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SYMPOSIUM

Mastication and the Postorbital Ligament: Dynamic Strain in Soft Tissues

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Synopsis Although the FEED database focuses on muscle activity patterns, it is equally suitable for other physiological recording and especially for synthesizing different types of information. The present contribution addresses the interaction between muscle activity and ligamentary stretch during mastication. The postorbital ligament is the thickened edge of a septum dividing the orbital contents from the temporal fossa and is continuous with the temporal fascia. As a tensile element, this fascial complex could support the zygomatic arch against the pull of the masseter muscle. An ossified postorbital bar has evolved repeatedly in mammals, enabling resistance to compression and shear in addition to tension. Although such ossification clearly reinforces the skull against muscle pull, the most accepted explanation is that it helps isolate the orbital contents from contractions of the temporalis muscle. However, it has never been demonstrated that the contraction of jaw muscles deforms the unossified ligament. We examined linear deformation of the postorbital ligament in minipigs, *Sus scrofa*, along with electromyography of the jaw muscles and an assessment of changes in pressure and shape in the temporalis. During chewing, the ligament elongated (average 0.9%, maximum 2.8%) in synchrony with the contraction of the elevator muscles of the jaw. Although the temporalis bulged outward and created substantial pressure against the braincase, the superficial fibers usually retracted caudally, away from the postorbital ligament. In anesthetized animals, stimulating either the temporalis or the masseter muscle in isolation usually elongated the ligament (average 0.4–0.7%). These results confirm that contraction of the masticatory muscles can potentially distort the orbital contents and further suggest that the postorbital ligament does function as a tension member resisting the pull of the masseter on the zygomatic arch.

Introduction

The contraction of the adductor muscles of the jaw in mammals is the *sine qua non* of mastication. These immensely strong, multipinnate muscles close the jaws and generate occlusal force, and their nuanced activity patterns maneuver the mandibular teeth into and across the maxillary teeth to break down foods of all types. However, these massive generators of force have secondary effects as well. In addition to jaw movement and occlusal force, substantial reaction loads are placed on the temporomandibular joint, often requiring structural reinforcements such as the postglenoid process in carnivorans (Maynard Smith and Savage 1959). Loading at the muscle attachment points as well as at the teeth and at the jaw joints causes stress and strain in the skull, again requiring anatomical adjustments such as reinforced bones and interdigitated sutures. Moreover, muscles approximate incompressible volumes, so when they shorten, their girth increases, placing orthogonal pressures against adjacent hard and soft tissues. Just as occlusal force can be measured using transducers and skull surface strain can be assessed using strain gages, pressures against the skull's surface can be quantified using flat pressure transducers. In studies on pigs, even areas of muscle attachment have proved to be under positive pressure resulting from the increased girth of the overlying fibers, with pressures ranging from ~8 kPa under the buccinator attachment to alveolar bone (Dutra et al. 2010) to ~112 kPa under the temporalis origin from the temporal fossa (Teng and Herring 1998). These "side"

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effects of muscular contraction are probably not useful to the organism, but rather should be viewed as the inevitable consequence of large muscles contracting in small spaces.

The jaw muscles are not completely enclosed in bony compartments, so they exert orthogonal pressure against soft tissues as well as against skull bones. Curvature of muscle fibers and the presence of internal tendons are features that probably increase intramuscular pressures (Hill 1948; van Leeuwen and Spoor 1992). These features are found in all adductors, but are particularly marked in the temporalis, which probably accounts for the very high pressures on the wall of the temporal fossa in pigs (Teng and Herring 1998). Undoubtedly, high pressures are also exerted against the soft tissues adjacent to the temporalis muscle. The area is covered by the temporal fascia, an investing layer that spans the skull roof and the zygomatic arch and gives rise to the origin of some temporalis fibers. Behind the orbit the temporal fascia is thickened into a postorbital ligament connecting the postorbital processes of zygomatic and frontal bones (Fig. 1, inset), and then turns medially as a septum between the temporal fossa and the orbit. Pigs have no bony separation between the temporal fossa and the orbit, and thus the question arises as to whether temporalis contraction disturbs the contents of the orbit during chewing.

