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Occlusal Force and Craniofacial Biomechanics During Growth in Rhesus Monkeys

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ABSTRACT The masticatory muscles in 132 anesthetized male and female rhesus monkeys ranging in age from juvenile to adult were unilaterally stimulated. Muscle forces and speeds were measured with a bite force transducer positioned at the incisors, premolars, and molars during twitch and tetanic contractions. Lateral cephalographs of all animals were used to estimate the orientation and mechanical advantage of the masticatory muscles. Results showed that maximal occlusal forces increased at a greater rate than body weight during growth. However, maximal occlusal forces increased isometrically relative to mandibular length. Mean forces at the incisors ranged from 70.3 newtons (n) in juveniles up to 139.9 n in adult males. Forces at the molars were 2–2.5 times greater than at the incisors. Time-to-peak tension decreased with increasing body size from 44.1 msec in juveniles to 37.4 msec in adult females to 31.0 msec in adult males. Regression analysis showed that adult males have faster muscles than adult females or juveniles even when corrected for body size. Temporalis and masseter orientation was found to change little throughout growth. The mechanical advantage of the masseter and temporalis muscles for producing occlusal forces on the distal molars improved between juveniles and adults, which is contrary to findings of Oyen et al. (Growth *43:*174–187, 1979). Among adults, females had a greater mechanical advantage of the masseter muscles than males.

Function plays a vital role in the growth and form of vertebrate tissues. However, its precise role in modulating developmental and adaptive processes is one that requires study of specific anatomical regions and tissue types from the molecular to the gross level. In studies of primate craniofacial growth, much research has focused on description of changes in skeletal form (for a review, see Sirianni and Swindler, 1979), without particular emphasis on concurrent functional changes or growth mechanisms. Other studies have stressed growth rates or ontogenetic allometry of craniofacial skeletal structures (Byrd and Swindler, 1980; Cochard, 1985; Enlow, 1966; Shea, 1985; Swindler and Sirianni, 1977), with the emphasis on understanding how alterations in growth curves lead to interspecific or sexual differences in craniofacial size and form.

Function has been important in creating a theoretical framework for understanding control of craniofacial growth and form (Klaauw, 1952, 1963; Moss, 1960, 1973; Scott, 1952). Studies have examined the effect of altered function on craniofacial features such as muscle attachments, overall skeletal size, and osseous structure (Avis, 1961; Bouvier and Hylander, 1981, 1982; Hendricksen et al., 1982; Herring and Lakars, 1981; Kilaridis, 1986; Moore, 1965, 1967, 1973; Moss and Simon, 1968). Several studies have inferred that biomechanical changes during craniofacial growth produce discrete morphological changes (Oyen 1982; Oyen and Rice, 1980; Oyen et al., 1979).

Although studies have examined the biol-

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ogy of growing muscles (Goldspink, 1968, 1972, 1980; Jolesz and Sreter, 1981; Ontell and Dunn, 1978; Rowe and Goldspink, 1969; Swatland, 1976, 1979, 1980, 1981; Timson, 1982; Villa-Moruzzi et al., 1979), including the masticatory muscles (Carlson, 1983; Gagnot et al., 1977; Herring, 1985a,b; Houston, 1974; Hurov et al., 1988; Maeda et al., 1981; Maxwell et al., 1979; McNamara, 1974; Nakata, 1981; Rayne and Crawford, 1971, 1972, 1975; Weijs et al., 1987), little is as yet known about growth changes in the physiology of the masticatory muscles and the relationship of these growth changes to the biomechanics of the craniofacial skeleton. This information is of great interest because it is vital for understanding how biomechanical systems in primates and other vertebrates grow and adapt and because it aids in interpreting craniofacial structure in extant and fossil primates.

This investigation was undertaken to quantify growth changes and sexual differences in the physiology and biomechanics of the muscles of mastication in rhesus monkeys. The investigation focuses on answering the following questions: 1) How does maximum occlusal force vary between ages and sexes in rhesus monkeys? 2) How does the speed of contraction of the masticatory muscles vary with growth and body size in rhesus monkeys? 3) Do differences in the form of the craniofacial skeleton between male and female rhesus monkeys and during growth alter the biomechanical efficiency of the masticatory muscles for producing occlusal force?

MATERIALS AND METHODS

Description of sample

The sample consisted of 132 juvenile and adult rhesus monkeys (*Macaca mulatta*) that entered the experimental animal pool at the University of Michigan (121 animals) between 1982 and 1987 and Baylor College of Dentistry (11 animals) during 1986 and 1987. Rhesus monkeys were housed individually and were cared for according to standards of The University of Michigan Laboratory Animal Care Program. Diets consisted of Purina monkey chow supplemented with apples and bananas.

Animals were categorized by dental development and sex into one of three groups: 1) juvenile (n=36; 34 males and two females); 2) adult female (n=81), and 3) adult male (n=15). Dental development among the juveniles ranged from complete deciduous dentition only to deciduous dentition with first permanent molars in occlusion. Dental development in the adult animals was complete, with the exception of a few animals that did not have full occlusion of the third molars. The two female juvenile monkeys were combined with the 34 male juvenile monkeys into a single group because t tests did not indicate any statistically significant differences for the various morphological and physiological parameters.

Occlusal force recording procedure

Measurements of masticatory muscle force and speed of contraction were made using a bite force transducer and muscle stimulation procedure similar to that reported by Dechow and Carlson (1983). This stimulation procedure was designed to stimulate maximally the masticatory muscles unilaterally during twitch and tetanic contractions. Prior to each set of measurements, monkeys were anesthetized with a combination of ketamine HCl (7–15 mg/kg) and Rompun (xylazine; 1–2 mg/kg). Muscle stimulation and force recording were usually done on the animal's right side.

Force recordings were measured at three occlusal positions along the tooth row: 1) at the central incisors, 2) at the anterior premolars just posterior to the canine, and 3) at the most posterior occluding molar cusps (M_3s in adults and dM_2s in juveniles). The bite force transducer required a 9 mm distance between the opposing occlusal surfaces. Following each recording session, monkeys were returned to their cages and allowed to recover from the anesthetic. The monkeys seemed to suffer no ill effects from this procedure. All animals behaved and ate normally shortly after recovery from anesthesia.

Two stimulation procedures were used: one produced a single twitch contraction of the masticatory muscles; the second produced a fused tetanus. The twitch contraction was stimulated with a single pulse of .8 msec duration and sufficient voltage for maximal unilateral masticatory muscle contraction (25–50 V). The tetanic contraction was produced by stimulating with a series of pulses at 80 Hz for 400 msec. Pulses were produced with a Grass model 48 square pulse stimulator coupled with a Grass SIU5 stimulus isolation unit. Readings from the transducer were amplified with a Vishay

2100 strain gage amplifier and displayed and photographed on a Tektronics 5113 dual-beam storage oscilloscope. Sample sizes vary because twitch readings were not recorded for the first half of the animals studied.

Several measurements were taken from the oscilloscope traces (Fig. 1). Measurements taken from twitch contractions included the peak twitch tension (PT), the time to peak twitch tension (TPT), one-half of the relaxation time from peak twitch tension (HRT), and the amount of passive tension that resulted from placing the bite force transducer between the upper and lower teeth. Peak tetanic tension (PO) was measured from traces of the tetanic contractions.

