.9	16.7	0.087	14.1 \pm 3.1	13.8 \pm 1.7	2.6	0.700
NPCSA (cm ²)	3.4 \pm 0.8	3.2 \pm 0.5	6.7	0.541	6.3 \pm 1.4	5.8 \pm 0.9	7.8	0.574
Temporalis								
Anterior NL_f (mm)	13.2 \pm 0.5	13.9 \pm 2.7	5.3	0.660	31.2 \pm 3.5	30.3 \pm 3.9	3.3	0.620
Posterior NL_f (mm)	14.4 \pm 2.9	14.3 \pm 1.2	1.2	0.921	32.3 \pm 8.8	34.1 \pm 6.8	5.1	0.700
NPCSA (cm ²)	8.5 \pm 0.8	8.5 \pm 1.5	0.6	0.956	14.0 \pm 2.6	14.2 \pm 3.1	1.4	0.679

^a %Change represents the % increase in normalized fiber length, and the % decrease in normalized PCSA, in the gaped compared with the occluded sides.

compared with male *M. mulatta* (Fig. 4).

Both male *M. fascicularis* and *M. mulatta* have significantly wider maximum jaw gapes compared with female conspecifics (Hylander, 2013) and the internal architecture of their jaw adductors likely mitigates the stretch-related loss of muscle force at wide jaw gapes.

Specifically, the longer fibers of males, with more sarcomeres in series, minimize the amount of muscle stretch needed to achieve a given amount of angular rotation at the temporomandibular joint. This, in turn, presumably minimizes loss of force as fibers would remain closer to the peak of the L-T curve. Because the longer fibers of male *M.*

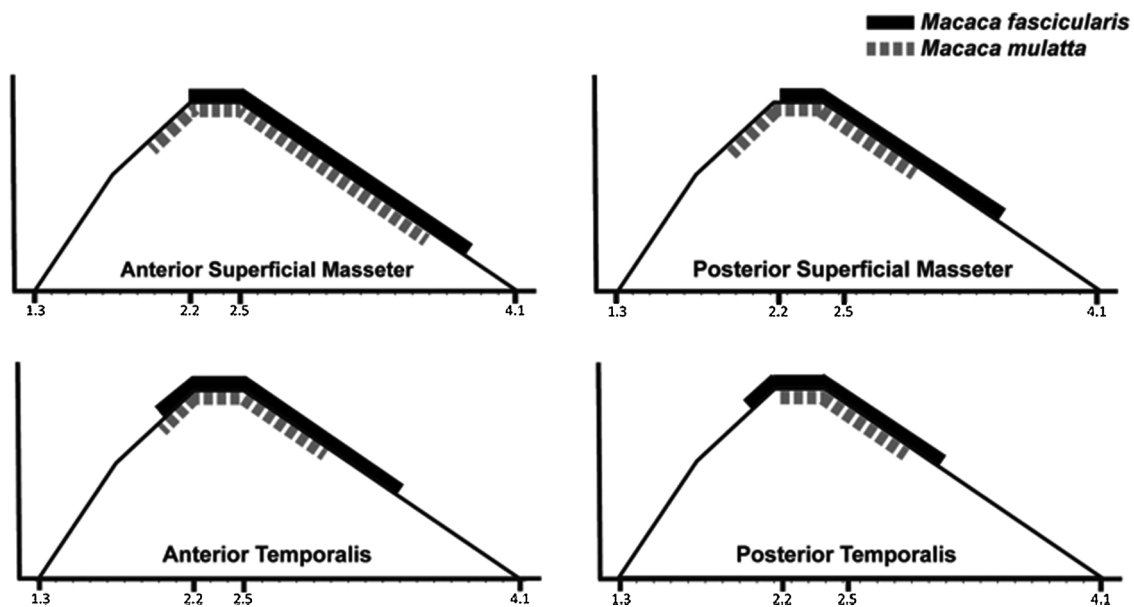


Fig. 4. Masseter and temporalis sarcomere length operating ranges for *M. fascicularis* (solid black line) and *M. mulatta* (hatched grey line) superimposed on a length-tension curve for rhesus macaque myofilament lengths (Walker & Schrodt, 1974). Operating range was interpolated from L_x values at occlusion and maximum gape. Male *M. mulatta* sarcomere lengths operated over narrower ranges and were shifted to the left compared with female *M. fascicularis*, reflecting the longer male fibers. With more sarcomeres in series to minimize the amount of stretch during angular rotation of the joint, fibers remain closer to the peak of the length-tension curve, minimizing loss of force.