Although open continuity between the orbit and temporal fossa is primitive for mammals, a bony postorbital bar has evolved independently numerous times, including in other ungulate members of the Cetartiodactyla, the order to which pigs belong (Heesy 2005). An ossified bar is characteristic of the order Primates, and in tarsiers and anthropoid primates ossification extends through the entire postorbital septum. Following arguments originally marshaled by Cartmill (1972, 1980) and failure of competing theories, the consensus is that by completing the lateral margin of the orbit, an ossified postorbital bar generally protects vision from the effects of contraction of the jaw muscles (Ross and Hylander 1996; Noble et al. 2000; Ravosa et al. 2000b; Heesy 2005; Nakashige et al. 2011). For a simple bar, this protection is clearly not total insulation from the temporal fossa, but rather the provision of a stiff lateral surface that provides attachment for eye-stabilizing structures (Heesy 2005). A complete bony septum could potentially eliminate the need for such stabilization, an advantage for stereoscopic perception of depth (Menegaz and Kirk 2009). In species such as pigs, which have an unossified ligament, it may be that the lack of frontation and convergence of the orbits prevents the jaw muscles from disturbing vision (Heesy 2005), or it may be that perturbation of vision is simply not important in such animals, which have little, if any, binocular vision and rely more on other senses.

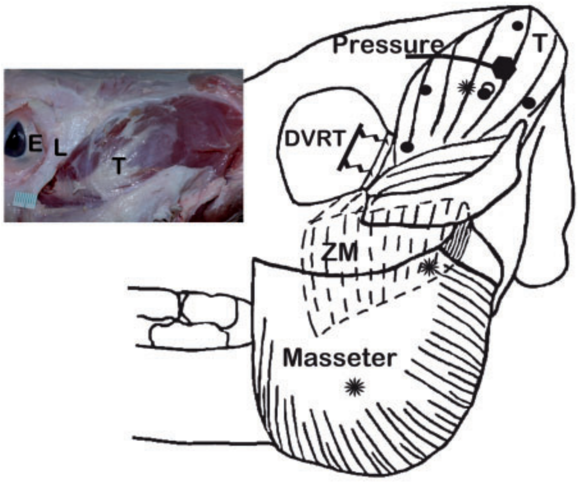

Fig. 1 Muscles of mastication in the pig, *Sus scrofa*, and sensors employed. The inset is a dissection showing the postorbital ligament (L, note the millimeter scale close to the ligament's ventral attachment) and its relationship to the eyeball (E). The temporal fascia, which is continuous with the caudal border of the ligament, has been removed to reveal the temporalis muscle (T). In the drawing, the starbursts show the approximate location of EMG electrodes in masseter, temporalis and zygomaticomandibularis (ZM), rendered as if the masseter and zygomatic arch were transparent. Length of the postorbital ligament was recorded with a DVRT placed with its two barbs at the upper and lower attachments of the ligament. The pressure transducer (hexagon with a wire) lay beneath the temporalis on the surface of the temporal fossa. The crystals for sonometric measurement of temporalis dimensions are shown as small circles, solid for the five superficial locations (rostral–dorsal, rostral–ventral, caudal–dorsal, caudal–ventral and central) and open for the central deep crystal, which was fastened to the temporal fossa.

Orbital shape and all characteristics of masticatory muscles are strongly associated (Cox 2008), so it is not obvious whether any one muscle is of primary importance. Cartmill (1980) proposed that the masseter muscle was the primary agent tensing the temporal fascia and thus the pull on the orbital margin would be caudal and medial, although the temporalis probably aided in tensing the fascia. Many subsequent workers have reiterated that the masseter muscle is positioned to place significant tension on the postorbital tissues (Greaves 1985; Rosenberger 1986; Ross and Hylander 1996). Nevertheless, recent attention has emphasized the temporalis muscle, particularly the anterior temporalis, as being primarily important in distorting the orbit (Ross and Hylander 2000; Heesy 2005), perhaps by pulling caudally on the fascia (Ross and Hylander

1996) as Cartmill had envisioned the masseter doing. However, a bulging of the fascia rostrally seems equally plausible, if the contracting temporalis increases its girth rostro-caudally as well as mediolaterally. The precise deformation of the temporalis is difficult to predict, because pressures differ among various intramuscular regions (Otten 1988; van Leeuwen and Spoor 1996), and the temporalis is a complex muscle with fibers running in a variety of orientations. Notably, either caudal or rostral deviation of the temporal fascia would force the postorbital structures into a curve, producing tension in the ligament/bar (Heesy 2005). Thus, both the masseter and the temporalis could theoretically tense the postorbital connective tissues during mastication.

