LENGTH–TENSION RELATIONSHIPS OF MASSETER AND DIGASTRIC MUSCLES OF MINIATURE SWINE DURING ONTOGENY

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Summary

At incremental whole muscle lengths, active isometric and passive elastic forces were recorded from the masseter and digastric muscles of anaesthetized miniature pigs (Hanford) weighing 2·0–20·0 kg. Wet muscle mass and maximum tetanic tension values for masseter exceed those for digastric and increase more rapidly with body mass (age). At any body mass, masseter exceeds digastric in the ratio of optimum length (that length at which maximum tetanic tension is produced) to *in situ* muscle length (that length which corresponds to the jaw in a closed position) and the proportion of passive tension comprising total (passive plus active) tension. Passive elastic tension begins to rise in masseter at lengths as short as 87 % of optimum (in younger pigs). In digastric, passive tension is absent until the muscle is stretched to a length slightly longer than optimum in younger pigs but occurs at shorter lengths in older pigs.

Contractile properties explain functional differences between masseter and digastric more clearly than they explain ontogenetic changes in either muscle. The behavioural transition from infant suckling to adult mastication of solid food is best characterized by a disproportionate increase in mass (and force) of the masseter, relative to digastric, and increased reliance upon active (rather than passive) tension.

Introduction

It is a relatively well documented, empirically observed physiological phenomenon that tetanic tension increases to its maximum (P_0) at an optimum length (L_0) as a whole muscle or fibre is stretched and then declines with further lengthening (e.g. Ramsey & Street, 1940; Gordon *et al.* 1966; Close, 1972, citing others). Although readily perceptible for muscles having their fasciculi arranged in parallel with the direction of whole muscle contraction, the length–tension relationship

becomes somewhat obscured with increasing complexity of muscle architecture. Despite recent advances using comprehensive examination of the contractile properties of unipinnate muscles (e.g. Goslow *et al.* 1977; Muhl *et al.* 1978; Walmsley & Proske, 1981; Muhl, 1982), the effect of multipinnate or complex fibre architecture on the relationship between tension and whole muscle excursion, especially within the range in which a muscle can be expected to perform work, remains enigmatic.

Contractile properties of whole pinnate muscles are best known for those studied in the hindlimb, especially as applied to understanding the functional consequences of muscle length changes during locomotion (e.g. Goslow & Van DeGraaff, 1982; Stephens *et al.* 1975; De Koning *et al.* 1987). However, with rare exceptions (e.g. Nemeth *et al.* 1986), the few studies of the masticatory muscles that are available indirectly measured tension and usually correlated forces measured on the jaw with gape position following direct stimulation of individual whole muscles (e.g. Nordstrom & Yemm, 1974; Yemm & Nordstrom, 1974; Thexton & Hiiemae, 1975; MacKenna & Turker, 1978). This approach was probably used because of the experimentally cumbersome geometry of the head and oral apparatus and the nonfusiform shape of most jaw muscles, which tend to make length manipulation for isometric tension measurements difficult at best. One attempt to circumvent this problem has been to measure contractile properties of small muscle bundles, but this necessitates severe extrapolation of the results (Faulkner *et al.* 1982; Maxwell *et al.* 1982). However, contraction of the muscle by direct stimulation less closely resembles the normal physiological condition than does contraction by stimulation of the muscle nerve.

The masseter and digastric muscles of miniature domestic pigs (*Sus scrofa*) present an interesting comparison of changes in muscle function during postnatal ontogeny. The transition from infant suckling behaviour to juvenile and adult mastication is characterized by increasing complexity of electromyographic activity in the masseter (Herring & Wineski, 1986), whereas the adult EMG pattern in digastric resembles that observable in the newborn. In this study, isometric and passive tension and whole muscle lengths were recorded from masseter and digastric following stepwise stretches and direct stimulation of the muscle nerve. The characteristic isometric contractile properties of these two muscles account for their functional differences and behavioural changes during ontogeny.

Materials and methods

Preparation and apparatus

Active and passive tetanic tension were measured at increasing muscle lengths in the masseter and digastric muscles of miniature swine (minipigs) of either sex and various strains (Table 1). Each animal was anaesthetized by gas inhalation (1 % halothane, nitrous oxide/oxygen), initially administered with a snout cone

Table 1. *Compilation of parameters considered in this study arranged in ascending order of body masses*