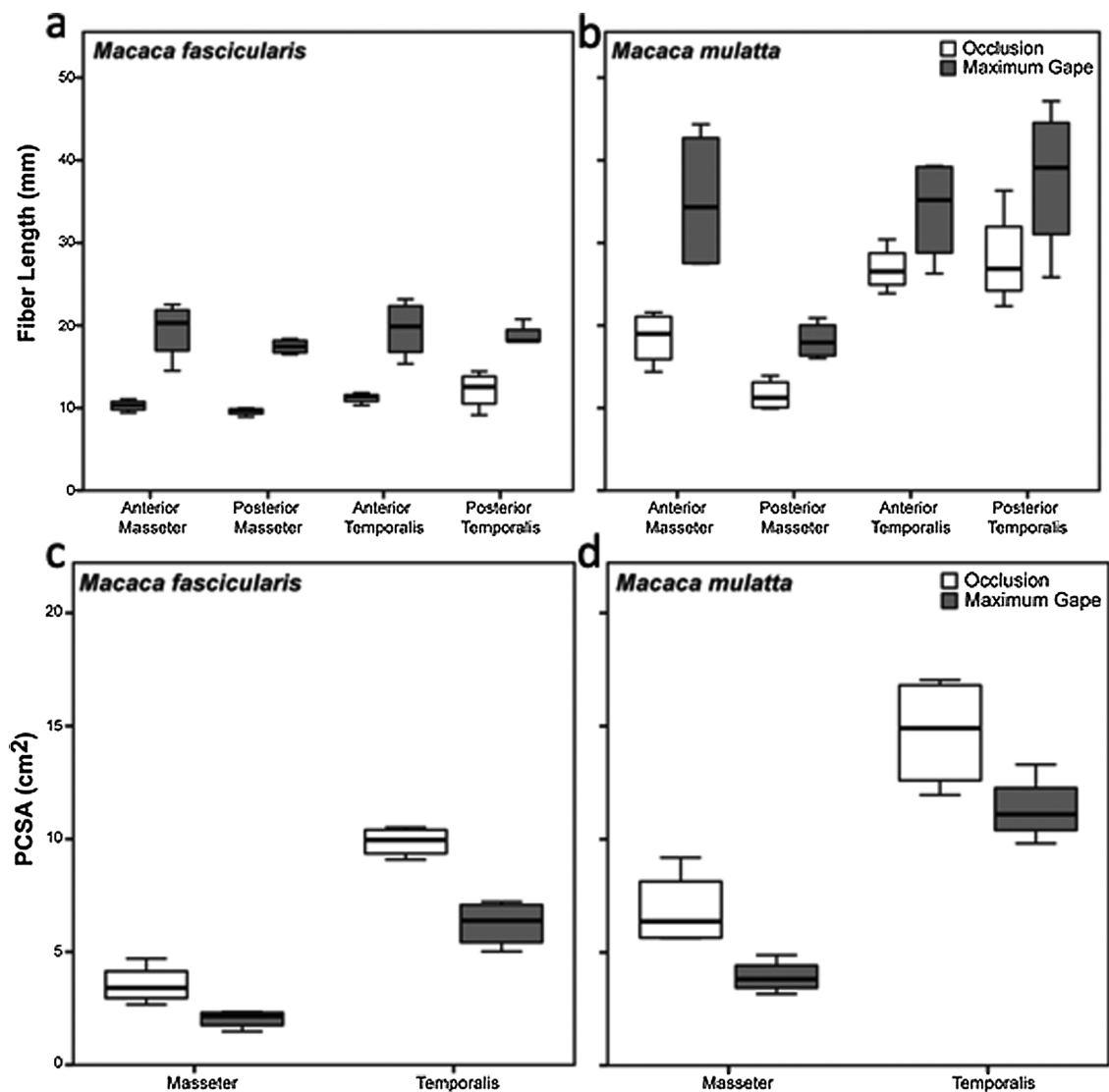


Fig. 5. Box plots of masseter and temporalis fiber lengths (a–b) and PCSAs (c–d) at occlusion and maximum jaw gape. Fibers were significantly longer ($p < 0.05$) and PCSAs significantly smaller ($p < 0.05$) at maximum jaw gape compared with fibers and PCSAs at occlusion, in both species for all muscle regions (see Table 3). As fibers were stretched (and pinnation angles decreased; Supplementary Table S2), muscle PCSAs decreased as a function of change in jaw position.

mulatta distribute lengthening over more sarcomeres, their fibers operate over a narrower L_0 OR, and are shifted to the left of the L-T curve, compared with female *M. fascicularis*. As an important first approximation, these *in vitro* L_0 OR estimates justify future *in vitro* and *in vivo* studies to determine the operating ranges of the jaw adductors and where these muscles operate along the L-T curve during feeding and active gape display behaviors.

3.4. Comparison of masseter and temporalis L_0 ORs with other species

Many skeletal muscle fibers likely operate over a wide range of sarcomere lengths during contraction (Burkholder & Lieber, 2001; Eng et al., 2009; Herring, Grimm, & Grimm, 1984; Nordstrom et al., 1974; Son, Indresano, Sheppard, Ward, & Lieber, 2018; Ward et al., 2006; Weijs & van der Wielen-Drent, 1982, 1983). A survey of L_0 ORs across a variety of vertebrates (Burkholder & Lieber, 2001) reported a substantial amount of variation among limb and jaw muscles within and among species. Portions of the ascending and descending limbs of the L-T curve commonly were included in the L_0 OR in different species' muscles, indicating that many species have the ability to operate over a wide range of the L-T curve. The functional consequences of operating