A potential problem with the stimulated bite force technique was the change in masticatory muscle length when the bite force transducer was positioned at different points along the tooth row. For instance, when the transducer is placed between the molars, the mouth is opened to a wider gape, and consequently the masticatory muscles are stretched more than when the transducer is placed between the incisors. Measurements taken on radiographs of a sample of 38 monkeys of various ages and sexes indicated that the anterior portion of masseter increased in length by 12.8% (sd 4.3%) when the transducer was moved from the incisor to the molar position.

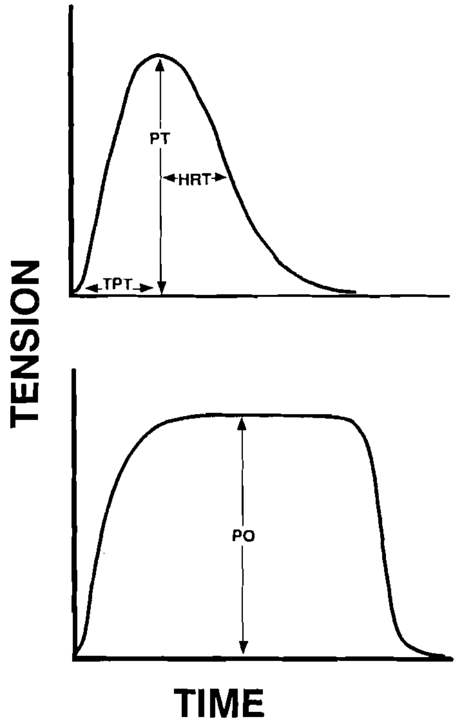

Fig. 1. Measurements taken from twitch and tetanic muscle force recordings. The upper panel is an example of a twitch. Three values were recorded: PT, peak twitch tension (peak amplitude); TPT, time to peak twitch tension; and HRT, half relaxation time. The lower panel is an example of a fused tetanic contraction, in which peak tetanic tension was measured.

The effects of changing masticatory muscle length on TPT were investigated by measuring twitch contractions on the sample of 38 monkeys at two incisal gape positions. The first gape position was that normally resulting from placing the transducer between the incisors. The second gape position was a larger incisal gape that corresponded to the amount of incisal gape when the transducer was placed between the molars. TPT was measured at this larger incisal gape by adding small metal bars to the biting end of the transducer until the appropriate dimension was achieved (Dechow and Carlson, 1982).

TPT was increased by an average of 2.0 msec (sd 2.9 msec), which was a statistically significant increase (T=4.4; $P<.001$). This result suggests that much of the increase in TPT between occlusal positions can be accounted for by this factor. This suggestion is also supported by studies on postcranial muscle (see Woittiez et al., 1984, for a review), which demonstrate that twitch contraction times are influenced by muscle length.

Dechow and Carlson (1986a) examined changes in stimulated tetanic bite force in rhesus monkeys with changes in gape and showed that force declines considerably at larger gapes. However, within the narrow range of muscle lengthening caused by different transducer positions here, differences in force are <5% and are not statistically significant.

Cephalometric procedure and biomechanical model

The cephalometric procedures and biomechanical model were similar to those described by Dechow and Carlson (1986b). Care was taken to ensure repeatable radiographic protocols, including similar distance constants between the X-ray tube and the primate subject, throughout the course of the study. Lateral cephalograms of each monkey were traced on acetate paper, and the cartesian coordinates of craniometric points were measured with a digitizer and microcomputer. Cephalometric angles and distances were computed using programs written for this purpose in Microsoft fortran and SYSTAT basic.

The biomechanical model differed from Dechow and Carlson (1986b) in that 1) bite forces were considered at both the incisors and the most posterior molar cusps and 2) some information on the position and orientation of the temporalis muscle and the masseter muscle were included (Fig. 2). The following points were digitized on each radiograph (Fig. 2).

1. Bite points—incisal bite point (IBP), premolar bite point (PBP), and molar bite point (MBP): IBP is located at the anteroinferior edge (occlusal tip) of the upper central incisors. PBP is located at the most inferior aspect of the most anterior premolar cusp (P^3 in adults; variable in juveniles). MBP is located at the most inferior aspect of the most posterior molar cusp (M^3 in adults; dM^2 or M^1 in juveniles).
2. Superior condylion (TMJ): point at the most superior aspect of the mandibular condyle.
3. Temporalis points–temporalis origin points one and two (TO1 and TO2) and temporalis insertion point one (TI1): TO1 is located at the most anterosuperior aspect of the superior temporal line. TO2 is directly above the external auditory meatus. This point lies near the most posteroinferior fibers of temporalis. TI1 is located at the most superior aspect (tip) of the coronoid process.
4. Masseter points–anterior masseter origin point (MO1) and masseter insertion points one and two (MI1 and MI2): MO1 is located at the most anteroinferior aspect of the zygomatic arch. MI1 is the most inferior point on the angle of the mandible, whereas MI2 is the most posterior point on the angle of the mandible. These points bear a consistent relationship to the attachments of masseter along the zygomatic arch and the mandibular angle. We demonstrated this radiographically in six monkeys by surgically exposing the masseter muscle and implanting muscle markers in the muscle and bone markers in the adjacent bone (for marker techniques, see Carlson, 1983).

The craniometric points were used to calculate the following planes and measurements relevant to the mechanical properties of the masticatory systems (Figs. 2A, B).

1. Mandibular length: the distance between points TMJ and IBP. This dimension was used as a measurement of craniofacial size.
2. Occlusal plane: plane passing through points MBP and PBP. Point IBP usually lay 1–3 mm superior to this plane.
3. Muscle angles: the angle of the occlusal plane with lines representing the position of the masseter or temporalis muscles. The sine of these angles represents the proportion of force directed along the muscle line that would be converted to force normal to the occlusal plane.

a. Masseter muscle angle: the angle of the occlusal plane to a line between points MO and MI (Fig. 2A). MO was one-third of the distance between MO1 and TMJ. Dissections of the masseter muscle in several rhesus monkeys showed that the masseter originates from approximately the anterior two-thirds of the zygotic arch. No attempt was made to distinguish between superficial and deep masseter. Superficial masseter arises from much of the anterior two-thirds of the zygomatic arch in rhesus monkeys, whereas deep masseter arises more posteriorly. MI was halfway between MI1 and MI2. MI is located near the center of the inferior extent of the masseter insertion on the angle of the mandible. Thus the point MA is located approximately at the center of the masseter origin in the midportion of the mandibular ramus.

b. Temporalis muscle angle: the angle of the occlusal plane to a line between points TO and TI (Fig. 2B). Point TO was found by taking a point midway between points TO1 and TO2, which are located at the anterior and posterior limits of the origin of temporalis. Temporalis inserts on the coronoid process, of which point TI is the tip.

4. Biting and muscular moment arm lengths: moment arm lengths were measured along the occlusal plane. This was done because the measured bite force was normal to this plane. Vertical moments were not considered because these would lead to movements parallel to the occlusal plane and to horizontal reaction forces at the TMJ.