In vivo masticatory strain has been recorded in the postorbital bar of prosimians (*Otolemur*, Ravosa et al. 2000a, 2000b) and in the equivalent location in the postorbital septum of anthropoids (*Aotus* and *Macaca,* Ross and Hylander 1996; Ross et al. 2011). Strain levels have been found to be moderate with peak shear strain averaging 200–600 $\mu\varepsilon$ and complex strain orientations confirming tension as well as torsion and bending. An interesting study tracking eye movement as a response to muscle tetany in *Otolemur* and domestic *Felis catus,* one of which had a completely ossified bar, showed substantial deflections of the globe, especially in the cats, in which the eye protruded and moved laterally 0.3–0.5 mm in response to stimulation of the temporalis (Heesy et al. 2007). These findings imply that loading on the postorbital bar is not trivial and that the postorbital tissues undergo considerable masticatory deformation even when a bar is present. Presumably, distortion would be much greater in the absence of ossification. However, no studies so far have addressed the *in vivo* behavior of an unossified postorbital ligament. Indeed this area is surprisingly unstudied, with a single histological analysis of the postorbital ligament in rabbits, which reported its composition as elastic fibrocartilage (Jasarevic et al. 2010), again suggesting that masticatory deformation might be both regular and considerable.

In this study, we explore the mechanics of the unossified postorbital ligament using the pig as an example of this primitive morphology. The basic question was whether and how the ligament deforms during mastication, and to answer this we measured linear strain in the ligament. We also attempted to determine whether ligamentary strain was produced by the temporalis or by the masseter muscle and to describe the 3D pattern of the distortion of the temporalis that accompanies ligamentary strain.

Materials and methods

Data were collected from seven female and four male juvenile Hanford minipigs, in the age group of 3–7 months, from Sinclair Research Farms (Columbia, MO, USA). All procedures were approved by the University of Washington Institutional Animal Care and Use Committee. Each pig was acclimated 4–7 days through daily feeding in the laboratory. In most cases baseline electromyographic (EMG) patterns were recorded in a session involving brief anesthesia by gas to implant fine-wire electrodes in the temporalis, masseter, and zygomaticomandibularis (ZM) muscles (Fig. 1), followed by recording while the pigs ate pig chow pellets. Electrodes were removed after the session. These baseline records served to verify that animals had typical alternating chewing patterns and chewed at typical rates. The experiment took place a few days later and included surgery to install instrumentation for measuring length of the postorbital ligament, pressure on the wall of the temporal fossa, and dimensions and EMG of the temporalis (Table 1 and Fig. 1). Some pigs had additional sensors placed in other locations, primarily strain gages on the mandible; these had no apparent effect on the results and are not reported here.

On the day of the experiment, pigs were anesthetized by inhalation of isoflurane and nitrous oxide. The temporalis muscle and postorbital ligament were exposed by a dorsocaudal incision. In some experiments (Table 1), flat pressure transducers (Model P19F-S-NSL Konigsberg Instruments Inc., Pasadena CA, USA) were placed under the temporalis muscle against the braincase. In all experiments, differential variable reluctance transducers (DVRT), (Microstrain, Williston VT, USA) were installed along the long axis of the postorbital ligament via two penetrating barbs. The distance between these barbs is reported as a voltage with a resolution of 0.001 mm. Piezoelectric crystals (Sonometrics, London, ON, Canada) were placed in the temporalis muscle to measure changes in shape. These transceiver crystals record distance as ultrasound time-lapse signals with a resolution of 0.02 mm. Five crystals were sutured near the superficial surface of the temporalis: central, caudal–dorsal, caudal–ventral, rostral–dorsal, and rostral–ventral (Fig. 1). The central crystal was typically a few millimeters rostral and ventral to the location of the pressure transducer. Distances between these five crystals monitored the changing surface dimensions of the temporalis. The sixth crystal was placed deep to the central crystal via a small peg that was inserted in a hole drilled in the