over a wide L_0 OR are enhanced fiber (and presumably whole muscle) excursion while at some expense to a muscle's force-generating capacity. Synergistic muscle groups are one way to counteract the reduction in force of any single muscle.

Sarcomere length operation range has been estimated *in vitro* for the masseter and temporalis muscles in humans (van Eijden, Korfage, & Brugman, 1997; van Eijden & Raadsheer, 1992) and in a handful of small mammals (Eng et al., 2009; Hertzberg, Muhl, & Begole, 1980; Nordstrom & Yemm, 1972; Nordstrom et al., 1974; Weijs & van der Wielen-Drent, 1982, 1983) (Table 1). Collectively, these L_0 OR estimates suggest that the jaw-closing muscles have the capacity to operate over a wide range of sarcomere lengths and well into the descending limb of the L-T curve, where sarcomeres are stretched and active force is diminished (Fig. 1). This configuration translates into the ability to generate a relatively wide jaw gape, a performance that is essential for feeding (Vinyard, Wall, Williams, & Hylander, 2003), predatory (Kiltie, 1984; Slater & Van Valkenburgh, 2009; Williams, Peiffer, & Ford, 2009) and gape display behaviors (Deputte, 1994; Verheyen, 1954). From a functional standpoint, wide gapes likely move jaw-closing muscle fibers onto the descending limb of the L-T curve, where the overlap of actin-myosin filaments is decreasing, and active force is declining, relative to