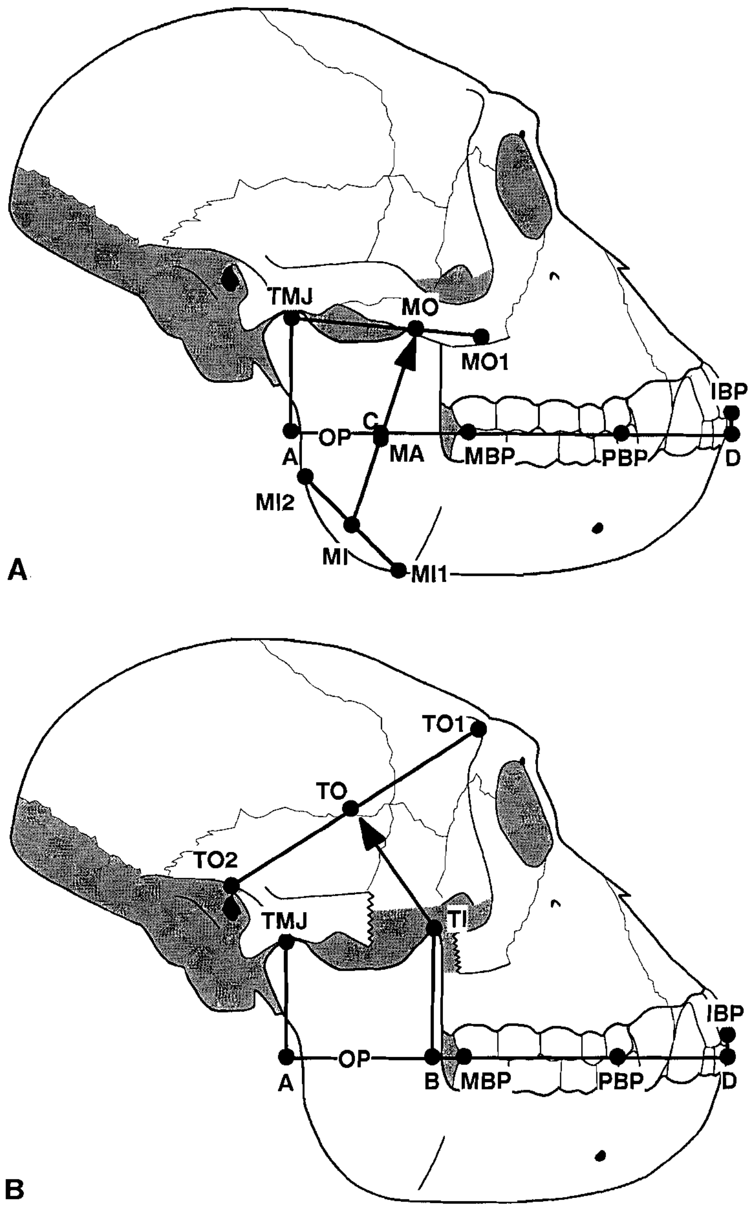

Fig. 2. Cephalometric points and biomechical model. A: Points and lines relating to the masseter muscle. B: Points and lines relating to the temporalis muscle. Abbreviations of craniometric points: IPB, incisal bite point; MBP, molar bite point; MI1 and MI2, masseter insertion points 1 and 2; MO1, anterior masseter origin point; PBP, premolar bite point; TI, temporalis insertion point; TMJ, superior condylion; TO1 and TO2, anterior temporalis origin points 1 and 2. Additional abbreviations include: A, point at the intersection of the occlusal plane and a line normal to this plane that also intersects point TMJ; B, point at the intersection of the occlusal plane and a line normal to this plane that also intersects point TI; C, point at the intersection of the occlusal plane and a line normal to this plane that also intersects point MA; D, point at the intersection of the occlusal plane and a line normal to this plane that also intersects point IBP; MA, masseter point, which is midway between MO and MI; MO, masseter origin point, which is one-third of the way from MO1 to TMJ; OP, occlusal plane; TI, temporalis insertion point, which is midway between TI1 and TI2; TO, temporalis origin point, which is midway between TO1 and TO2. Arrows indicate the orientation of the temporalis (between TO and TI) and the masseter (MO and MI) relative to the occlusal plane (OP).

Neither horizontal or vertical reaction forces at the TMJ were measured in this study. Moment arm lengths were measured by computing the distances between the intersection of the occlusal plane and a line normal to this plane that also intersects point TMJ (point A; Fig. 2A,B) and various other points associated with masticatory muscles and bite positions. The following moment arm lengths were calculated.

a. Moment arm length for incisor biting: the distance between point A and the intersection of the occlusal plane with a line normal to this plane that passes through point IBP (point D; Fig. 2A,B).

b. Moment arm length for molar biting: the distance between points MBP and A. By definition, point MBP is on the occlusal plane (Fig. 2A,B).

c. Masseter moment arm length: the distance between points C and A (Fig. 2A). Point C was determined by first finding point MA, the midpoint between points MO and MI. Point MA approximates the center of the masseter insertion on the ramus of the mandible. Point C is the intersection of the occlusal plane with a line normal to this plane that passes through point MA.

d. Temporalis moment arm length: the distance between points A and B (Fig. 2B). Point B is the intersection of the occlusal plane with a line normal to this plane that passes through point TI, the representation of the temporalis insertion.

5. Mechanical advantage: the mechanical advantage of a muscle is defined as the ratio of the lever arm to the load arm. The lever arms are the moment arm lengths for the masticatory muscles while the load arms are the moment arm lengths for the various bite positions. Mechanical advantage was calculated for both the masseter and the temporalis at two biting positions, at the incisors and at the molars.

6. Percent of muscle force contributing to bite force: the approximate amount of muscle force that contributed to biting force was calculated for each bite position by multiplying the sine of the masticatory muscle angles by the mechanical advantage of the muscle. The remaining masticatory muscle forces are horizontal forces along the tooth row and horizontal reaction forces at the temporomandibular joint or vertical reaction forces at the temporomandibular joint.

7. Estimates of masticatory muscle force: estimates of the actual forces produced by the masticatory muscles in rhesus monkeys were calculated using a mechanical analysis. Separate estimates were produced using biting forces measured at 1) the incisors and 2) the molars. The following equation was used to make these estimates:

$$(TF*PT + MF*PM)/100 = BF,$$

where TF is temporalis muscle force, MF is masseter muscle force, PT is the percent of temporalis muscle force contributing to bite force, and PM is the percent of masseter muscle force contributing to bite force. Since there are two unknown values in this equation, a further approximation was used to estimate the ratio of temporalis to masseter muscle force. This ratio was based on actual muscle forces of the masticatory muscles measured using a whole muscle contractile property technique (Dechow and Carlson, 1986b; Dechow et al., 1987). In 20 rhesus monkeys of various ages and sexes, it was found that the combined forces of the masseter and medial pterygoid muscles were on average 94% of the force of the temporalis muscle. Medial pterygoid was included here because it also contributes to occlusal force (BF). Calculations of medial pterygoid force were combined with masseter because its position is similar to masseter in a lateral projection. Combining these muscles was necessary because we were unable to derive a satisfactory method of determining medial pterygoid position from radiographs.

RESULTS

Body and cranial size

Significant differences in body weight and mandibular length were found between groups (Table 1). On average, adult males weighed 1 kg (16%) more than adult females and had mandibles that were 9.1 mm (11%) longer. Juveniles had significantly smaller weights and cranial dimensions than either adult males or females.

The relationship between mandibular length and the cube root of body weight for all groups combined appeared curvilinear (Fig. 3) and was modeled as an exponential relationship yielding the equation:

$$ML = -66.03 + e^{[4.389 + (.3462 \times CRWT)]},$$

TABLE 1. Size measurements[1]

	Group	Mean	sd	N
Body weight (kg)	Juvenile	3.1	.7	36
	Adult female	6.3	1.4	81
	Adult male	7.3	1.7	15
	F	93.7		
	Tukey tests	1,2,3		
Mandibular length (mm)	Juvenile	63.3	6.9	36
	Adult female	86.9	5.1	81
	Adult male	96.0	9.0	15
	F	232.9		
	Tukey tests	1,2,3		

[1] All F values are significant at $P<.001$. Results of posthoc Tukey tests at $P<.05$; 1, juvenile different from adult female; 2, juvenile different from adult male; 3, adult female different from adult male.