Table 1 Subjects and recorded instrumentation

Pig no., sex (M/F), weight (kg)	Fossa pressure	Temporalis dimensions	Postorbital ligament	Mastication	Muscle stimulation
347, M, 26	–	Left	Left	Yes	Yes
348, M, 29	–	Left	Left	Yes	Yes
368, F, 9	–	–	Left	Yes	Yes
380, M, 13	Right, Left	Right	Right	Yes	Yes
381, M, 11	Right, Left	Right	Left	Yes	Yes
382, F, 10	Right, Left	Right	Right, Left	Left only	Yes
383, F, 11	Right, Left	Right	Right, Left	Right only	Yes
384, F, 11	Right, Left	Right	Right	Yes	Yes
385, F, 11	Right, Left	Right	Right, Left	Yes	Yes
425, F, 18	–	Left	–	Yes	No
426, F, 18	–	–	Right, Left	Yes	Right only

bone of the temporal fossa. The distance between this crystal and the central (superficial) crystal measured thickness of the temporalis. The incisions were closed, leaving exit channels for the lead wires. Sterile bipolar fine-wire electrodes (nickel–chromium alloy, 0.05 mm diameter, 1 mm bared tips) were placed via hypodermic needles into the temporalis, masseter, and ZM muscles. Lidocaine was infiltrated into the incision, and analgesics (ketorolac and buprenorphine) were administered intramuscularly.

Animals were allowed to awaken and feed without restraint. Pig chow was the only food offered. EMG, pressure, and DVRT signals were sampled at 1000 Hz and saved digitally (AcqKnowledge, Biopac Systems Inc., Goleta, CA, USA). Digital data from the ultrasound crystals were saved to a separate computer. After ~15 min of feeding had been recorded, animals were anesthetized again and placed prone with the teeth in occlusion for the stimulation procedure. Pairs of stimulating needle electrodes were placed in each masseter and temporalis muscle. Muscles were tetanized at 0.5/s by 600 ms trains of 5 ms pulses delivered at 60 pps while signals were recorded as before. Stimulation was begun at low voltage (typically 20–30 V) and gradually increased until contraction spread beyond the stimulated muscle, with three repetitions at each level. Simultaneous stimulations of masseter and temporalis were also carried out, but these resulted in poor recordings and so were not analyzed. Then, in most cases, the mandible was passively manipulated (open–close, protrude–retrude, left–right). Manual pressure was placed on the eye and temporalis to see whether this was sufficient to alter the length of the postorbital ligament. Following these procedures, the animals were terminated and the placement of the instruments was verified.

Analysis began by identifying several sequences of 10–20 consecutive chews that had consistent signals from the implanted devices. EMG patterns were used to determine the chewing side; the working side masseter and balancing side temporalis have later offsets than their counterparts. Measurements of the ligament and of pressures were made at the peak of the ligament's (DVRT) deformation. After subtracting a baseline value, these measurements were converted from voltages to millimeters or Pascals using previously acquired calibration equations. DVRT values were converted to postorbital ligament strain by dividing the changes in length by the original distance between the implanted barbs. Ultrasound dimensions were analyzed similarly by subtracting baseline distance from peak distance and converting to strain. Since EMG could not be recorded adequately to the Sonometrics system, these recordings lacked information on side of chewing, and the analyzed sequences were in general not the same as those analyzed with AcqKnowledge.

Results

With one exception (#384, which refused food but chewed on a silastic tube), pigs fed with normal appetite, chewing rate, and right–left alternation. Breakage or slippage of instruments marred several recordings and accounted for variation in sample size.

Mastication

During mastication, the postorbital ligament reliably showed a pattern of cyclic changes in length.