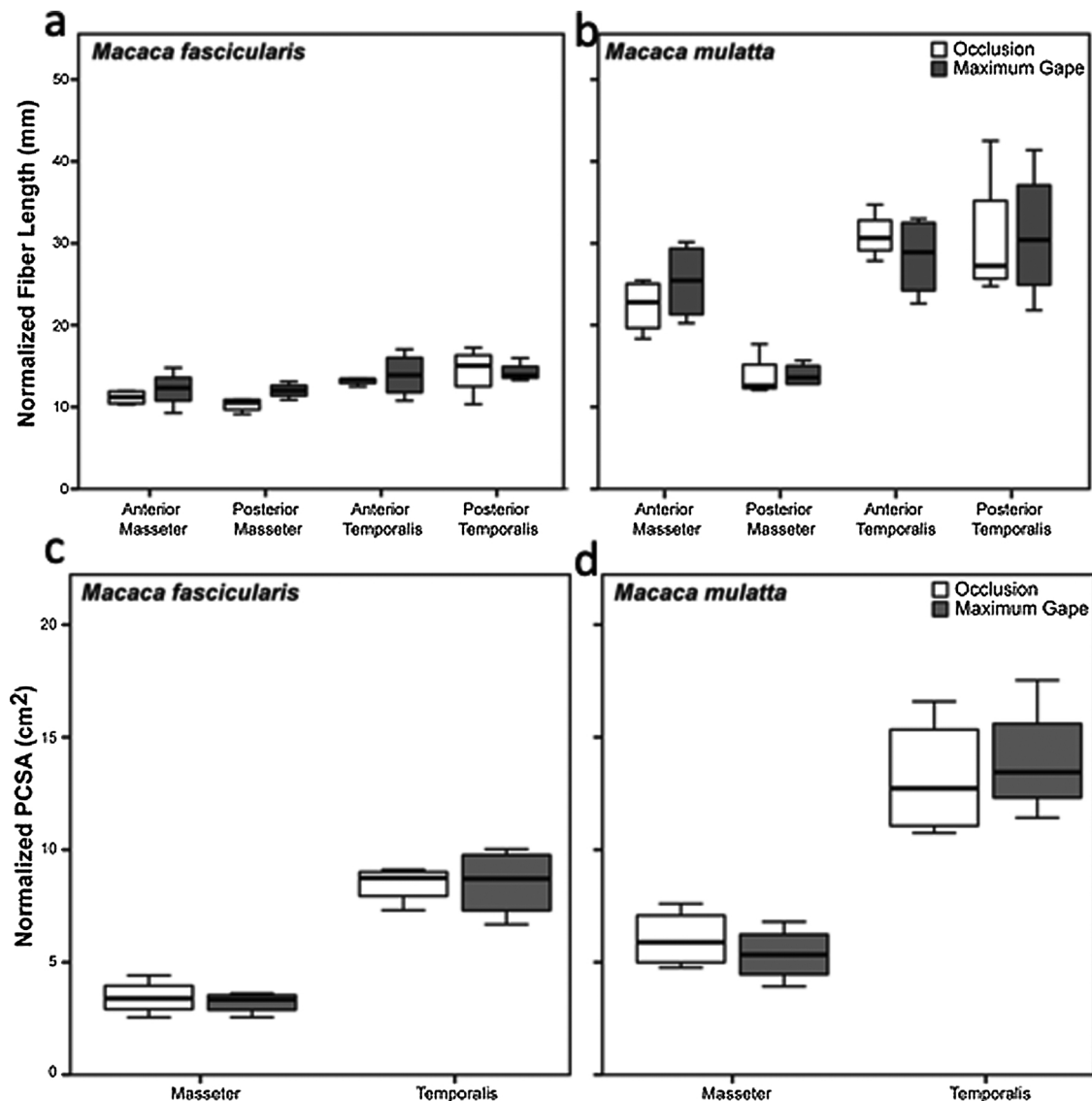


Fig. 6. Box plots of masseter and temporalis fiber lengths (a–b) and PCSAs (c–d) at occlusion and maximum jaw gape, normalized to a standard sarcomere length of 2.41 μm . The absence of significant differences ($p > 0.05$) in fiber lengths and PCSAs between the occluded and maximally-gaped sides indicates that L_s -normalization has effectively eliminated the impact of position-dependent variation in fiber lengths and PCSAs in these jaw muscles (see Table 4).

the plateau region (Fig. 1). Given that where muscles operate along the L-T curve has implications for force production, an understanding of how sarcomere length changes during movement can provide important insights into how muscle-joint complexes are structured to facilitate muscle function. For the masticatory apparatus, this includes performance at extreme joint postures, such as generating adequate bite forces at wide jaw gapes. We note that, due to the absence of sensory feedback (e.g., muscle spindles, golgi tendon organs), maximum L_s ORs estimated *in vitro* are likely to be greater than maximum active or passive ranges estimated *in vivo* and we currently lack data on L_s OR throughout the gape cycle during active behaviors such as chewing or biting.

