

Masticatory muscle fiber length and position influence relative maximum jaw gapes in the sexually-dimorphic *Macaca fascicularis*.

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INTRODUCTION

Relative to the great apes, early hominins have 1) decreased canine crown height; 2) decreased sexual dimorphism in canine size; 3) loss of the canine/P3 honing complex; and 4) increased apical wear of the canines (e.g., Greenfield, 1990; Plavcan, 2001; Kimbel et al., 2006; White et al., 2009). Reduced canine size and dimorphism have been linked by some (Reno et al., 2003; White et al., 2009) to decreased male-male competition in early hominins, and by others (e.g., Jolly, 1970; Hylander, 1988; Teaford and Ungar, 2000) to changes in feeding behavior and diet.

Hylander and Vinyard (2006) hypothesize that canine crown height was reduced in early hominins as a consequence of selection for increased bite force along the postcanine dentition, which resulted in a reduction in relative maximum jaw gape. This hypothesis is supported by a strong correlation in canine crown height and gape across catarrhines, indicating that most males have relatively larger maximum jaw gapes than do females (Hylander et al., 2008). Among catarrhines, the exceptions are humans and hylobatids, both of which have little canine height dimorphism. Here we present a preliminary test of the soft and bony tissue correlates of this hypothesis in male (n = 5) and female (n = 5) *Macaca fascicularis* (Figure 1). In this highly sexually dimorphic species, male gapes are 113% of jaw length compared to 80% of jaw length in females.



Figure 1. Photographs of female and male superficial masseter and temporalis muscles *in situ*. Both specimens are scaled to the same size.

RESEARCH PREDICTIONS

We examine the following (non-mutually exclusive) predictions regarding features that may facilitate relatively wider maximum jaw gapes in male *M. fascicularis*. Compared to females, males will display:

- Relatively longer superficial masseter and temporalis fibers to facilitate increased muscle excursion (range of motion).
- Relatively more caudally positioned masticatory muscles.
- Relatively longer mandibles and/or a TMJ positioned closer to the occlusal plane.
- Relatively anteroposteriorly (AP) elongated TMJ surfaces areas.

MATERIALS AND METHODS

Muscle architecture measurements

- Prior to removal, muscles were cleaned, and their positions measured as in Table 1 and Fig. 1.
- Muscles were removed, weighed, and their internal architecture quantified following Taylor and Vinyard (2004, 2009) (Table 2).
- The superficial masseter (SM) and temporalis (Temp) muscles were sectioned as shown in Figure 2; at each cross-section, we measured muscle fiber length (Lf) and pinnation angle for up to ten adjacent fibers at two separate sampling sites.
- We corrected for differences in jaw posture at the time of fixation by normalizing muscle fiber length (Lf) to a standard sarcomere length (Ls) of 2.41 μ m, the empirically derived optimal Ls for macaque limb muscle (Walker and Schrodt, 1974). Normalized Lf was used in all subsequent calculations involving fiber length (Felder et al., 2005).

Bony measurements of the mandible and temporomandibular joint

- Bony masticatory measurements from a separate sample of 12 females and 11 males (Terhune, 2010) were taken on skulls of adult wild caught specimens (Table 3).

Analytical methods

- For all analyses (except pinnation angle), variables were scaled by mandibular length as the relevant biomechanical standard for size adjustment (Hylander, 1979). Mandibular length was standardized by dividing by a geometric mean of cranial size.
- One-tailed Student's t-tests followed by the sequential Bonferroni adjustment (employed per muscle, per hypothesis), were used to test for significant differences between males and females.

Table 1. Muscle position variables and their predicted differences.

Measurement	Abbrev.	Definition	Prediction
Masseter origin position	ASMO	Condyle to anterior-most origin of SM	F>M
Masseter insertion position	ASMI	Condyle to anterior-most insertion of SM	F>M
Temporalis origin position	ATO	Condyle to anteroposterior-most origin of temporalis	F>M
Temporalis insertion position	ATI	Condyle to insertion of temporalis on coronoid process	F>M

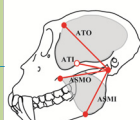


Fig. 2. Muscle position measurements.

Table 2. Muscle architecture variables and their predicted differences.

Measurement	Abbrev.	Unit	Prediction
Muscle fiber length	Lf	mm	M>F*
Physiological cross sectional area	PCSA	cm ²	No pred.*
Pinnation angle	PinnAngle	degrees	F>M
Muscle weight	TempWt	g	M>F

*We made no prediction for posterior masseter fiber length (because of its position close to the mandibular center of rotation) or for PCSA (because of competing demands for muscle excursion and force production). T-tests for these variables were two-tailed.