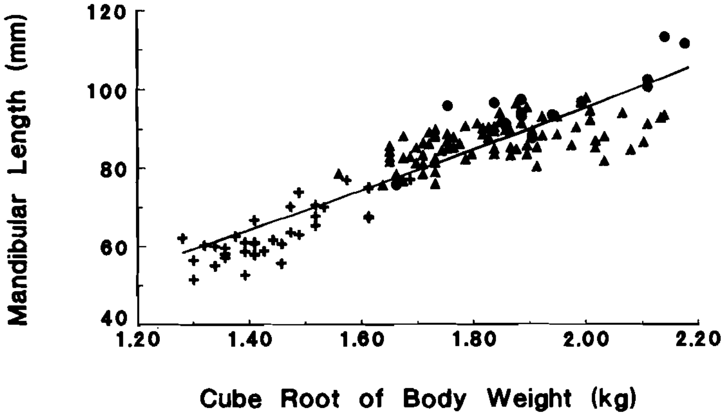

Fig. 3. Plot of a measure of craniofacial size, mandibular length, with a measure of body size, the cube root of body weight. The crosses are juvenile animals; the triangles are adult females; and the circles are adult males. The line is a plotting of an exponential relationship between the two variables. Note that adult males fall primarily above the line compared to adult females, which do not. This demonstrates that males have significantly longer mandibles than do adult females of comparable body weight. We suggest that this is a reflection of the development of the canine-sectorial premolar complex in adult male monkeys.

where ML is mandibular length and CRWT is the cube root of body weight. Examination of the residuals about this line resulted in significant differences ($F=11.0$, $P<.001$), where the juvenile mean was below the line, the adult male mean was above the line and the adult female mean did not differ significantly from zero.

A closer examination of the data in Figure 3 revealed that this line, which was fitted simultaneously for all groups, does not adequately describe growth of the face compared to body size. If each group is examined separately, it is apparent that there is a leveling off of mandibular length in adult females in the upper half of their range of body weights. A significant regression line was computed for the adult females alone ($ML=47.7+21.3*CRWT$), and residuals were calculated for adult males and adult females. A t test on these residuals revealed that adult males have mandibles that are, on average, 7 mm longer than those of adult females at comparable body weights ($T=5.5$, $P<.001$).

Examination of other craniofacial dimensions and the force dimensions revealed similar patterns when plotted against body weight. However, when the craniofacial or force measurements are plotted against mandibular length, most of the differences between the juveniles, adult females, and males are smaller or not present. To minimize the effects of relative differences in body size and cranial size between adult males, adult females, and juveniles, mandibular length (as a measure of skull size) rather than body weight was used as a general size variable in subsequent analysis.

Contractile properties

Twitch readings and speed of contraction. Twitch recordings were similar to those generated using isolated in vitro muscle preparations (Fig. 4A) (Dechow et al., 1987). All recordings showed a fast contractile speed, which averaged between 30 and 50 msec for both TPT and HRT for the three groups at various jaw positions (Table 2). On average, TPT was 1–4 msec slower than HRT. Although several of these differences were statistically significant, they are probably of little significance physiologically.

Examination of TPT and HRT between jaw positions indicated that measured contraction speed increased as the bite point was moved anteriorly in some groups (Table 2). Analysis of variance with repeated factors (for jaw position) revealed that these differences were statistically significant for TPT in the juvenile (F=58.2; $P<.001$), adult female (F=72.3; $P<.001$) and adult male (F=5.1; $P<.014$) groups. HRT was significantly different between jaw positions for adult females (F=18.4; $P<.001$) but not for juveniles (F=3.7; $P<.089$) or adult males (F=.189, $P<.829$).

There was a significant decrease in TPT or HRT for all jaw positions between juveniles and both adult groups and between female and male adults. This decrease corresponded to increases in cranial and body size. A regression of TPT against mandibular length (Fig. 5) gave a negative slope of −.33 (constant=79.6; r=.58; $P<.001$). Analysis of the residuals around this regression line revealed significant differences by age-sex group (F=7.3; $P<.001$). Juveniles and adult females did not differ significantly from each other and were scattered proportionately about the regression line. However, adult males differed significantly from both juveniles and adult females and were found, on average, to be positioned 5.2 msec (sd 4.0) below the regression line.

Peak twitch and tetanic tension. Analysis of peak twitch and tetanic tension data yielded similar differences between jaw positions and between age-sex groups. The following describes differences in peak tetanic tension alone. This is appropriate since peak tetanic tension, as a measure of maximal masticatory muscle force, is an important measurement functionally. Conversely, peak twitch tension is less significant, since it is primarily a byproduct of the twitch stimulation protocol. However, peak twitch tension usually maintains a constant ratio to peak tetanic tension so that analysis of its values leads to similar relative differences between groups as peak tetanic tension.

It is evident that maximal tetanic bite

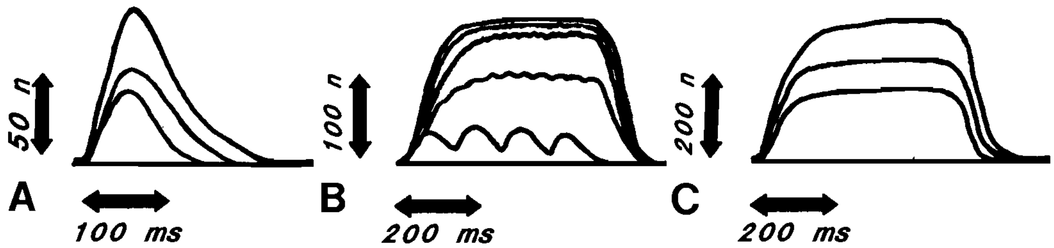

Fig. 4. Tracings of raw masticatory muscle twitches and tetani redrawn from oscilloscope photographs following a session of stimulated bite force measurement in an adult female rhesus monkey. A: Three superimposed twitches. The twitch of least amplitude was taken with the bite force transducer positioned at the incisors, middle amplitude at the premolars, and greatest amplitude at the molars. A slightly greater TPT is evident at molar biting compared to incisal biting. B: Force-frequency relationship following a series of stimulations at 10, 25, 40, 60, 80, and 100 Hz with the bite force transducer positioned at the incisors. Fused tetanus was obtained by stimulating at 80 Hz in this animal. Thus the tetanus following stimulation at 100 Hz overlies that from stimulation at 80 Hz. C: Three fused tetani with the bite force transducer positioned at the incisors (trace of least amplitude), at the premolars (trace of intermediate amplitude), and at the most posterior molar cusp (trace of greatest amplitude).