Minimum L_s estimates for the macaque superficial masseter and temporalis muscles were similar to those previously measured for humans, rabbits, and rats (with the exception of rat temporalis). Alternatively, minimum L_s fell well above those reported for other anthropoid primates such as common marmosets and cotton-top tamarins (Tables 1 and 2), suggesting that in occlusion, the marmoset and tamarin jaw muscles were markedly shortened (Eng et al., 2009). By contrast, maximum L_s for macaque anterior and posterior superficial masseter and temporalis exceeded those reported for all other species

with the exception of humans (Tables 1 and 2). We note that maximum L_s for human (van Eijden & Raadsheer, 1992), common marmoset, and cotton-top tamarin (Eng et al., 2009) masseter and temporalis are modeled estimates. Given that at $\sim 4.3 \mu\text{m}$, human actin and myosin filaments have likely reached the point of no overlap (Lieber, Loren, & Fridén, 1994), the modeled maximum L_s for human masseter of 4.80 μm may be an overestimate.

Minimum and maximum relative L_s (computed as percent optimal length, L_0), have an average range of 81–107% across a sample of 51 vertebrate limb and jaw muscles (Burkholder & Lieber, 2001). Following Burkholder and Lieber (2001), we estimated minimum and maximum relative L_s for our macaque data by dividing our *in situ* L_s measurements from the occluded and gaped sides by an optimal L_s estimate of 2.41 μm . Results showed that the superficial masseter had an average range of between 87–143% and the temporalis between 88–130% of optimal L_s (Fig. 7). These findings indicate that maximum relative L_s for these macaque jaw muscles falls well above the upper end of the range for vertebrate limb and jaw muscles (Burkholder & Lieber, 2001), and above the upper end of the range for relative masseter (88–127%) and temporalis (84–108%) sarcomere lengths previously reported for rabbit and rat masseter and temporalis (Burkholder &

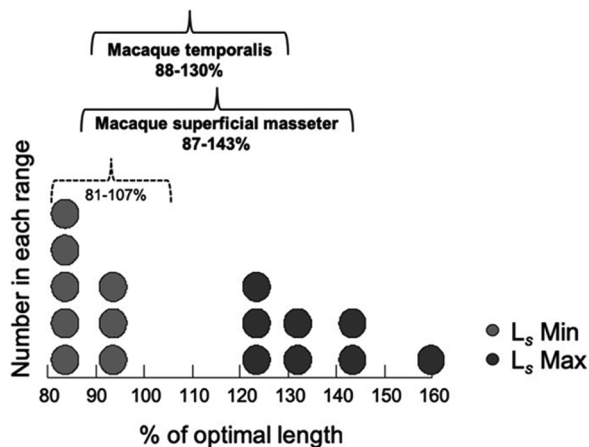


Fig. 7. Dot density histogram of relative sarcomere lengths (measured sarcomere length divided by a standard sarcomere length of 2.41 μm ; reported as % of optimal length, L_0) for macaque anterior and posterior superficial masseter and anterior and posterior temporalis muscles. Light grey dots represent relative L_s Min (at occlusion) and dark grey dots represent relative L_s Max (at maximum jaw gape), for each muscle region, averaged by species. The average range was 87–143% L_0 for macaque masseter and 88–130% L_0 for the temporalis (solid black brackets). The range for relative sarcomere lengths for these macaque jaw adductors included a large portion of the descending limb of the L-T curve, and was both wider and shifted to the right of the L-T curve in comparison with the range previously reported for jaw and limb muscles (81–107%; dotted black bracket) across a variety of vertebrates (Burkholder & Lieber, 2001). The macaque pattern may be characteristic of facially prognathic primates and other mammals that generate relatively wide maximum jaw gapes.

Lieber, 2001).