Pig no.	Body mass (kg)		L_i (cm)	Wet muscle mass (g)	P_0 (N)	L_0/L_i ×100	Muscle length at passive tension onset (%L_0)	Passive/total tension at P_0 (%P_0)
55	2·0	M	3·05	2·81	2·60	105	90·3	20·5
		D	2·38	0·40				
60	2·5	M	3·42	3·31	2·21	110	91·3	7·5
		D	3·67	0·92	0·55	102	100·0	4·2
61	2·7	M	3·54	4·53	2·63	99	97·7	23·8
		D	3·72	0·83	0·58	100	100·0	2·2
69	2·7	D	3·66	0·56	0·61	103	104·8	0·0
68	3·0	M	4·23	6·47	7·85	104	89·3	8·7
		D	3·92	0·91	0·91	100	100·0	1·6
62	3·2	M	3·83	4·01	4·63	109	84·5	26·7
		D	4·00	0·95	1·09	109	100·0	1·4
52	3·6	M	3·84	4·46	6·35	99	96·6	12·8
		D	3·69	0·86	0·46	101	100·0	3·9
73	5·5	M	4·90	6·62	8·83	115	89·6	17·5
		D	4·35	1·30	1·15	103	100·0	1·9
77	6·3	M	4·21	7·79	10·02	108	87·1	19·8
		D	4·92	1·28	1·08	105	99·0	4·0
53	6·8	M	4·66	14·49	19·30	100	97·0	5·5
		D	5·07	2·69	3·05	99	98·8	1·4
50	9·1	M	5·30	15·00	26·93	103	92·0	6·0
		D	4·33	2·06	3·29	100	100·0	1·0
54	11·4	M	5·66	17·27	20·94	109	89·8	13·0
		D	6·42	3·53	2·24	100	96·0	3·2
70	12·3	M	6·31	16·20	22·44	106	86·7	11·0
		D	5·73	1·96	2·39	104	93·6	3·0
42	14·5	M	5·63	19·40	15·41	105	98·9	3·7
		D	5·93	2·55				
71	15·9	M	6·27	20·53				
		D	6·11	2·89				
59	17·0	M	6·99	27·63	26·93	106	94·3	9·4
		D	6·74	4·90	3·14	100	97·0	2·8
44	18·6	M	6·66	48·07	40·40	106		
		D	6·85	4·47	7·85	104		
45	19·1	M	6·98	50·64	44·88	110	91·4	10·1
		D	6·40	4·57	5·06	100	92·0	1·7

D, digastric; M, masseter.

led from a Drager veterinary anaesthesia machine (North American Drager, Telford, PA).

The forehead, cheeks and ventral neck were shaved and cleansed with 70 % ethanol; an overhead heat lamp helped to maintain body temperature as monitored by a rectal thermometer. The ventral neck skin was incised from the mandibular symphysis to the jugular notch. The trachea was exposed by blunt dissection and cannulated 0·5 cm below the larynx; maintenance of surgical-plane anaesthesia was immediately relegated to the tracheostomy. A sagittal incision of the forehead skin and underlying periosteum allowed a headholder (25 mm × 20 mm o.d. stainless-steel tubing) to be applied to the frontal bone between the orbits. This was accomplished by obliquely inserting 6–8 jeweller's screws (0, 0·48–0·95 cm) in a circular formation slightly larger than the outer circumference of the tube. A flange was created by cementing the tube within the circle of screws using standard dental acrylic (Lang Dental Manufacturing Co., Chicago).

With the animal lying on its side, the masseter was exposed and a fine black silk suture (000, Ethicon, Somerville, New Jersey, USA) was carefully tied into the deep fascia at the mandibular attachment of the muscle at gonion. A second suture was placed into the tendinous attachment to the zygomatic arch at the opposite end of a stress line (perceptible in the superficial aponeurotic tendon of masseter) from gonion. The distance between the sutures was defined as the *in situ* length of the muscle belly (L_i) measured with the jaws in occlusion. Without injury to the masseter, the zygomaticomaxillary and temporal roots of the arch were cleaned and detached from the skull and the zygomaticomandibularis muscle was scraped from the internal surface of the arch. The masseteric nerve was exposed by blunt dissection and stimulated with silver hook electrodes led from a Grass SIU-5A stimulus isolation unit (Grass Instrument Co., Quincy, Massachusetts, USA) driven by a Grass S-48 stimulator. Positive identification of the nerve was by direct observation of muscle contraction and palpation of the detached arch.

The arch was clamped to an adjustable rigid bar led from a 114 kg capacity force transducer (±0·03 linearity) (Omega Engineering, Inc., Stamford, CT, USA). The transducer was mounted on an adjustable collar which surrounded a 35 mm × 400 mm vertical stainless-steel rod. The base of this upright was a rectangular slide that could be secured anywhere along the edge of a stainless-steel plate (450 mm × 780 mm × 20 mm). Thus, the attitude of the transducer was adjustable by translation in the vertical and horizontal planes and by horizontal rotation. A calibrated adjusting screw connecting the muscle and the force transducer allowed changes in length of up to 20 mm.

The cranium was stabilized by fastening (with a set screw) a 1 cm diameter rod into the headholder. The rod extended from a fully adjustable ball joint mounted on the base plate. The lower jaw was fixed by an adjustable clamp mounted on a second 25 mm × 245 mm upright rod whose attachment to the base plate could also be manipulated. The compliance of the apparatus (bar, force transducer, jaw holder) was 0.092 mm kg^{-1}.

Force and length measurements of the digastric either preceded or followed

completion of the masseter portion of the protocol. With the pig lying on its back, the digastric was exposed with blunt dissection. Sutures were tied into the most rostral attachment of the muscle belly to the mandible and into the extrinsic tendon at the attachment of the most caudal muscle fibres; L_i was measured and recorded. The branch of the mylohyoid nerve that innervates the digastric was dissected and verified by stimulation at low voltage. The tendon was detached from the skull, leaving a small fragment of the paracondyloid process in the severed end, and tied to a wire hook with a silk ligature. The hook was attached to the rigid bar that led from the force transducer.