TABLE 2. Masticatory muscle twitch and tetanic measurements[1]

		Incisor			Premolar			Molar		
	Group	Mean	sd	N	Mean	sd	N	Mean	sd	N
Time-to-peak tension (TPT) (msec)	Juvenile	44.1	5.3	15	40.6	4.3	5	50.1	8.6	13
	Adult female	37.4	4.4	24	39.6	7.8	37	43.2	5.1	49
	Adult male)	31.0	3.7	13	30.7	4.3	13	32.9	2.7	13
	F	29.2			8.5			31.9		
	Tukey tests	1,2,3			2,3			1,2,3		
Half relaxation time (HRT) (msec)	Juvenile	40.2	9.8	15	36.2	4.6	5	49.4	16.2	13
	Adult female	33.2	4.2	24	38.2	7.0	37	38.7	6.6	49
	Adult male	28.5	4.4	13	28.0	3.6	13	28.1	4.1	13
	F	12.3			13.0			19.4		
	Tukey tests	1,2			2,3			1,2,3		
Peak twitch tension (PT) (n)	Juvenile	16.9	5.7	16	30.1	9.0	5	36.9	10.4	12
	Adult female	31.0	8.6	24	50.1	10.1	37	73.4	16.7	49
	Adult male	34.5	8.1	13	63.2	15.2	13	99.3	24.1	13
	F	23.3			15.9			40.6		
	Tukey tests	1,2			1,2,3			1,2,3		
Peak tetanic tension (PO) (n)	Juvenile	70.3	18.7	34	97.8	32.6	36	139.8	39.9	36
	Adult female	133.1	31.6	52	184.6	40.5	81	286.2	64.0	81
	Adult male	151.1	42.9	14	242.4	57.9	15	369.3	101.9	15
	F	57.8			84.7			92.2		
	Tukey tests	1,2			1,2,3			1,2,3		

[1] All F values are significant at $P < .001$. For key to Tukey tests, see table 1.

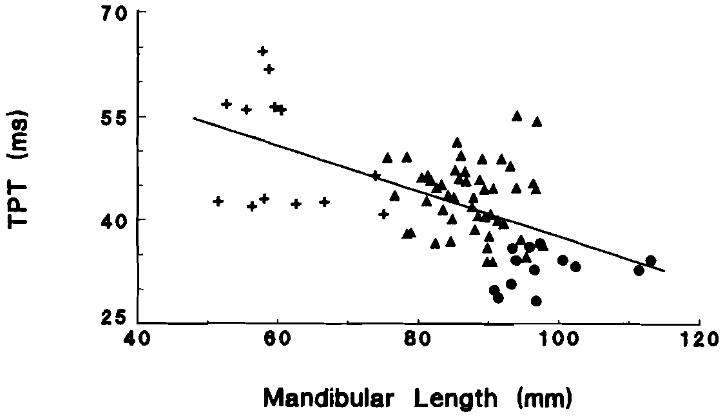

Fig. 5. Time-to-peak tension (TPT) vs. mandibular length in 75 rhesus monkeys. All values of TPT in this graph were recorded with the bite force transducer positioned at the most posterior molar cusp. Symbols for age-sex groups are the same as in Figure 3. Note that the adult male values fall primarily below the regression line, whereas the juvenile and adult female values are distributed proportionately about the line. Thus adult males have shorter TPTs than would be expected given their mandibular length.

forces should increase as the bite point is moved posteriorly from the incisors to the molars, since the load arm for biting is decreasing while the lever arms for the muscles of mastication remain constant. This trend can be seen in all groups (Table 2, Figs. 4C, 6). There was a tendency for the bite force to increase more in the larger monkeys. For instance, in the juveniles, the bite force increased 100% at the molars compared to the incisors; in the adults, it increased 115% (females 115%, males 114%).

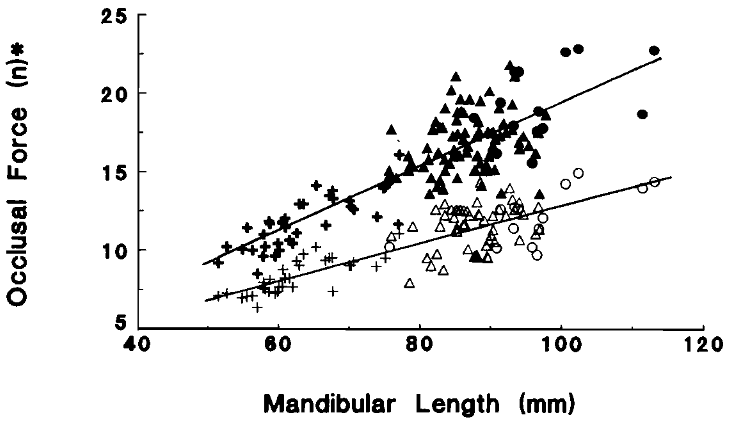

Fig. 6. Occlusal force vs. mandibular length in rhesus monkeys. Occlusal force is given as the square root of the maximum stimulated tetanic bite force in newtons. Symbols for age-sex groups are the same as in Figure 3. The lower regression line and the lighter and open symbols are for force values measured with the transducer positioned at the incisors; the upper regression line and the darker and solid symbols are for force values measured with the transducer positioned on the most posterior molar cusps. A regression line (not illustrated here) intermediate between these two and with similar scatter of data was also found for stimulated bite force measured at the premolars vs. mandibular length. The slope for incisal occlusal force vs. mandibular length was .12 (r=.83, $P<.01$) and for molar occlusal force vs. mandibular length was .20 (r=.84, $P<.001$). The constants were not significantly different from zero. Analysis of residuals about these regression lines did not demonstrate any significant differences between juveniles, adult females, and adult males. In other words, increases in maximum stimulated occlusal force can be accounted for by increases in cranial size regardless of age or sex.

Peak stimulated occlusal forces were much larger in adult monkeys than in juveniles and were moderately larger in adult males than in adult females (Table 2, Fig. 6). Differences were not apparent when occlusal force was regressed against mandibular length (Fig. 6) and size-related effects were removed. Analysis of the residuals by age-sex groups for each of the regression lines in Figure 6 (and for the regression line for premolar occlusal force vs. mandibular length, not shown) demonstrated no significant differences.

In addition, we calculated the coefficients of allometry according to Huxley's equation using the natural log of the square root of biting force vs. 1) the cube root of the log of body weight and 2) the log of mandibular length. Using this method, a coefficient of 1.0 indicates isometry. Coefficients were calculated for bite force vs. mandibular length because it was suspected that, although bite force increases at a faster rate than body weight (Dechow and Carlson, 1986b), bite force may increase isometrically with facial size, especially facial length. We suspect this on theoretical grounds because the amount of muscle force that is being converted to bite force is proportional to the moment arm length of biting, which is similar to facial length.

The allometric coefficients demonstrated that this hypothesis is supported. Coefficients of allometry for bite force (dependent variable) at the incisors, premolars, and molars vs. body weight (independent variable) were, respectively, 1.27 (standard error .06), 1.39 (.07), and 1.41 (.07), all of which were significantly greater than isometry (1.0 at $P<.01$). Coefficients for bite force vs. mandibular length were, respectively, 0.92 (.06), 1.07 (.05), and 1.08 (.05), none of which were significantly different from isometry (1.0 at $P<.05$). This analysis shows that bite force increases at a faster rate than body weight. However, bite force increases isometrically relative to facial size, in particular mandibular length. Furthermore, analysis of residuals shows that adult males, females, and juveniles are all equally distributed about the regression line (as can also be seen in a nonlog plot, Fig. 6). This suggests that differences in maximal masticatory muscle force or bite force between our age and sex groups reflect isometric scaling with increasing facial length.

Growth and jaw mechanics

Muscle angle. The sine of the muscle angles for the anterior portion of the masseter and the anterior portion of the temporalis (Table 3) suggest that the majority of forces from these muscles can be used to exert a biting force normal to the occlusal plane. Significant differences between groups suggest that masseter is more optimally situated to produced occlusal forces in adult female rhesus monkeys than in juveniles or adult males, whereas temporalis is better situated in juveniles. The differences between groups for muscle angles are small and probably do not have great physiological significance. Correlation coefficients of muscle angles with mandibular length revealed significant ($P<.05$) but weak relationships (masseter angle $r=.403$; temporalis angle $r=.360$). This suggests that shifts in muscle orientation relative to the occlusal plane are evident but minor throughout growth.