There are several possible explanations for why our *in vitro* maximum L_s estimates are longer in comparison with those in the same muscles in other species. One possibility is that small mammals like rabbits and rats do not generate relatively wide maximum jaw gapes akin to those of facially prognathic macaques, with the net effect being that less strain is imposed on the sarcomeres when stretched during wide-mouth opening. That said, maximum sarcomere length estimates compiled in Burkholder and Lieber (2001) for these mammals do not appear to have been measured with the jaws in maximum gape. Maximum angular gapes estimated *in vivo* for rabbits range between 20–25° (Weijs & Dantuma, 1981) but the L_s estimate used in Burkholder and Lieber (2001) was from a maximum angular gape of 8.5° (Weijs & Wielen-Drent, 1983). Likewise, the rat data are from jaws fixed in linear gapes up to 16.5 mm (Nordstrom et al., 1974) but in Nordstrom and Yemm (1974) rats achieved maximum linear gapes of up to 20.9 mm. Thus, it seems likely that the maximum L_s reported in the literature for these muscles in these species are underestimates, resulting in underestimates of their L_s ORs.

Facial configuration influences the position of the jaw adductors on the skull and their capacity for muscle stretch (Herring & Herring, 1974). Long, prognathic faces, like those of macaques, are correlated with the production of relatively wide maximum jaw gapes (Hylander, 2013), which is facilitated by muscle stretch. Similar to other sexually dimorphic and prognathic Old World monkeys, macaques generate relatively wide jaw gapes as part of their behavioral repertoire of engaging in agonistic canine display (or 'yawning') (Deputte, 1994). Thus, macaque facial morphology may also contribute to their greater maximum L_s . Our current findings indicate that their passive superficial masseter and temporalis L_s ORs are both wider and shifted to encompass more of the descending limb of the L-T curve as compared with other mammals. Additional work is needed on other primates and nonprimate mammals to determine whether this finding reflects a macaque morphotype or whether this pattern is characteristic of moderate- to large-

bodied prognathic mammals that generate relatively wide maximum jaw gapes.

3.5. Divergence in L_s OR between the superficial masseter and temporalis muscles

In both macaque species, L_s ORs were greatest for the anterior superficial masseter compared to other muscle regions (Table 2). In *M. fascicularis* the posterior superficial masseter also had a wider L_s OR compared with the anterior and posterior temporalis (Table 2). These findings suggest that when fibers are stretched during mouth opening, sarcomere strain is greatest in the superficial masseter, particularly the anterior region of this muscle. Likewise, in both species the anterior superficial masseter operated over a greater portion of the descending limb of the L-T curve compared with the temporalis, facilitating muscle stretch and the production of wide mouth opening. Alternatively, the temporalis operated over a more favorable region of the L-T curve for generating muscle and bite force.

The differences in L_s OR between the superficial masseter and temporalis can be added to a suite of physiological and morphological features that support functional divergence between these two muscles. Previous work evaluating jaw adductor muscle-activity patterns during chewing suggests the superficial masseter may have evolved diverse functional roles in different groups of primates, while temporalis muscle function appears more evolutionarily conserved for generating vertical bite force (Hylander, Ravosa, Ross, Wall, & Johnson, 2000; Hylander et al., 2005; Vinyard et al., 2007; Vinyard, Wall, Williams, & Hylander, 2008; Ram & Ross, 2018). Work relating masseter and temporalis fiber architecture and electromyography in primates shows similar functional relationships (Vinyard & Taylor, 2010). Our findings of a wider sarcomere length operating range for the masseter, while the temporalis is restricted closer to the plateau region of the L-T curve where sarcomere overlap is optimal for maximizing muscle and bite force, support these EMG patterns. Architectural studies of the jaw adductors in anthropoid primates (e.g., common marmosets, crab-eating macaques) likewise indicate a functional partitioning of the masseter and temporalis (Taylor et al., 2009; Terhune et al., 2015).