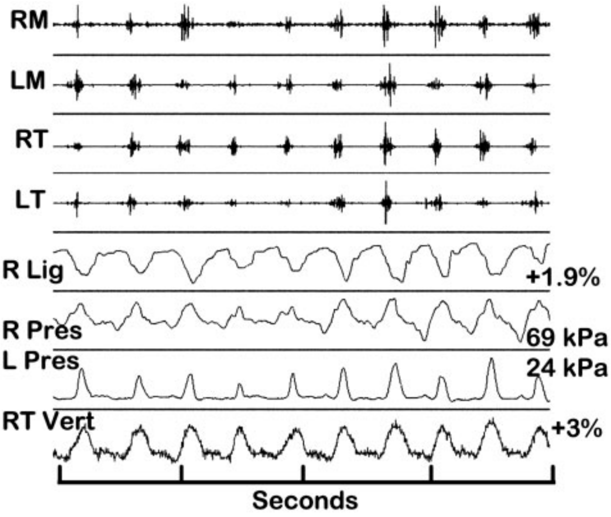

Fig. 2 Example of mastication (pig 380). The first four channels are EMG of right and left masseter (RM, LM) and temporalis (RT, LT). The animal was not chewing hard for the first five cycles, but amplitude of the signals increased for the final five cycles, which show typical alternation (right–left–right–left–right). R Lig is the DVRT signal from the right postorbital ligament. Downward deflections of this channel represent elongation. Elongation increased with EMG in the final five cycles but did not differ for left versus right cycles; average elongation in this animal was 1.9%. Pressure of the temporalis on the temporal fossa differed on the right (R Pres) and left (L Pres) sides, but both sides showed increased pressure (upward deflections) in the final five cycles. The bottom channel (RT Vert) is the vertical height (caudal–dorsal crystal to caudal–ventral crystal) of the right temporalis; the signal is noisy because it is analog output of the digital sonomicrometric measurement. Throughout the 4 s of recording, the end of the EMG bursts, the elongation of the ligament, pressure on the fossa, and deformation of the temporalis are synchronous.

The onset of elongation corresponded to the onset of activity of the jaw-closing muscles, with maximum length occurring towards the end of the adductor burst. The elongated condition was sometimes sustained as a short plateau, and the ligament shortened to reach its original minimum length during the opening phase (Fig. 2). There were no consistent differences for side of chewing, so data for working-side and balancing-side cycles are combined in Table 2. Although the pattern of elongation was highly consistent, the degree of stretching was low (0.94% average strain for the total sample, 1.05% if the low outlying value of #382 is omitted) and varied greatly among (but not within) animals (0.06–2.8% strain).

Peaks in pressure accompanied each chewing cycle, with the rise lagging slightly behind the onset of EMG and the initiation of elongation of the postorbital ligament (Fig. 2). Peak pressure was roughly simultaneous with stretching of the ligament and was never sustained as a plateau. Pressures averaged 57 kPa (Table 2), very comparable to results obtained in our previous study (62 kPa, Teng and Herring 1998) and, as in that study, there was a nonsignificant tendency for pressure under the working-side temporalis (55.9 kPa) to be lower than pressure under the balancing-side temporalis (59.2 kPa, $P = 0.08$ in a paired *t*-test). This trend underlines the role of the balancing-side temporalis in producing mandibular movement toward the balancing side. Unexpectedly, there was a very pronounced difference between right and left sides. The right side, which had also been instrumented with sonomicrometry crystals, evinced much higher pressures (83.5 ± 23.3 kPa) than did the left side (31.2 ± 25.1 kPa) which was not instrumented (calculated from Table 2).

During mastication, the dimensions of the temporalis changed simultaneously with adductor EMG signals, stretching of the postorbital ligament, and the rise of pressure on the temporal fossa (Fig. 2). Dimensional changes were consistent from cycle to cycle in each individual, but varied among animals (Table 2), probably because it was not possible to position the crystals identically with respect to the orientation of the fibers or to the depth of implantation. Thickness was recorded well in only three experiments, but each of them showed thickening during muscle contraction, with an overall average of 7%. Dorsal–ventral heights decreased in seven experiments (average −5%) but increased in two (average +3%). Rostral–caudal lengths were even more variable, with a range from −7% to +16%. Since the first two experiments had been carried out a few months earlier than the other experiments and produced unusual results (+16% and +14%, Table 2), there may have been some systematic but unrecognized change in placement of the crystals. The entire sample produced an average rostral–caudal strain close to zero; without the first two experiments the average would have been −3.8% ± 2.6%, clearly a shortening.

Stimulation of muscles and manipulation of the jaws and soft tissues

Stimulation of muscles were repeatable, but the patterns of muscular deformation often altered as the tetanus increased in intensity; sometimes a supramaximal stimulus could not be achieved because the stimulus had spread to other muscles. The maximal responses of the postorbital ligament to muscle stimulations are summarized in Table 3. The postorbital ligament usually elongated in response to

Table 2 Mastication summary data (combined working and balancing sides)