Core temperature was maintained with a heating pad and monitored with a rectal thermometer. The muscle was kept damp with a saline-soaked gauze sponge and the nerve preparation was bathed in mineral oil.

Physiological measurements

The remainder of the procedure was the same for either muscle. Resting length was re-established and twitch contractions were induced by direct stimulation (6 ms pulses) of the nerve at increasing voltage (10 V increments). The signal from the force transducer was amplified through a Grass 7P1G low-level d.c. preamplifier and 7DAG d.c. driver amplifier and displayed on a Tektronix 5116 digital oscilloscope (Tektronix, Inc., Beaverton, Oregon, USA). The oscilloscope was equipped with a Tektronix 5D10 dual-cursor waveform digitizer that enabled direct measurement of amplitude and time course of the signal. The voltage at which the amplitude of the twitch contraction no longer increased was selected for tetanic stimulation.

The muscle length was shortened 3–5 mm below L_i and the length of the muscle and passive tension, if present, were recorded. The nerve was stimulated with a 400–600 ms train at 40 Hz using the same pulse settings as before; active tetanic tension (P) was recorded from the muscle. The muscle was lengthened 1 mm on the scale and the procedure was repeated after a 1 min interval. This continued until tetanic tension fell below maximum twitch tension. At the end of the experiment, both masseter and digastric were removed, trimmed of extrinsic tendon (digastric), blotted dry, and weighed. The pig was then administered a lethal dose of sodium pentobarbital intraventricularly.

Data analysis

An equation to transform electrical data from the oscilloscope to force was derived by least-squares linear regression. For each experiment, passive and active tension values were normalized by expressing each as a percentage of maximum or optimum tetanic tension (P_0) observed during that experiment. Muscle lengths were normalized by expressing each as a percentage of optimum length L_0 (the measured length corresponding to P_0 at the maximum discrepancy between active and passive tension).

Length–tension curves and related plots were generated with an IBM system 370 computer at the University of Illinois at Chicago using the Statistical Analysis

System (SAS Institute, Cary, North Carolina, USA). SAS was also used for the computation of statistics for the data analysis.

Results

Representative oscilloscope traces of fused tetani recorded from masseter and digastric muscles of a 3·2 kg minipig are presented in Fig. 1. Traces are included for muscle lengths approaching L_0 (Fig. 1A,D), approximately at L_0 (Fig. 1B,E) and following L_0 (Fig. 1C,F). The curves typify those observed for most subjects regardless of body mass.

The slight declinations of the plateaux at L_0 are similar for both muscles and exhibit a slight 'sag', thought to be correlated to the presence of alkaline-stable myosin adenosine triphosphatase, i.e. fast-twitch fibres (Burke *et al.* 1971; Reinking *et al.* 1975; Kernall *et al.* 1983). At lengths below L_0, the 'sag' is much more pronounced in digastric. However, at lengths greater than L_0, the plateau is more horizontal, i.e. the sag is absent.

The results of least-squares regressions of P_0 and wet muscle mass on body mass for masseter and digastric muscles are shown in Figs 2 and 3. Although P_0 and wet muscle mass are highly correlated with body mass for both masseter and digastric, only for digastric do the regressions appear to be linear. For both parameters for masseter, the portion of the curve corresponding to pigs $\leqslant 16$ kg has the most gradual slope with the steepest portion corresponding to pigs >16 kg. The slopes of the overall ontogenetic increases in both P_0 and wet muscle mass are considerably steeper in masseter than in digastric.
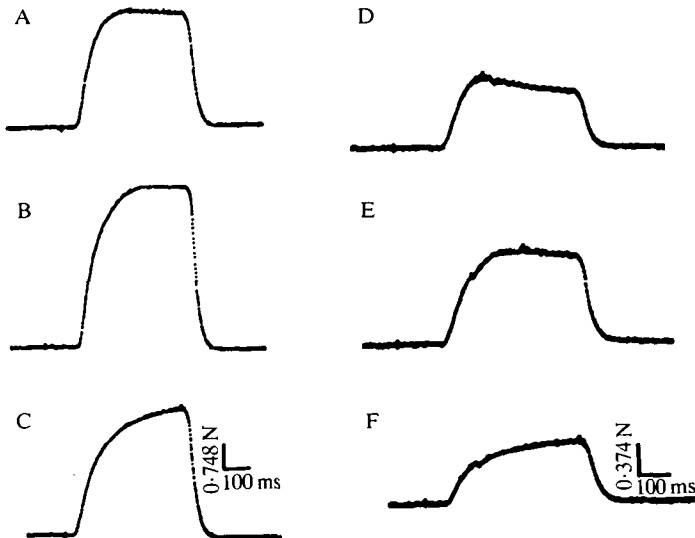