Moment arm length. Moment arm lengths for masseter and temporalis (lever arms) showed differences between juveniles and adults but not between adult males and females (Table 4). On the other hand, moment arm lengths for incisor and molar biting (load arms) were significantly different between all three age-sex groups.

Mechanical advantage. Absolute differences in the mechanical advantage of the masseter and temporalis muscles between groups for incisor biting were small. Small F values indicated minimal statistical significance (Table 5). Likewise, absolute differences for mechanical advantage of temporalis muscle for molar biting only showed significant differences between juveniles and adult females. On the other hand, absolute differences for mechanical advantage of masseter and molar biting were larger between all groups and were highly statistically significant. Juveniles had small mechanical advantages, which increased in adults and were the largest in adult females. A correlation coefficient of .45 demonstrated that the mechanical advantage of masseter for molar biting increased with craniofacial size (mandibular length).

Percent of muscle force contributing to bite force. Analyses of the percent of masseter and temporalis muscle force contributing to

TABLE 3. Biomechanical measurements: Sine of muscle angle[1]

	Group	Mean	sd	N
Sine of masseter muscle angle	Juvenile	.88	.04	36
	Adult female	.93	.03	81
	Adult male	.90	.04	15
	F	20.8		
	Tukey tests	1,2,3		
Sine of temporalis muscle angle	Juvenile	.94	.06	35
	Adult female	.87	.07	81
	Adult male	.91	.08	15
	F	13.9		
	Tukey tests	1		

[1] All F values are significant at $P < .001$. For key to Tukey tests, see Table 1.

TABLE 4. Biomechanical measurements: Moment arm lengths[1]

	Incisor			Molar			Masseter			Temporalis		
Group	Mean	sd	N	Mean	sd	N	Mean	sd	N	Mean	sd	N
Juvenile	54.6	7.2	36	27.4	4.4	36	12.9	2.2	36	14.8	2.6	36
Adult female	78.0	4.1	81	31.5	3.2	81	19.0	2.0	81	19.8	2.6	81
Adult male	85.3	8.7	15	35.8	5.5	15	19.4	2.7	15	20.7	4.0	15
F	250.8			27.5			111.4			44.2		
Tukey tests	1,2,3			1,2,3			1,2			1,2		

[1] All F values are significant at $P < .001$. For key to Tukey tests, see table 1.

bite force for incisor and molar biting showed similar differences between age-sex groups, as did the analyses of mechanical advantage (Table 6). This is expected since these percentages were a product of the sine of the muscle angle and the mechanical advantage. Since the sine of the muscle angle did not have differences as great as for mechanical advantage, the latter is the primary influence on differences in the percent of muscle force contributing to bite force. Also, these differences were similar to those of mechanical advantage since there are some similarities in the pattern of variation between groups in mechanical advantage and muscle angle; i.e., adult females had both the most advantageous muscle angles and muscle mechanical advantages for the masseter muscle.

Estimated masticatory muscle forces. Masticatory muscle forces were estimated for the masseter and medial pterygoid muscle complex and for the temporalis muscle with the biomechanical model and stimulated bite force measurements (Table 7). Between age-sex groups, these followed a predictable and statistically significant pattern of increase in muscle force. There was also great congruence between muscle forces estimated from incisor biting and molar biting. This congruence suggests validity of the biomechanical model used in this study.

DISCUSSION

Masticatory muscle force

In a recent publication (Dechow and Carlson, 1986b), we determined that bite force increases at a faster pace than body weight during growth. We calculated the coefficient of allometry of stimulated bite force at the molars vs. body weight. The coefficient (1.09) was significantly greater than .66, which is

TABLE 5. Biomechanical measurements: Muscle mechanical advantage[1]

		Incisor biting			Molar biting		
	Group	Mean	sd	N	Mean	sd	N
Mechanical advantage of masseter	Juvenile	.24	.02	36	.47	.06	36
	Adult female	.24	.02	81	.60	.07	81
	Adult male	.23	.02	15	.55	.09	15
	F, *P*	4.9, <.01			45.3, <.001		
	Tukey tests	3	1,2,3				
Mechanical advantage of temporalis	Juvenile	.27	.04	36	.54	.08	36
	Adult female	.25	.03	81	.63	.09	81
	Adult male	.24	.04	15	.59	.12	15
	F, *P*	5.6, <.01			12.6, <.001		
	Tukey tests	2	1				

[1] All F values are significant at $P < .001$. For key to Tukey tests, see Table 1.

TABLE 6. Biomechanical measurements: Percent of muscle force contributing to bite force[1]

		Incisor biting			Molar biting		
	Group	Mean	sd	N	Mean	sd	N
Percent of masseter muscle force contributing to bite force	Juvenile	21	2	36	42	7	36
	Adult female	22	3	81	56	7	81
	Adult male	20	2	15	49	10	15
	F, *P*	8.9, <.001			45.5, <.001		
	Tukey tests	3	1,2,3				
Percent of temporalis muscle force contributing to bite force	Juvenile	25	4	35	51	8	35
	Adult female	22	2	81	54	7	81
	Adult male	23	3	15	53	11	15
	F, *P*	18.8, <.001			3.0, NS		
	Tukey tests	1,2					

[1] All F values are significant at $P < .001$. For key to Tukey tests, see Table 1.

TABLE 7. Biomechanical measurements: Estimated masticatory muscles forces (in newtons)[1]

		Incisor biting			Molar biting		
	Group	Mean	sd	N	Mean	sd	N
Masseter and medial pterygoid	Juvenile	146.7	40.8	33	142.3	38.1	33
	Adult female	293.1	69.4	52	267.1	62.9	52
	Adult male	351.0	97.7	14	356.0	83.4	14
	F	67.1			76.7		
	Tukey tests	1,2,3			1,2,3		
Temporalis	Juvenile	156.0	43.4	33	151.4	40.6	33
	Adult female	311.8	73.8	52	284.2	66.9	52
	Adult male	373.4	103.9	14	378.8	88.7	14
	F	67.1			76.7		
	Tukey tests	1,2,3			1,2,3		

[1] All F values are significant at $P < .001$. For key to Tukey tests, see Table 1.

the expected value for an isometric relationship between an area measurement, bite force, and a volumetric measurement, body weight. Bite force was taken to be an area measurement since it is expected to be proportional to the cross-sectional area of the contracting muscle fibers. The coefficient indicated that bite force increased faster than body weight throughout a mixed age and sex series of rhesus monkeys.

In the present study, even though our sample size was more than doubled, allowing a more accurate calculation of this coefficient, its value was similar. However, additional analysis revealed that bite force increases in size isometrically with facial length. This result corresponds with findings by Cochard (1985) concerning differences in scaling of most skeletal facial dimensions between male and female macaques. Despite differences between males and females in relative postcanine teeth dimensions, the majority of viscerocranial dimensions scale similarly during growth in both sexes. Likewise, the results presented here suggest that masticatory muscle growth occurs in such a way as to maintain maximal bite forces that are proportionate for a given facial size.