Pig no., side	Ligament stretch (mm)	Ligament strain (%)	Temporalis strain			Temporalis Pressure (kPa)
			Thickness (%)	Dorsal–Ventral[a] (%)	Rostral–Caudal[a] (%)	
347, Left	0.006	ND	+10	−12	+16	–
348, Left	0.007	ND	+3	−6	+14	–
368, Left	0.172	0.91	–	–	–	–
380, Right	0.165	1.94	ND	+3	−4	69.0
Left	ND	ND	–	–	–	23.5
381, Right	ND	ND	ND	−2	ND	126.5
Left	0.208	2.78	–	–	–	18.2
382, Right	ND	ND	ND	−5	−7	66.2
Left	0.004	0.06	–	–	–	18.1
383, Right	0.049	0.61	ND	−1	−4	72.9
Left	ND	ND	–	–	–	81.9
384, Right	ND	ND	ND	−5	−4	94.2
Left	ND	ND	–	–	–	18.1
385, Right	0.067	0.74	ND	−5	+1	72.1
Left	0.023	0.29	–	–	–	27.3
425, Left	ND	ND	+8	+3	−5	–
426, Right	0.087	0.94	–	–	–	–
Left	0.016	0.20	ND	ND	ND	–
Mean, SD	0.07 ± 0.08	0.94 ± 0.89	7.0 ± 3.6	−3.3 ± 4.7	0.9 ± 9.0	57.3 ± 35.8

Notes: Instrument not implanted. ND: No data, usually because of instrument malfunction.

[a] Dorsal–Ventral is either the rostral or the caudal vertical height or, if both were available, their average. Similarly, Rostral–Caudal is either the dorsal, the ventral, or the average horizontal length (Fig. 1).

contractions of individual muscles, but less consistently than for mastication and with lower values. The ipsilateral masseter always had a measurable effect, averaging ~0.5%. Increasing the voltage usually increased the strain in the postorbital ligament, suggesting a causal relationship. The ipsilateral temporalis was the next most regular contributor, averaging 0.7% (0.4% if the outlying #426 is omitted), and increasing stimulation to this muscle often produced a dose response in the ligament as well. To ascertain whether the ipsilateral masseter and/or temporalis might be the direct cause of masticatory strain in the postorbital ligament, correlation coefficients were calculated for masticatory strain and stimulated strain for the seven ligaments in six pigs that had data for both conditions. Strain from ipsilateral masseter stimulation was found to have a positive relationship with masticatory strain ($r = 0.80$, $P = 0.03$), whereas strain from ipsilateral temporalis stimulation was not correlated with masticatory strain ($r = 0.17$, $P = 0.71$).

The contralateral muscles were much less consistent than the ipsilateral muscles in deforming the postorbital ligament and typically did not show a relationship between stimulus voltage and ligament strain (Table 3). In particular, most stimulations of the contralateral temporalis did not cause a measurable response from the ligament. The contralateral masseter usually elongated the ligament, but to a lesser degree than did the ipsilateral muscles.

Of the various manipulations, only jaw opening/closing produced consistent strain in the postorbital ligament. These were recorded as polarity only (Table 3) because of variations in magnitude between repetitions of the movement. In six of the nine cases, the postorbital ligament elongated during opening and shortened on closing; the other three showed the reverse pattern. Jaw opening was invariably accompanied by low to moderate increases of pressure on the temporal fossa.

Stimulations of temporalis muscles instrumented for sonomicrometry allowed a comparison of deformation of this muscle during mastication and during isometric contraction. These were found to be similar. Thickness increased 2% (SD 1%, $n = 7$), dorsal–ventral height was variable ($0\% \pm 3\%$, $n = 5$), and rostral–caudal length tended to decrease ($-2\% \pm 2\%$, $n = 9$). To test the association between

Table 3 Strain of the postorbital ligament during stimulation of muscles and during opening of the jaw[a]

	Temporalis		Masseter		
Pig ID	**Ipsilateral (%)**	**Contralateral (%)**	**Ipsilateral (%)**	**Contralateral (%)**	**Jaw opening**
347, Left	−0.62	ND	+2.76	ND	ND
348, Left	+1.35	ND	−0.25	ND	+
368 Left	−0.01	−0.007	+0.17	−0.01	ND
380 Right	+1.81	+2.12	+0.73	+1.94	+
381 Left	+0.83	0	+2.06	+0.23	−
382 Right	0	0	+0.04	0	+
Left	−0.07	0	−0.02	0	−
383 Right	+0.15	0.61	+0.12	0	+
Left	+0.002	0	+0.14	+0.10	ND
384 Right	+0.42	0	+0.72	+0.64	+
385 Right	+0.59	0	+0.77	+0.25	+
Left	0	0	+0.18	+0.06	−
426 Right	+4.25	+3.36	−0.52	+0.19	ND
Mean (SD)	0.67 (1.26)	0.50 (1.14)	0.53 (0.92)	0.31 (0.57)	—
Omit #426	0.37 (0.68)	0.21 (0.67)	0.62 (0.91)	0.32 (0.60)	—

Notes: ND: no data.