Fig. 1. Typical oscilloscope trace of maximum tetanic tension in a 3·2 kg miniature pig for the masseter muscle at (A) approx. 89 % L_0, (B) approx. 99 % L_0 and (C) approx. 104 % L_0; and the digastric muscle at (D) approx. 94 % L_0, (E) approx. L_0 and (F) approx. 103 % L_0.
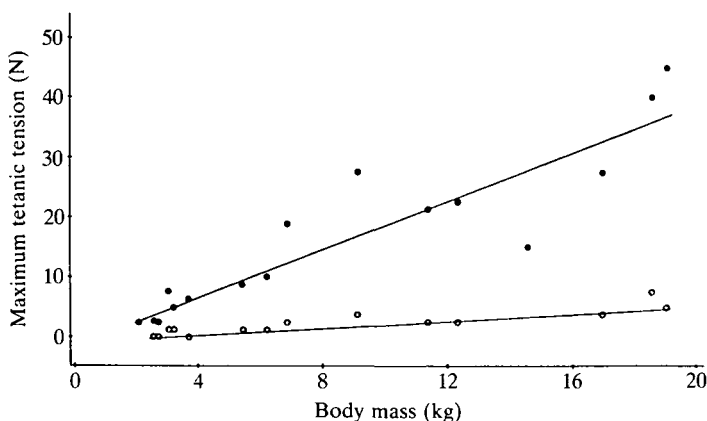
Fig. 2. Bivariate plot of maximum tetanic tension *versus* body mass for masseter (●) and digastric (○) muscles. Least-squares linear regression is included for masseter: correlation coefficient $(r) = 0.92$ $(P < 0.0001)$, slope ± s.e. $(k) = 2.004 \pm 0.236$, y-intercept ± s.e. $(b) = -0.837 \pm 2.456$; and digastric: $r = 0.87$ $(P < 0.0001)$, $k = 0.296 \pm 0.047$, $b = -0.210 \pm 0.047$.
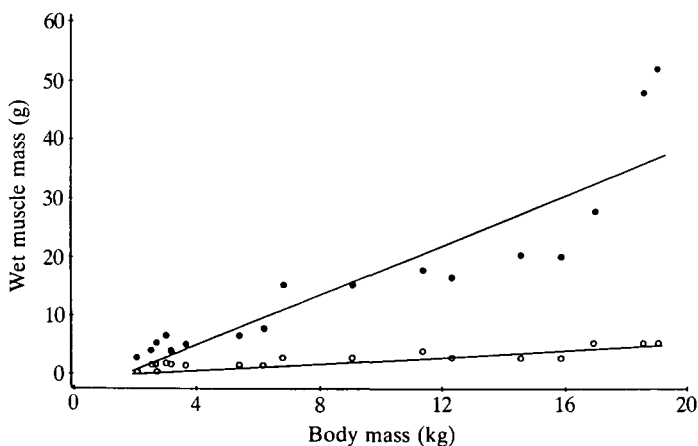

Fig. 3. Bivariate plot of wet muscle mass regressed on body mass for muscles removed from pigs used in this study (see Table 1). Least-squares linear regression is included for masseter (●): $r = 0.91$ $(P < 0.0001)$, $k = 2.141 \pm 0.259$, $b = 3.491 \pm 2.802$; and digastric (○): $r = 0.93$ $(P < 0.0001)$, $k = 0.221 \pm 0.022$, $b = 0.173 \pm 0.236$ (see legend to Fig. 2).

The negative residuals of masseters in intermediate-sized pigs probably indicate a naturally occurring, temporary slackening of the growth rate because the regression of P_0 on wet muscle mass is linear and highly correlated $(P < 0.0001)$ for both masseter $(r = 0.95)$ and digastric $(r = 0.83)$. However, when P_0 is regressed on wet muscle mass, the slope is steeper in digastric $(k = 1.116 \pm 0.205)$ than in

masseter ($k = 0.846 \pm 0.074$) (means $\pm$ S.E.). In addition, *in situ* muscle belly lengths are highly correlated with body mass (masseter, $r = 0.96$; digastric, $r = 0.93$), $P < 0.0001$, with both muscles sharing virtually identical slopes and intercepts (masseter, $k = 0.204 \pm 0.015$, $b = 3.183 \pm 0.161$; digastric, $k = 0.200 \pm 0.019$, $b = 3.148 \pm 0.205$). Thus, relative to digastric, more of the masseter's ontogenetic increase in mass may be to increase fibre length, and therefore velocity of contraction, rather than force.

Age-related differences in the shape of the length–tension plots were not obvious for either muscle, and normalizing length and tension allowed superimposition of records for all subjects. Normalized length–tension curves for 16 masseter and 15 digastric muscles are presented in Fig. 4. On the ordinate, active and passive forces are each expressed as a percentage of P_0. On the abscissa, the measured length of the muscle is expressed as a percentage of L_0 (as defined in Materials and methods). The scatter is attributed to individual (but not age-dependent) variation and/or experimental error.

To compare overall differences in the length–tension relationship between masseter and digastric, the plotted data shown in Fig. 4 were separated into ascending limb, descending limb and passive tension components, and regressed on their corresponding lengths. Individual regression lines are shown in Fig. 5. For the ascending limb, active tension data points include the first point on the plateau of the length–tension curve. For the descending limb, active tension data points include the last point on the plateau. Before regression, the tension and length values were transformed to natural logarithms to facilitate comparisons between slopes and between intercepts.