3.6. The impact of position-dependent variation on fiber architecture

Our findings demonstrated that variation in joint position at the time of fixation has the potential to introduce substantial variation in architectural estimates of muscle excursion/contraction velocity (L_f) and muscle force (PCSA) (Table 3). Previous reports of fiber length increases in rat limb muscles from neutral to extreme plantarflexion (160°) fall well within these ranges (~53–75% for the tibialis anterior, extensor digitorum longus and soleus; Felder et al., 2005). In our sample, we estimated the variance in L_f between the occluded and gaped sides. Averaged across individuals, this ranged between 30.2–106.1 mm² across the four muscle regions examined (Table 3). Sarcomere-length normalization substantially reduced this variance to 1.6–4.9 mm² (Table 4). We likewise observed reduced variance for PCSA (3.2–8.1 cm for raw PCSA compared with 0.4–0.9 cm² for PCSA normalized for L_s) (Tables 3 and 4).

In this study, our focus has been on position-dependent variation that translates into error for estimating fiber lengths at a consistent position on the L-T curve. We recognize that there are other sources of error associated with estimating fiber architecture. For example, beyond standard measurement error, estimates of pennation are a source of error. This is because fibers rotate during muscle contraction and this rotation impacts force generation and fiber contraction velocity that cannot be accounted for in static estimates of pennation (Azizi & Roberts, 2014; Azizi, Brainerd, & Roberts, 2008). Additionally, architectural estimates of muscle force do not take into account parallel or series elastic components, such as connective tissues and tendons, which can increase force following stretch of an active muscle (i.e.,