Table 3. Mandible and TMJ variables and their predicted differences.

Measurement	Abbrev.	Unit	Prediction
Jaw length	JawLg	mm	M>F
TMJ height	TMJHt	mm	F>M
Glendoid fossa length (AP)	GlenLg	mm	M>F
Condyle length (AP)	CondLg	mm	n/a
Translation ratio	TransPot	n/a	M>F

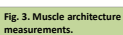


Fig. 3. Muscle architecture measurements.

RESULTS

Absolute values for jaw length and muscle architecture variables are presented in Table 4. Results of significance tests for relative differences in fiber architecture, muscle position, and TMJ measures are presented in Table 5 and Figures 4 through 9.

Table 4. Absolute values for jaw length and the measures of muscle architecture and weight.

	Females		Males	
	Mean	SD	Mean	SD
Jaw length	80.28	\pm 7.84	101.14	\pm 8.58
Anterior Lf	12.53	\pm 2.70	21.14	\pm 3.00
Posterior Lf	10.81	\pm 1.53	12.80	\pm 1.92
PinnAngle	12.87	\pm 2.68	15.34	\pm 3.05
PCSA	3.22	\pm 0.65	5.61	\pm 1.69
SMWt	4.07	\pm 0.93	11.00	\pm 4.36
Lf	15.78	\pm 3.89	26.83	\pm 5.03
PinnAngle	10.07	\pm 1.52	9.80	\pm 1.99
PCSA	8.16	\pm 0.94	18.19	\pm 4.36
TempWt	13.70	\pm 3.15	53.40	\pm 19.82

Table 5. Results of the Student's t-tests for significant differences between males and females. Shaded p-values are significant.*

Variable	Predicted Difference**	As predicted?	Significant difference?
Anterior Lf	M>F	Yes	p=0.0001
Posterior Lf	n/a	n/a	p=0.308
PinnAngle	F>M	No	p=0.105
PCSA	n/a	n/a	p=0.366
SMWt	M>F	Yes	p=0.070
ASMO	F>M	Yes	p=0.119
ASMI	F>M	Yes	p=0.032
Lf	M>F	Yes	p=0.005
PinnAngle	F>M	Yes	p=0.407
PCSA	n/a	n/a	p=0.015
TempWt	M>F	Yes	p=0.0001
ATO	F>M	Yes	p=0.466
ATI	F>M	Yes	p=0.261
JawLg/GEOM	M>F	Yes	p=0.0001
TMJHt	F>M	Yes	p=0.016
GlenLg	M>F	Yes	p=0.174
TransPot	M>F	Yes	p=0.168

*All values except pinnation angle were scaled by jaw length and jaw length was scaled by a geometric mean of cranial size to create dimensionless ratios; we took the square root of PCSA and the cubed root of muscle weight before dividing by jaw length.
**We predicted specific directional differences for all variables except Lf for the posterior masseter (because of its position close to the center of rotation of the mandible, we expected either no difference between sexes or a relative increase in Lf in males), and PCSA (where we could expect either F or M to give competing functional demands for this variable).

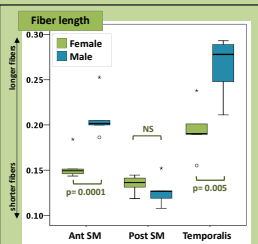


Fig. 4. Box plots of relative fiber length for the anterior and posterior superficial masseter and temporalis. As predicted, males have relatively longer muscle fibers than females. There is no significant difference in Lf for the posterior masseter, as these fibers are positioned closer to the mandibular center of rotation.

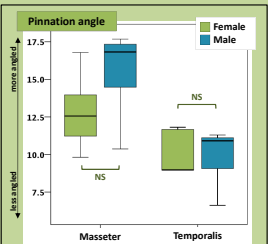


Fig. 5. Box plots of pinnation angle (in degrees) for the superficial masseter and temporalis. No significant differences between males and females were found in pinnation angle for either the masseter or temporalis muscles.

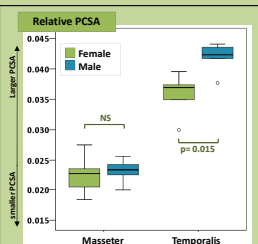


Fig. 6. Box plots of relative PCSA for the masseter and temporalis. Males have absolutely and relatively larger PCSAs than females, but only significantly so for the temporalis muscle (p-value shown is two-tailed; see Table 2).