The slopes of the ascending limb ($P < 0.001$), descending limb ($P < 0.01$) and passive tension ($P < 0.001$) components of the length–tension curve of digastric are all significantly steeper than the corresponding components for masseter (Zar, 1984). Although the absolute values of the slopes of the ascending and descending limbs are not significantly different for either masseter or digastric, the y-intercept of the descending limb is significantly lower ($P < 0.001$) than that of the ascending limb in both muscles (Zar, 1984). This asymmetry is probably an artefact of the normalization process because, in each experiment, L_0 corresponded to the length of the muscle at the earliest occurrence (first value on the plateau) of maximum tetanic tension.

Several differences between masseter and digastric with regard to their respective length–tension relationships recur during ontogeny (Figs 6–8; Table 1). First, although maximum tetanic tension occurs at lengths slightly greater than *in situ* length in both muscles, the difference is significantly exaggerated in masseter ($P < 0.01$). For masseter, the ratio $L_0 : L_i$ averages $105.9 \pm 4.3\%$ (Fig. 6). For digastric, L_0 is only $102.0 \pm 2.7\%$ of L_i. The ratio is not correlated with body mass for either muscle. Second, the onset of passive tension as each muscle is stretched is characteristically different for masseter and digastric (Fig. 7). The smallest mean length at which passive tension can be discerned is significantly ($P < 0.001$) shorter for masseter ($91.8 \pm 4.3\% L_0$) than for digastric ($99.7 \pm 3.2\% L_0$); in digastric this
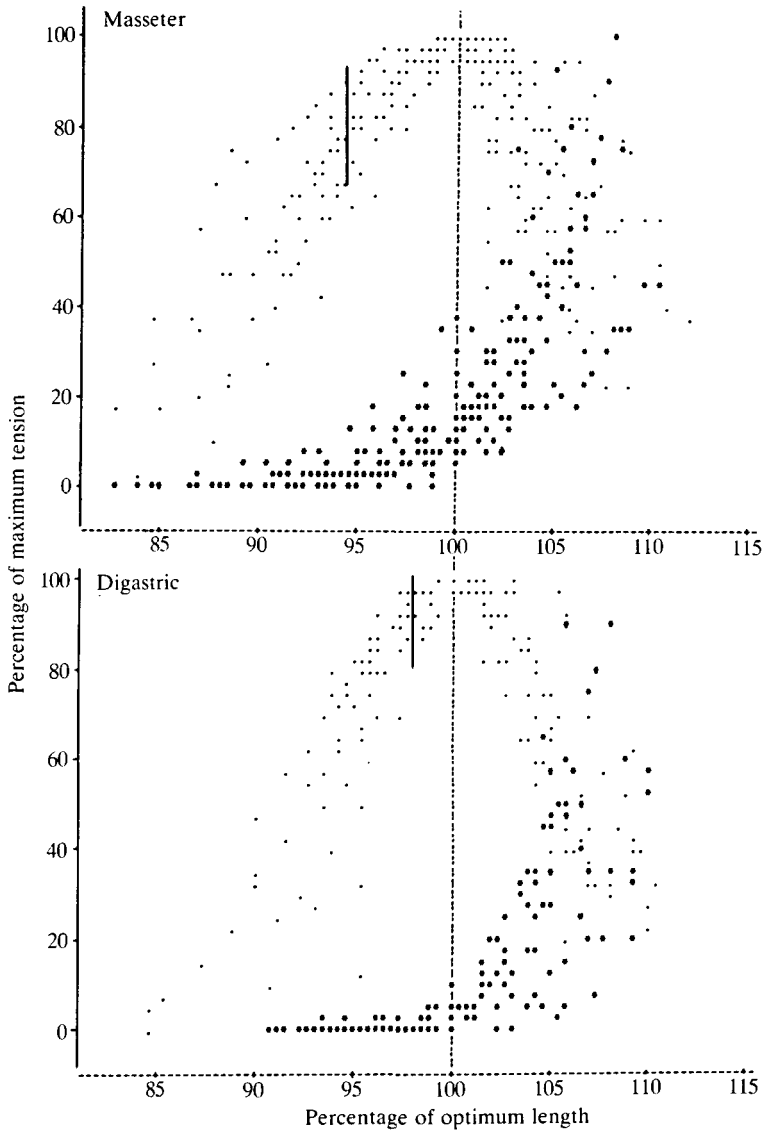
Fig. 4. Composite length–tension curves for 16 masseter and 15 digastric muscles in miniature pigs. A vertical dashed line transects optimum length (100 %). Mean muscle *in situ* length (with teeth in occlusion) is indicated by the short vertical line to the left of optimum. Dots are active tetanic force produced at each muscle length; asterisks are passive force that occurred at each consecutive stretch of the muscle.