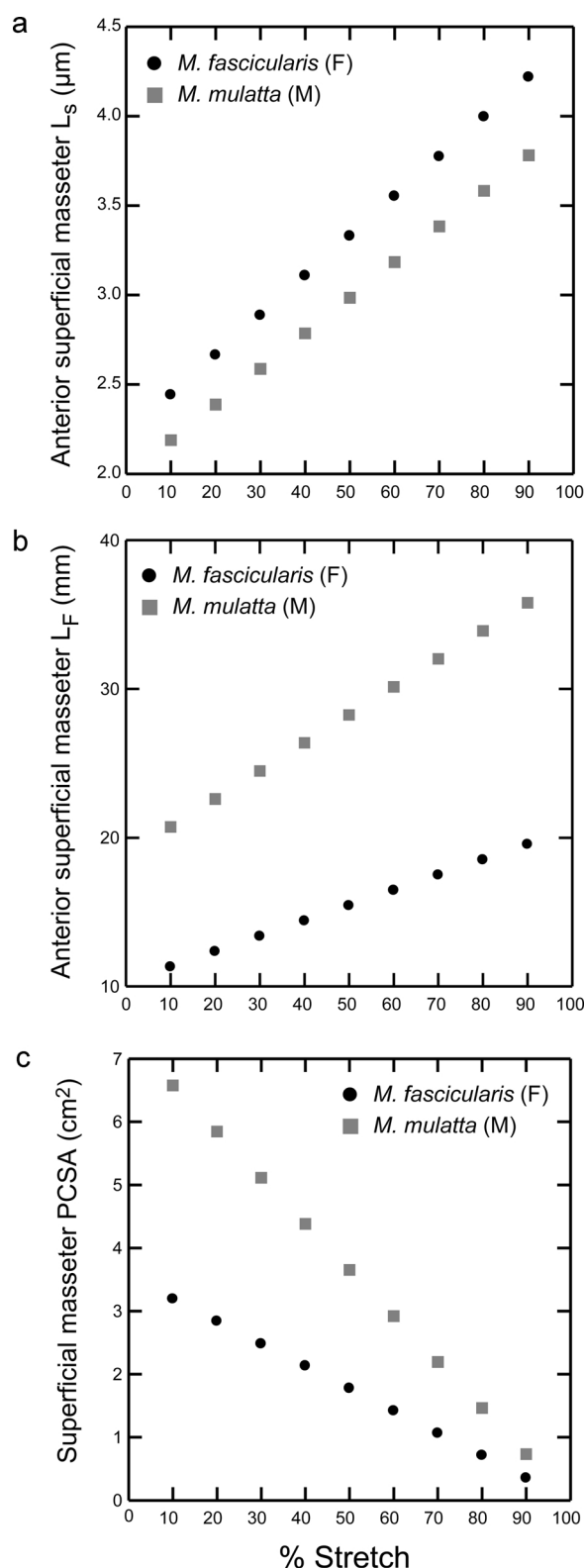


Fig. 8. Plots of changing a) sarcomere length (L_s); b) fiber length (L_f); and c) PCSA as a function of percent fiber stretch for the anterior superficial masseter. Fiber stretch was interpolated in 10% increments from occlusion to 90%. For every 10% increase in stretch from occlusion, sarcomeres lengthen by ~ 8 –9%, and fibers lengthen between 1–3 mm, depending on muscle region. Sarcomere and fiber lengths measured *in vitro* at maximum jaw gapes fell within our estimated ranges for sarcomeres stretched by as much as 70–80%, and fiber stretched by as much as 90%, respectively, from occlusion. (Supplementary Table S3).

residual force enhancement; Rode, Siebert, Herzog, & Blickham, 2009).

Although the variances reported here were associated with joints fixed in extreme positions, our data showed that even with incremental fiber stretching (e.g., 10% increments), sarcomeres demonstrated moderate increases in length (Supplementary Table S3). These incremental increases varied across muscle regions, ranging between 0.204–0.226 μm for *M. fascicularis* and 0.199–0.225 μm for *M. mulatta* (Fig. 8a). This equates to approximately 8–9% of resting length per sarcomere (assuming an average resting length of ~ 2.41 – $2.5 \mu\text{m}$ (Huxley, 1957, 1972; Walker & Schrodt, 1974). These sarcomere-length increases translated into increases in fiber length and decreases in PCSAs. For example, anterior superficial masseter fibers underwent an average increase in length of ~ 1 mm in *M. fascicularis* and ~ 1 –2 mm in *M. mulatta* per 10% fiber stretch (Fig. 8b). For the anterior and posterior temporalis, the average increase in fiber length per 10% stretch was greater, ranging between ~ 1 –3 mm. Notably, our sarcomere lengths measured *in vitro* at maximum jaw gapes fell within these estimated ranges for sarcomeres stretched by as much as 70–80% for the anterior superficial masseter, 40–50% for the posterior superficial masseter, 40–60% for the anterior temporalis and 30–50% for the posterior temporalis. Our fiber lengths measured at maximum gape fell within the estimated ranges for fibers stretched by as much as 90% for the anterior superficial masseter and our superficial masseter PCSAs measured at maximum gape fell within the estimated ranges for fibers stretched by 40–50% (Fig. 8c; Supplementary Table S3). Given that maximizing an opportunistic sample is likely to require including specimens with jaws fixed in a variety of positions, these findings demonstrate the importance of a correction factor for position-dependent variation, such as normalizing fiber length measurements to a standard sarcomere length.

4. Conclusion

Sarcomere length operating ranges for macaque jaw adductors varied between 1.96–2.26 μm and 2.92–3.85 μm for the masseter, and between 2.04–2.28 μm and 2.93–3.40 μm for the temporalis. Macaque operating ranges were wider and shifted to the right of the descending limb of a representative length-tension curve compared with other mammals. These wider operating ranges may be functionally linked to agonistic canine display behaviors in male macaques that require jaw-muscle stretch to facilitate production of wide jaw gapes. Significant position-dependent variation in architectural estimates of muscle excursion and muscle force were effectively eliminated by normalizing fibers to a standard sarcomere length.

Funding

This work was supported by grants from the National Science Foundation (BCS 1723041) and the National Skeletal Muscle Research Center at UCSD (NIH R24 HD050837).

Conflict of interest

None declared.

Ethics approval

Not required. No animals were sacrificed for purposes of this study. All specimens were used secondarily to other research projects pertaining to drug addiction and cognitive function that were approved by the 2003 National Research Council Guidelines for the Care and the Use of Mammals in Neuroscience and Behavioral Research and with approval by the Animal Care and Use Committee of Wake Forest University.

Acknowledgements

We thank Dr. William Hylander, Duke University, and Dr. Michael Nader and the Nader Lab, Wake Forest School of Medicine, for providing the cadaveric specimens. The comments of two reviewers and the Editor improved the quality of this manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.archoralbio.2019.05.015>.

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