[a] Values for stimulation of each muscle are maxima. It was difficult to perform manual movement consistently, so only the polarity of strain is reported for opening. Closing movements had opposite polarity.

deformation of the postorbital ligament and rostral–caudal length of the temporalis, a correlation coefficient was calculated for the eight cases with both measurements; this proved to be negative ($r = -0.51$), but statistically insignificant ($P = 0.19$). In a few cases the temporalis was uncovered during stimulation, and these observations revealed that each pig had a unique pattern of surface deformation and that changes in muscle shape were surprisingly local. For example, thickening of the dorso–caudal part of the muscle could accompany thinning of the ventro–rostral part.

Dimensions of the temporalis were also assessed during jaw opening, omitting the first two experiments because of large excursions which accompanied movement and were not seen in the other experiments. Clear patterns were not seen. Opening tended to thin the muscle ($-3\% \pm 4\%$, $n = 3$), but dorsal–ventral height was highly variable ($1\% \pm 4\%$, $n = 5$), as was rostral–caudal length ($2\% \pm 5\%$, $n = 6$).

Discussion

Technical considerations

Both the DVRT and the sonometric crystals share the drawback of producing linear measurements, whereas the actual deformation of the postorbital ligament and the temporalis is likely curved. The barbs of the DVRT were inserted near the attachments of the ligament to the frontal and zygomatic bones, and thus would have underestimated any elongation that was not collinear with them. Less than optimal positioning of the barbs probably accounts for the variable magnitude of tensile strain seen in the ligament during mastication. Therefore, the maximal values recorded, 2–3% strain (pigs 380 and 381, Table 2), may be a better estimate of the true stretch of the postorbital ligament than is the calculated average of 1%.

As the focus of this study was on deformation of the ligament, the placement of the sonometric crystals was intended to reflect the overall shape of the temporalis in the temporal fossa, not to track the length or width of muscle fasciculi. However, this strategy would only have been completely successful if the muscle contractions were isometric, because changes in length did affect the results, accounting for higher variability in chewing and in opening/closing than for muscle stimulation. Coupled with the difficulty in applying linear measures to curvilinear distortions, little meaning can be attached to the precise values for muscle strain. Nevertheless, these measurements were useful in showing general patterns of deformations of the temporalis.

Surprisingly, higher pressures were measured on the right temporal fossa than on the left one

(Table 2). This makes no sense biologically, because the animals were chewing normally on both sides. The finding is probably artifactual. In previous work with pressure transducers (Teng and Herring 1998; Dutra et al. 2010), we have noted that readings are greatly attenuated unless the transducer is firmly seated flat against the bone. Due to the additional implantations on the right side, exposure was better and more care was taken in the positioning of the device. Another possibility is that the additional implantations caused an unintentional change in location of the transducer to a higher-pressure region. It is also conceivable that there was more traumatic swelling on the right side, but this should have affected the baseline as well.

Deformation of the postorbital ligament during chewing

The main finding of this study is that the postorbital ligament invariably stretched with every masticatory cycle. The initiation of ligament stretch was closely coupled to EMG from the adductor muscles and the initial changes in dimensions of the muscle. The peak deformation coincided with the later part of the EMG burst, the peak deformation of the temporalis, and peak pressure. Thus, stretching of the ligament accompanies the power stroke of mastication.

The magnitude of strain averaged ~1% during mastication with a maximum of ~3%. These values are not small when it is considered that the measurement was likely an underestimate (see above). Furthermore, muscle tendons, which, like the rabbit's postorbital ligament (Jasarevic et al. 2010), usually have elastin as well as crimped collagen (Herring et al. 2002), show typical functional strains of only 2–4% (Riemersma et al. 1988; Loren and Lieber 1995; Herring et al. 2002). Thus, a strain of 1–3% for a ligament is reasonable, and is at least an order of magnitude larger than strains typically observed in facial bones during mastication.

What stretches the postorbital ligament?