length is also inversely correlated to body mass. Third, at L_0, the portion of total (active plus passive) tension attributable to passive tension is significantly ($P < 0.001$) higher in masseter ($13.1 \pm 7.0 \%$) than in digastric ($2.3 \pm 1.2 \%$) (Fig. 8).
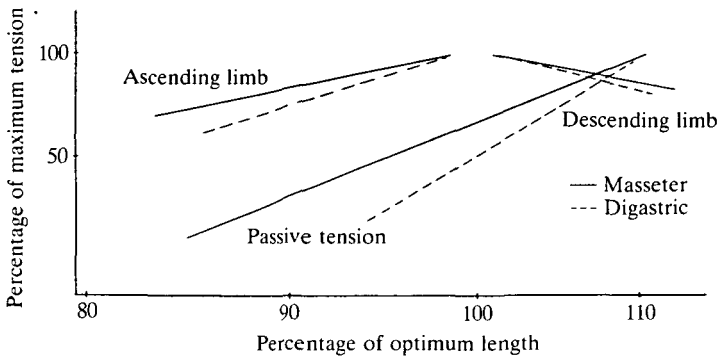
Fig. 5. Least-squares linear regression of percentage of maximum tetanic tension on percentage of optimum length for ascending and descending limbs of the active length–tension curve and the passive tension curve for all pigs in this study. Data have been log-transformed (base e) to enable comparisons of slopes and intercepts. Ascending limb: masseter, coefficient of determination $(r^2) = 0.636$, $k = 9.039 \pm 0.588$, $b = -36.867 \pm 2.676$; digastric, $r^2 = 0.717$, $k = 13.850 \pm 0.928$, $b = -58.996 \pm 4.234$. Descending limb: masseter, $r^2 = 0.474$, $k = -8.776 \pm 0.898$, $b = 45.049 \pm 4.17$; digastric, $r^2 = 0.637$, $k = -13.236 \pm 1.111$, $b = 65.719 \pm 5.164$. Passive tension: masseter, $r^2 = 0.794$, $k = 21.674 \pm 0.761$, $b = -97.255 \pm 3.505$; digastric, $r^2 = 0.677$, $k = 32.515 \pm 2.203$, $b = -148.281 \pm 10.214$.
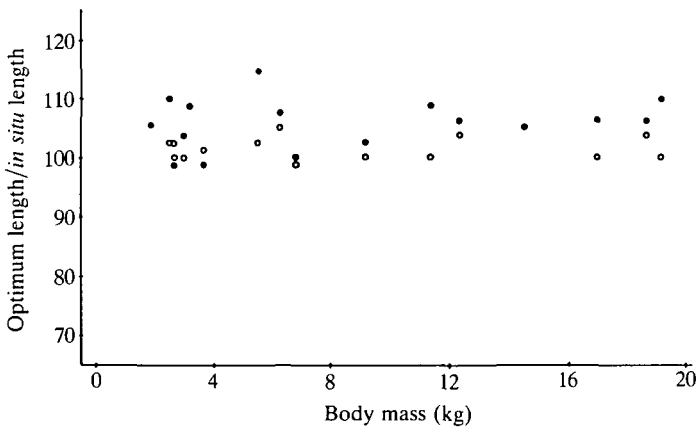

Fig. 6. Bivariate plot of percentage optimum length/*in situ* length *versus* body mass. Masseter, (●) $r = 0.19$ $(P > 0.48)$; digastric, (○) $r = -0.16$ $(P > 0.5)$ (see legend to Fig. 2).

Discussion

Methodology

Accurate measurement of the contractile properties of the masseter muscle is complicated by both its gross anatomy and fibre architecture (figs 1 and 2 in Herring, 1980). Because the broad aponeurotic tendon of origin attaches along the
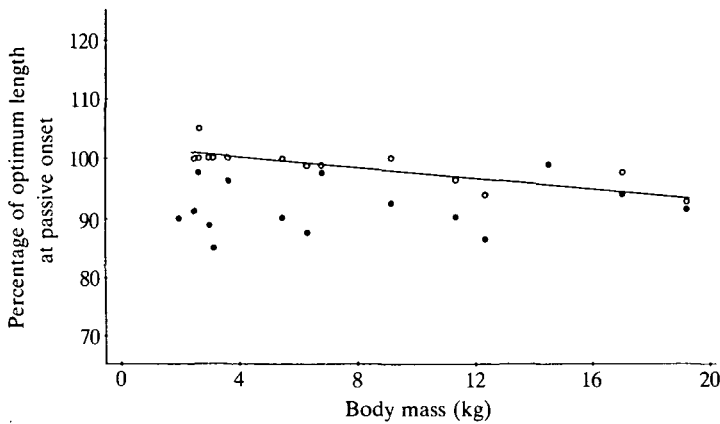
Fig. 7. Bivariate plot of percentage of optimum length at onset of passive tension *versus* body mass. Masseter, (●) $r = 0.15$ $(P > 0.6)$; digastric, (○) $r = -0.83$ $(P < 0.0002)$, $k = -0.475 \pm 0.093$, $b = 102.226 \pm 0.852$ (see legend to Fig. 2).
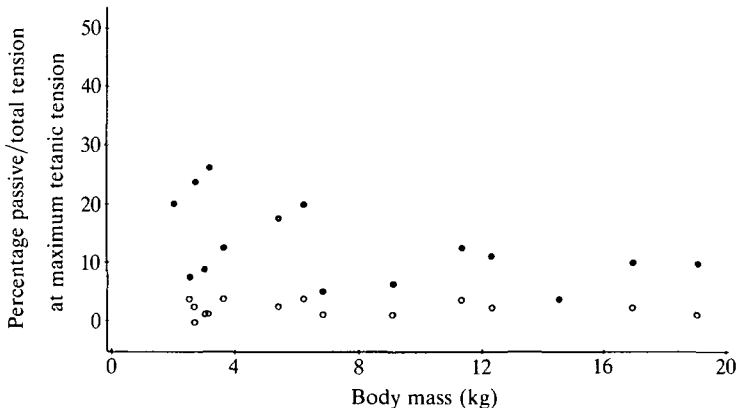