Evidence in the literature suggests that the muscles of mastication increase in size differentially throughout growth in rats (Houston, 1974), mice (Nakata, 1981), and humans (Schumacher, 1962). Differences in muscle proportion have also been reported between various species of primates (Strzalko and Malinowski, 1972). On the other hand, Cachel's (1984) study of dry weights of masticatory muscles in a series of different primates over a large range of body sizes indicates isometric interspecific scaling of all muscles with body weight. In a study comparing adult males and females of the rhesus monkey, Grant (1973) reports that posterior temporalis is proportionately larger in adult males than in adult females when compared with anterior temporalis and superficial masseter. Cochard (1985) reports a scaling difference between male and female rhesus monkeys in bizygomatic breadth, which he concludes is largely because of differences in temporal fossa size (and, by inference, temporalis muscle size). Cochard therefore speculates that similar differences in scaling between males and females in both bizygomatic breadth and canine size imply a link between relatively larger temporalis muscles in adult males and relatively larger canines. However, as Cochard suggests, the resolution of this problem requires further studies of changes in muscle proportions and structure throughout growth. This is especially true since it is possible that complex highly pennate muscles, such as the masticatory muscles, may increase their physiological cross-sectional area by adding length as well as adding width. It is also likely that complex muscles cannot double their force output simply by doubling their mass. Because of the restrictions of the locations of muscle origin, insertion, and position, packaging of muscle fibers may become a significant problem. This may require the addition of relatively more fibers, which are located in a less advantageous position, to effect an increase in muscle force. Given these constraints, it is possible that an isometric increase in maximal bite force with facial dimensions may actually require more complex growth changes in the masticatory muscles themselves, such as in relative proportions of various parts of the muscles, in muscle fiber and connective tissue orientation, and in contractile and histochemical properties (Carlson et al., 1982; Carlson and Poznanski, 1982).

Masticatory muscle contraction speed

Contraction speeds (TPT and HRT) of the rhesus monkey masticatory muscles measured with our technique suggest that these muscles are composed primarily of fast muscle fibers and are similar to those reported in the literature for other mammals (see Guelinckx et al., 1986, for a review of these values). Recent studies in our laboratories (Carlson et al., 1986; Dechow et al., 1987) indicate that TPTs measured with the bite force technique are not significantly different from those measured with an in vitro technique that assesses values for selected small bundles of masticatory muscles fibers. Attempts by us to measure directly the contraction values of whole masticatory muscles have resulted in TPTs that average about 10 msec greater than the values reported here (Carlson et al., 1986; Dechow et al., 1987).

The importance of the speed of the masticatory muscles for the physiology of mastication may be in the limitations placed on the rate of chewing. For instance, Hylander and colleagues (1987) suggested that the rate of unloading of the craniofacial skeleton during mastication corresponds directly with the contraction speed of the masticatory muscles. They also noted that the rate of loading probably includes other considerations, such as the timing of the recruitment of the masticatory muscles. Despite the general assumption that higher rates of mastication corresponded with more rapidly contracting masticatory muscles in smaller animals, note that masticatory muscle speed in our growth series of macaques did not decrease but rather increased as the animals became larger. Data on growth changes in chewing rates in rhesus monkeys would be interesting to study in this regard, as would interspecific data on growth rates of both masticatory muscle contraction speeds and chewing rates of mammals of a range of body sizes.

The difference in the contraction speed of the muscles of mastication over the size range from juvenile to adult male rhesus monkey consists of a shift of slightly greater than 15 msec. Physiologically, this probably does not represent a significant shift as the time-to-peak tensions are at least an order of magnitude faster than mastication rates in rhesus monkeys. Such a change may be indicative of changes in the histochemical characteristics of the masticatory muscles and other associated characteristics. For instance, a shift to a muscle with a greater proportion of fast fatiguable fibers from one with a greater proportion of slow or fast fatigue-resistant fibers would result in a concurrent increase in contractile speed coupled with lesser oxidative capacities and a decrease in fatigue resistance (Close, 1972). Some of the results of Maxwell and colleagues (1979) coupled with results of the current study support this suggestion as an explanation of growth changes in the contractile speed of rhesus masticatory muscles. Maxwell and colleagues found that the anterior masseter and anterior temporalis muscles of adult male rhesus monkeys had a significantly higher percentage of their cross-sectional areas made up of fast fatiguable fibers than adult females or juvenile monkeys. A similar trend was also seen in the posterior temporalis and posterior masseter but was not statistically significant. The authors did not find significant differences between adult females and juveniles in muscle composition of fast fatiguable fibers. By contrast, significant differences are evident between adult males, adult females, and juveniles for both TPT and HRT. We suspect that measurements of TPT using the stimulated bite force technique may be a more accurate way of assessing changes in the masticatory muscle properties than histochemical measurement due to problems associated with adequate typing and sampling. The stimulated bite force technique is not sensitive to individual parts of the masticatory system, but can give an average assessment of changes in the system as a whole.

Despite the evidence that muscle force varies isometrically with facial size, changes in the properties of the masticatory muscles with size cannot be considered to result solely from simple proportional increases in muscle mass during growth. One indication of this is that male rhesus monkey masticatory muscles appear to be faster than would be predicted on the basis of craniofacial dimensions alone. Several alternate explanations may be important to explain such results. One possibility is that sexual hormones have a distinct impact on the maturation of the masticatory muscles in male and female rhesus monkeys. Estrogen has been shown to have an inhibitory effect on muscle development in mice (Ihemelandu, 1981), although testosterone implants in rabbits have little effect on muscle composition (Grigsby et al., 1976). No experimentation has examined the impact of hormonal influences on masticatory muscle development. It is possible that such influences are species specific, having a greater importance in highly sexual dimorphic species such as Old World monkeys.

Another possibility to explain differences during growth in muscle speed relates to functional effects on muscle development. There are few data that show what proportion of maximal masticatory muscles forces are actually employed during mastication, but, for the majority of masticatory cycles, it is likely that the forces are relatively low but are maintained for high numbers of repetitions. Muscles that are well adapted for this sort of behavior would have increased fatigue-resistant properties in the muscle fibers that are most often recruited. Maxwell and colleagues (1979) found that the anterior masseter and anterior temporalis have a higher proportion of slow fibers, which are highly resistant to fatigue, compared to the posterior parts of these muscles. They suggest that these differences may relate to differences in the recruitment and function of these regions.

Studies by Cochard (1985) indicate that facial size is positively allometric compared to postcanine dental dimensions in a sample of adult rhesus monkeys. If our data showing that bite forces increase proportionate to facial size are also considered, this suggests that bite pressures (force per unit area) increase throughout a range of body sizes. Our data show this to be true. Using published dental width dimensions (Swindler, 1976), dental length dimensions collected from our radiographs, and our bite force data, we estimated bite pressures in rhesus monkeys. We found that juveniles had an average postcanine biting pressure of 1.36 newtons (n)/mm^2 (sd .39), adult females 1.45 n/m^2 (sd .33), and adult males 1.87 n/mm^2 (sd .41). These differences are statistically significant at $P<.001$ (F= 116). Since rhesus monkeys of all ages and sexes process similar food items (Clutton-Brock, 1977), there would be little need to have differences in postcanine biting pressures because of diet. If food items are similar, there would only be a need to maintain similar pressures. The most likely possibility is that these larger biting forces in larger animals, especially males, reflect adaptations to agonistic behaviors involving use of the large male canines. Since these activities are not highly repetitious like mastication, they can be effectively carried out without the extra metabolic cost of maintaining energy stores in the muscle fibers that are recruited during these behaviors. This line of reasoning would then suggest that adult male rhesus monkeys need only maintain a high resistance to fatigue in relatively smaller portions of their masticatory muscles that are most recruited during mastication. A byproduct of this pattern would be the faster contraction times and higher postcanine biting pressures that we see in adult males, although these characteristics probably have little specific importance by themselves.