The postorbital ligament stretches when adductor muscles contract, but the functional data do not make it clear whether this stretching is a "side effect" of contraction of the temporalis or whether it results from the downward pull of the masseter on the zygomatic arch (or both or neither). Comparison of the timing of stretch to EMG in the muscles was unrevealing because the events coincided. The situation was further complicated by the possibility that the movement itself or of the contralateral muscles could have caused the ligament to stretch. For this reason we performed additional observations on anesthetized animals.

Stretching of the postorbital ligament was not due to movement of the jaw, as shown clearly by passive manipulations. First, in six of the nine open/close recordings, the ligament shortened during closure of the jaws, whereas in mastication the ligament was stretched at closure. No other manipulations consistently affected the ligament. Furthermore, events in the temporal fossa differed from those during mastication. Pressure rose during passive opening (presumably because the temporalis was stretched) and fell during passive closing, whereas during chewing, the opposite pattern was seen. Distortion of the temporalis during passive manipulations corresponded to mastication only in that the muscle usually thinned during opening and thickened during closing.

By contrast, stimulation of either the ipsilateral masseter or the ipsilateral temporalis was successful in stretching the postorbital ligament. Both muscles usually showed a dose effect, with increasing tetanus causing increasing stretch of the ligament. Elongation was somewhat less than for mastication, however. Interestingly, each muscle seemed to contribute ~0.5% to the total elongation of ~1% (Tables 2 and 3). This finding suggests that the full masticatory elongation of the postorbital ligament requires the participation of both muscles. Unfortunately, attempts to test this by stimulating the muscles simultaneously were unsuccessful.

Of the two muscles, the masseter appeared to be more effective than the temporalis in stretching the postorbital ligament. Tensile strain was greater (or shortening less) for stimulation by the masseter than by the temporalis in 9 of 13 ligaments recorded (Table 3). Furthermore, masticatory strain in the ligament was significantly correlated with strain produced by tetanus of the masseter but showed no covariation with strain produced by tetanus of the temporalis. However, the remote location of the motor nerves makes it difficult to produce a complete tetanus of the temporalis. Also, if the temporalis forced the ligament into a curve, the DVRT would underreport strain of the ligament. Thus, the influence of the temporalis may be greater than indicated.

The mechanism by which the masseter stretches the postorbital ligament appears to be the ventral and caudal pull of the muscle on the zygomatic arch, as envisioned by previous authors (Cartmill 1980; Greaves 1985; Rosenberger 1986;

Ross and Hylander 1996). It is more difficult to explain why the contralateral masseter usually stretched the ligament as well, but this could have been a product of mandibular rotation around a rostral–caudal axis (Herring and Mucci 1991), which would passively stretch the masseter and pull the arch ventrally. Notably, these proposed ventral movements of the zygomatic arch would tense the entire temporal fascia, not just the postorbital ligament.

The action of the temporalis on the postorbital ligament is not a direct pressure from the increasing girth of the contracting muscle, because the rostral–caudal dimension did not expand. Indeed, this length most often decreased during contraction. The most salient observation is that the temporalis thickened, probably pressing on the enclosing temporal fascia. Thus, these data support Cartmill's (1972, 1980) original idea of the temporalis supplementing the masseter-derived tensile stress in the temporal fascia. Contraction of the contralateral temporalis cannot tense the fascia and does not cause mandibular rotation around a rostral–caudal axis, and so did not usually affect the length of the postorbital ligament.

In summary, contractions of both the masseter and the temporalis elongate the postorbital ligament, most likely by causing tension in the temporal fascia, with the masseter doing so more directly.

Is vision affected?

In the primitive mammalian condition and in pigs, the laterally facing orbit and temporal fossa are roughly in line (Heesy 2005). Cartmill suggested that such an arrangement would prevent masticatory tension in the temporal fossa from affecting the orbital contents (Cartmill 1972). This is clearly not true, at least for pigs. Despite the absence of convergence or frontation of the orbit in pigs, contraction of the jaw muscles caused significant distortion of the postorbital soft tissues. Since we did not study the eye itself, we have not proved that mastication disrupts vision in pigs, but it is highly likely to do so. Possibly such disruptions are small and can be corrected by oculomotor adjustments (Heesy 2005; Heesy et al. 2007). Vision is reasonably acute in pigs, but these animals are inattentive to visual information and learn much more rapidly using their other senses (Klopfer 1966). Given the orientation of the eyes, binocular vision is minimal at best. Thus, it seems likely that pigs are simply not inconvenienced by the visual disruptions that inevitably accompany chewing.

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