Fig. 8. Bivariate plot of passive tension (as a percentage of the total of active plus passive tension) at P_0 *versus* body mass. Masseter, (●) $r = -0.48$ $(P > 0.06)$. Digastric, (○) $r = 0.05$ $(P > 0.85)$ (see legend to Fig. 2).

entire ventral margin of the zygomatic arch, the exact direction of contraction of the whole muscle is difficult to ascertain. Correct alignment of the whole muscle for tension measurements was achieved by adjustment of the apparatus until deflection during tetani of the rigid bar linking the arch and the force transducer was eliminated.

The inherent heterogeneity of force production within the pig masseter presents a second problem. Architectural, histochemical and electrophysiological data suggest that intramuscular compartments of this muscle may function independently during feeding (Herring *et al.* 1979; Herring, 1980; Wineski & Herring, 1983; Anapol, 1985; Herring & Wineski, 1986). From several tendinous sheets

invaginating from the superficial aponeurosis, short fasciculi arise and attach obliquely into portions of other tendinous sheets that insert into the masseteric fossa of the mandible. When the jaw is in the closed position, sarcomeres in the anterior portion of the masseter are shorter than those in the posterior portion but become longer than the posterior sarcomeres as maximum gape is attained (Herring et al. 1979, 1984). Thus, it is doubtful whether maximum tension can be generated in all parts of the muscle concurrently. Instead, different regions of the muscle may reach their maxima at different times and according to functional requirements at any moment. This regional variation may explain why the slope of the ascending limb (Figs 4, 5) of the masseter length–tension curve is more gradual than that of the digastric. Not all sarcomeres are at the same length when the mouth is closed and those which initially rest at lengths shorter than maximum overlap are gradually stretched towards their plateau. Experimental control of intramuscular variability would require individual length–tension measurements for subdivided portions of the muscle and was not attempted in this study.

In contrast, digastric (fig. 8 in Herring & Scapino, 1973) has a fusiform muscle belly with a circumscribed proximal tendinous attachment, a configuration generally more conducive to in situ physiological studies (Muhl et al. 1978; Muhl, 1982; Anapol et al. 1987). This unipinnate jaw depressor is much less complex than the masseter. The thick, round and long extrinsic tendon of origin arises from the paracondyloid process of the occipital bone and broadens rostrally to ensheath the medioproximal surface of the muscle belly. Short fasciculi extend obliquely from the tendon to insert on the medial surface of the ventral border of the mandible. Most of the fasciculi arise from the lateral surface of the tendon with the remainder originating from the medial surface. The shape of the curves for the digastric of the pig are similar to those of comparable muscles, e.g. medial gastrocnemius of cat (Stephens et al. 1975; Walmsley & Proske, 1981) and rabbit digastric (Muhl et al. 1978).

Functional implications

In isolated muscle fibres, 80% of maximum tetanic tension is maintained between 0·8 and 1·2 times optimum length (Gans & Bock, 1965; after Ramsey & Street, 1940). In the current study, the range within which tetanic tension attained or exceeded 80% of maximum was limited to $0·92–1·06L_0$ in masseter and $0·93–1·07L_0$ in digastric. In fact, tension was negligible or absent outside the range $0·8–1·2L_0$ for either muscle. Other authors have argued that this shorter range may be a function either of pinnation (Goslow et al. 1977) or relatively longer muscle fibres (Muhl, 1982).

The striking physiological contrast between masseter and digastric parallels their architectural disparity. At maximum gape, the fibres of masseter stretch up to about 150% of their resting length (Herring et al. 1984), i.e. the working range of masseter begins at lengths greater than L_0. Because the excursion of the whole muscle terminates at L_i, it includes a portion of both descending and ascending limbs of the length–tension curve. In contrast, the working range of digastric

begins at L_i (which is shorter than L_0) and is limited to the ascending limb of the curve.

Statistically significant differences between masseter and digastric occur both in size-related variables, e.g. wet mass, and maximum tetanic tension, and in variables that are independent of body mass but address the relationships between resting and optimum length and between active and passive tension, such as the ratio of L_0 to L_i, the relative whole muscle length at which passive tension begins to rise, and the proportion of passive tension comprising total tension at L_0. In essence, L_i is further below L_0 on the length–tension curve in masseter than in digastric. Passive tension begins to increase at shorter muscle lengths and at a more rapid rate in masseter, and contributes more significantly to total maximum tension; in digastric, passive tension is inconsequential at lengths shorter than L_i.

The resting posture of masseter, at which the muscle is slightly longer than in the jaws-closed position (Herring *et al.* 1984), can be maintained against gravity at relatively little metabolic cost to the animal. Ample passive tension is present at lengths less than L_i, and may result from the series elasticity within the contractile machinery *per se* (Cavagna *et al.* 1980).