Estimated individual masticatory muscle forces

We attempted to use our biomechanical model to calculate estimates of how much force individual masticatory muscles can produce. We believe that these data are of interest as a minimal estimate of the capabilities of the masticatory muscles in macaques and are an improvement over published data in the literature on dry and wet muscle weights and estimates of muscle cross-sectional area. However, it should be stressed that these muscle forces are an underestimate of actual muscle forces, primarily because of limitations of taking relevant craniometric measurements from lateral cephalograms. However, this underestimate may not be large. One problem is that the muscles involved all have a mediolateral component that is not considered here. This component needs to be measured to ascertain the underestimation of force. The underestimation is probably not large because these muscles are much greater in dimension vertically than mediolaterally. More reliable estimates could also be derived if medial pterygoid and masseter were separated in the model.

Masticatory muscle position and orientation

Biomechanical changes in the masticatory apparatus can be divided into size-related shifts in 1) the orientation and 2) mechanical advantage of the masticatory muscles. The present study has divided these possible changes into their component parts (Tables 3–7). It is important to note that shifts in mechanical advantage or muscle orientation might also be effected physiologically by differential recruitment of regions within the masticatory muscles (Herring, 1985b).

There are a few reports in the literature of changes in the orientation of the masticatory muscles throughout growth. In humans, Moss and Simon (1968) suggested that growth changes in the inclination of the angular process of the mandible is linked functionally to a change in the orientation of the masseter muscle both in the coronal and sagittal planes. In the sagittal plane, Moss and Simon suggested that the masseter muscles change from a more vertical orientation in the neonate to a more oblique orientation in the adult. Gagnot and colleagues (1977) demonstrated age-related changes in the proportions of various parts of rabbit masticatory muscles that presumably would effect line of action. Weijs and colleagues (1987) showed changes in the biomechanics of rabbit masticatory muscle position during growth. Herring (1985b) cited an obscure thesis by Zey (1940) in which the transition from suckling to chewing in sheep is shown to be accompanied by shifts in the relative sizes and orientations of the masticatory muscles. Herring (1985b) also pointed out that, since bone growth is influenced by many factors besides muscle activity, adaptation in muscles may be a secondary response to the alterations in muscle orientation and position induced by skeletal growth. These muscle adaptations could include both differential growth in the masseter muscles and alterations in the pattern of muscle activity.

Work by Carlson and colleagues (1978) suggested that in macaques there are growth-related changes in the orientation of the temporalis muscle but not the masseter muscle (Carlson, 1983). The changes in temporalis were suggested to relate to adaptations during growth in the temporomandibular joint (Hinton and Carlson, 1983). The anterior component of the temporalis in young animals was reported to originate more posteriorly along the cranial vault and then expand in an anterior direction as the postorbital bar develops in juvenile animals. This morphological change is thought to coincide with shifts in masticatory muscle activity during growth that have been reported from EMG studies (McNamara, 1974).

In our current research, we found only a minimal shift in the orientations of the anterior portions of the masseter and temporalis muscles as the animals age from juvenile to adult stages. Even though we found some significant differences in masseter and temporalis orientation between age and sex groups, when we consider the impact of these changes to actual shifts in muscle force converted to bite force they are quite small, on the order of several percent. This result points out the importance of considering the orientation of the masticatory muscle relative both to its areas of attachment and to the bite plane and the direction of occlusal force. It is possible that a muscle might appear to shift orientation relative to its areas of origin and insertion but actually maintain a fairly constant orientation relative to the direction of functionally meaningful activity.

Changes in the mechanical advantage of primate masticatory muscles throughout growth have not been documented. However, a study by Oyen and colleagues (1979) suggested that in baboons the masticatory muscles become less efficient throughout growth due to the progressive elongation of the muzzle. They related incremental shifts in biomechanical efficiency of the masticatory muscles as the postcanine dentition erupts and the muzzle elongates to the development of the brow ridges. Data from macaque studies do not support this idea. Recent strain gage studies (Hylander and Johnson, 1987) suggested that brow ridges have very low strain values during incision and mastication. Our data show that the masticatory muscles of macaques do not become less mechanically efficient with an increase in cranial size during growth but conversely become more efficient in some cases. Adult macaques have more efficiently placed masseter muscles than juveniles for producing bite forces, especially distal motor forces as would be used in mastication. This is because the anterior extent of these muscles is more closely positioned to the distal molars and may result from 1) greater anterior growth of the masticatory muscles and/or 2) proportionately longer tooth rows as macaques mature. If adult macaques alone are considered, there is a size-related trend for smaller adults to have masseter muscles with greater mechanical efficiency than larger animals. For instance, in this study, the masseter and temporalis muscles were both better positioned for producing incisal and molar bite forces in adult females than in adult males. The reason for this was that muscle moment arms were similar between adult males and females but adult males had longer faces and thus longer moment arms for biting. If muscle moment arm lengths are primarily determined by neurocranial size (since the muscles originate on the neurocranium or cranial base and insert on the posterior portion of the mandible), then similarity in moment arm lengths between adult males and females would correspond with the minimal differences in neurocranial size between adult male and female macaques (Cochard, 1985). Conversely, temporalis has at best minimal shifts in mechanical efficiency throughout the range of juvenile and adult macaques.

SUMMARY

1. Maximal occlusal force is positively allometric to body weight in our sample of rhesus monkeys. Conversely, maximum occlusal force increases isometrically with a measurement of facial size, mandibular length. Neither juvenile nor adult female nor adult male rhesus monkeys showed a deviation from this pattern. An isometric increase of maximum bite force with facial size may not indicate a simple enlargement of the masticatory muscles during growth. Shifts in muscle architecture and differential growth of portions of the masticatory muscles may be necessary to accommodate isometric shifts in bite force.

2. Masticatory muscle contraction speeds decrease with increasing facial size in rhesus monkeys. Juveniles and adult females have similar contraction speeds when facial size is considered. However, adult males have faster speeds than would be predicted from facial size. We suspect that this difference relates to the relatively higher cross-sectional area of fast fatiguable fibers in the masticatory muscles of adult rhesus monkeys. These fibers would allow large forces for infrequent agonistic behaviors using the large male canines. A smaller core of fatigue resistant fibers would allow maintenance of occlusal forces for mastication similar to adult females and juveniles. It is possible that the development of differences in fiber types in the masticatory muscles of adult males relates to hormonal influences during growth.

3. Few meaningful differences are evident between juvenile, adult female, and adult male rhesus monkeys in the efficiency of their masticatory muscles for producing vertical occlusal forces. The percentages of masseter and temporalis muscle forces that contribute to incisal bite forces vary by only several percent between these groups and do not vary in a consistent pattern. No statistically significant differences were found for the percentage of temporalis muscle force contributing to molar bite force. This information is similar to that reported for humans by Sasaki and colleagues (1989). They found that voluntary bite forces in adults correlate with the cross-sectional areas of the masticatory muscles but not with other biomechanical measurements, such as lever arm length.

4. The major biomechanical difference between groups was in the percentage of masseter muscle force contributing to molar biting force. Adult masticatory muscles were better situated to produce molar biting forces than those of juveniles. This difference was an increase of 14% between juveniles and adult females and 7% between juveniles and adult males. Adults had masseter muscles that were more closely positioned to the most distal molars than juveniles. Adult females and males had similar moment arm lengths for masseter. However, males had more anteriorly placed molars, giving them a decreased advantage for molar biting compared to females. These data contradict claims by Oyen and colleagues (1979) for baboons. They suggest that the masticatory muscles of baboons become less mechanically efficient throughout growth due to the progressive elongation of the muzzle.

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