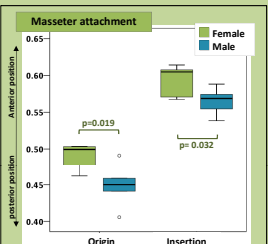


Fig. 7. Box plots of masseter origin (ASMO) and insertion (ASMI) position. As predicted the superficial masseter is positioned relatively more rostrally (i.e., anteriorly) in females than in males.

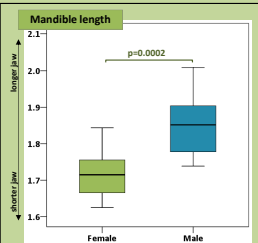


Fig. 8. Box plots of relative mandible length. As predicted, males have absolutely and relatively longer mandibles than do females.

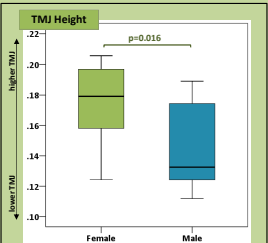


Fig. 9. Box plots of relative TMJ height above the occlusal plane. As predicted, the TMJ in females is positioned relatively further above the occlusal plane than in males.

SUMMARY OF FINDINGS

- Males have significantly relatively longer anterior superficial masseter and temporalis fibers than females (Fig. 4).
- There is no significant difference in pinnation angle between sexes (Fig. 5).
- Males have a relatively larger PCSA for the temporalis (but not superficial masseter) than females (Fig. 6).
- Females have more rostrally (i.e., anteriorly) positioned superficial masseter muscles relative to jaw length than males (Fig. 7).
- Males have relatively longer mandibles and TMJs situated relatively closer to the occlusal plane than do females (Figs. 8 & 9).
- There are no significant differences between males and females in AP dimensions of the TMJ.

DISCUSSION AND CONCLUSIONS

Point 1: *Macaca fascicularis* males and females exhibit a mosaic of muscular and bony features that impact both gape and force production. Muscle excursion and the capacity to generate relatively wide maximum jaw gapes are facilitated in males by 1) relatively longer superficial masseter and temporalis fibers; 2) a relatively more caudally positioned superficial masseter; and 3) relatively greater mandibular length and a TMJ positioned relatively closer to the occlusal plane. However, increased gape comes at some expense to force production, as a caudally positioned superficial masseter results in decreased mechanical leverage compared to females (cf. Dechow and Carlson (1990) for Rhesus macaques).

Point 2: Largely by increasing muscle mass without altering pinnation angle, males have relatively greater temporalis PCSAs compared to females. These results suggest that males compensate for decreased mechanical leverage of the superficial masseter by increasing relative maximum force production of the temporalis. By doing so, males and females are capable of generating similar maximum muscle (and bite) forces, consistent with Dechow and Carlson's (1990) experimental findings of peak occlusal forces in Rhesus macaques. These findings further support Dechow and Carlson's (1990) hypothesis that in the presence of inefficient leverage, rearrangement of the internal architecture of complex, pinnate-fibered muscles like the masseter and temporalis may be required to effect an increase in muscle force.

Point 3: Male *M. fascicularis* circumvent the predicted architectural trade-off between maintaining relatively large PCSAs (i.e., muscle forces) and relatively long fibers (i.e., muscle excursions). This finding emphasizes the variety of architectural arrangements in response to divergent ingestive and non-ingestive behavioral requirements (e.g., Eng et al., 2009; Taylor and Vinyard, 2009; Taylor et al., 2011).

Point 4: Our results provide support for the hypothesis (Hylander and Vinyard, 2006; Hylander et al., 2008) that male *M. fascicularis* have experienced selection to maintain a relatively large maximum jaw gape and attendant large canines, likely for social display behaviors. These results further emphasize the importance of considering gape as well as force requirements in functional and adaptive studies of primate masticatory apparatus form.

ACKNOWLEDGEMENTS

We thank Dr. Michael A. Nader, Department of Physiology & Pharmacology and Radiology, Wake Forest University School of Medicine, for the cadaveric material. Support for this work is provided by funds from the National Science Foundation (BCS 0452160, BCS 0962677, BCS 0752661), the National Institutes of Health (R24 HD050837-01), and the Leakey Foundation.



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