During jaw elevation, isotonic contraction of the masseter *from* L_i is, of course, impeded at occlusion. Its action more closely resembles the extensor muscles of the limbs than it does either the limb flexors or digastric in that it must be stretched considerably *beyond* L_i to generate maximum tetanic tension. This is analogous to the contractile properties of cardiac muscle. At end-systole, the sarcomeres of resting heart muscle are well below maximum overlap. As the heart becomes engorged with blood, the myocardium is stretched and the sarcomeres *approach* maximum overlap where submaximal tension is generated for systole; thus, work is performed only on the ascending limb of the length–tension curve (Grimm & Whitehorn, 1966). Similarly, during feeding the parted jaws are 'engorged' with food. The masseter is stretched towards or, perhaps, *beyond* the plateau of the length–tension curve (and probably beyond maximum sarcomere overlap) so that maximum tension to crush the bolus is produced during closing.

When the masseter is stretched to a length on the descending limb of the length–tension curve, the passive tension rises dramatically. This is probably attributable to the extensive tendons of attachment, which provide stiff, parallel resistance to maintain the integrity of the sarcomeres and return the muscle towards L_0. Thus, the large passive forces occurring over a broad range of muscle lengths both maintain resting posture and produce closing forces at wide gape.

The less complex architectural configuration of digastric more closely resembles a flexor muscle of the limbs. Physiologically, its resting state approximately coincides with the jaws-closed position and represents the beginning of its *in vivo* working range. Stretching beyond L_i to L_0 could only occur at the conclusion of the power stroke when jaw protrusion and contralateral deviation presage the beginning of opening (Herring & Scapino, 1973). In this position, the maximum amount of active force would be required for jaw depression.

In the digastric, passive tension at lengths less than or equal to L_i would be

counterproductive because the resting state of the closed jaw would be opposed. Whether digastric is ever stretched enough during mastication to generate functionally significant passive tension is doubtful. However, passive tension could resist minimal anterior disarticulation of the mandible during other, non-masticatory behaviours.

Ontogenetic changes

Several, but not all, of the parameters examined in this study change during postnatal ontogeny. As one would expect, wet muscle mass, maximum tetanic tension and *in situ* whole muscle length are highly correlated with body mass, and thus the age of the animal, for both masseter and digastric. Some of the increase in wet muscle mass in masseter may also reflect an increase in fibre length, and thus an increase in the velocity of contraction.

For digastric, the percentage of optimum length at which passive tension becomes perceptible decreases with body mass. The correlation coefficient is high, but the slope is slight and the onset of passive tension at decreasing muscle lengths may be attributable to the slight increase in muscle mass with age. The functional significance of this phenomenon may be to increase the effect of digastric on 'braking' jaw-closing as masticatory function increases in the maturing pig.

The proportion of passive tension comprising total (passive plus active) tension decreases with age in masseter. This must be a direct result of a larger increase in the contractile muscle tissue relative to the non-contractile elastic component (tendon, mysia) of the whole muscle and is functionally related to the behavioural transition from suckling to adult mastication.

The ratio of optimum length to *in situ* length was not correlated with body mass for either muscle and was higher for masseter in all but two subjects. The functional implication of this fundamental difference between masseter and digastric is discussed above.

Behavioural adaptations

Alteration of individual length–tension relationships through architectural elaboration of one or more muscles within a functional complex is a useful way in which a gross anatomical musculoskeletal bauplan can become adapted to accommodate a wide variety of behavioural demands. Variations among individual muscles and within entire muscle groups have been relatively well documented for the locomotor anatomy (e.g. Goslow, 1972; Goslow & Van DeGraaff, 1982).

The present findings demonstrate a strong physiological distinction between masseter and digastric in miniature pigs which is reconcilable with their *in vivo* functional requirements. As in other mammals, e.g. opossum (Thexton & Hiiemae, 1975), cat (MacKenna & Turker, 1978) and rat (Nordstrom & Yemm, 1974), the maximum forces in masseter are generated, not when the jaw is in the closed or resting position, but when maximum gape is approached. Whether maximum forces during feeding are actually produced at maximum gape, or

whether the instantaneous moment arm of the masseter is inversely proportional to the forces at any gape so that the moment about the craniomandibular joint is held constant, is still unclear.

The position at which maximum tension is produced in the digastric is similar to that reported in rabbits (Anapol *et al.* 1987) and in domestic cats (MacKenna & Turker, 1978), in that $L_0 > L_i$, i.e. optimum gape, is slightly less than $0°$. In contrast, optimum gape for digastric is $23°$ in opossum (Thexton & Hiiemae, 1975). Although greater optimum gape for digastric in more carnivorous species is probably adaptive for stabilizing the craniomandibular joint against struggling prey (Scapino, 1975), the adaptive significance of differences in optimum gape among species of different dietary habits remains enigmatic despite the available comparative data.

As in other mammals, masticatory development in pigs entails a behavioural transition from suckling to adult mastication of solid food (Herring, 1985). The results presented here indicate that this transition is best characterized as a shift in emphasis from the digastric (during suckling) to the masseter (during mastication) by a disproportionate increase in mass (and force) and increased reliance on active, rather than passive, tension during postnatal ontogeny.

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