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Jaw muscles and the skull in mammals: the biomechanics of mastication☆

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Abstract

Among non-mammalian vertebrates, rigid skulls with tight sutural junctions are associated with high levels of cranial loading. The rigid skulls of mammals presumably act to resist the stresses of mastication. The pig, *Sus scrofa*, is a generalized ungulate with a diet rich in resistant foods. This report synthesizes previous work using strain gages bonded to the bones and sutures of the braincase, zygomatic arch, jaw joint, and mandible with new studies on the maxilla. Strains were recorded during unrestrained mastication and/or in anesthetized pigs during muscle stimulation. Bone strains were 100–1000 $\mu\varepsilon$, except in the braincase, but sutural strains were higher, regardless of region. Strain regimes were specific to different regions, indicating that theoretical treatment of the skull as a unitary structure is probably incorrect. Muscle contraction, especially the masseter, caused strain patterns by four mechanisms: (1) direct loading of muscle attachment areas; (2) a compressive reaction force at the jaw joint; (3) bite force loading on the snout and mandible; and (4) movement causing new points of contact between mandible and cranium. Some expected patterns of loading were not seen. Most notably, strains did not differ for right and left chewing, perhaps because pigs have bilateral occlusion and masseter activity. © 2001 Elsevier Science Inc. All rights reserved.

Keywords: Bone strain; Mandible; Mastication; Masticatory muscles; Maxilla; Pig; Skull; Suture

1. Introduction

Although primitive jawed fishes had well ossified skulls with interlocking bones, the predominant evolutionary trend has been toward increasing flexibility and independent movability of parts (Schultze, 1993). Among living vertebrates, some degree of cranial kinesis is the rule. Rigid skulls are only found in taxa specialized for niches that require forceful use of the head, for example burrowing (Gans, 1974; Wake and Hanken, 1982; Rieppel, 1996) or feeding on resistant prey (Lauder, 1982; Wineski and Gans, 1984; De Vree and Gans, 1987; Hull, 1991; Turingan and Wainwright, 1993; Wild, 1997). The exception to the general rule of cranial kinesis is the Class Mammalia. Kinesis was present in early therapsids but lost in cynodonts, and recent mammals all have

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solid, tightly sutured skulls (Maier, 1999). Suckling and mastication are forceful cranial activities almost unique to mammals, and thus most workers believe that the akinetic mammalian skull originally evolved because of the mechanical requirements of feeding (Maier, 1999).

In the present study we examine the premises of this reasoning by investigating whether the skull is truly akinetic during mastication. In order to determine how the skull resists feeding loads, we measured bone and suture strain during in vivo mastication. These observations were followed by investigations intended to determine the most probable sources of the feeding loads, such as muscle contraction, bite force, or reaction forces at the jaw joint.

Our subjects are miniature pigs, *Sus scrofa*, of the Hanford strain, which resemble their feral ancestors (Porter, 1993) in having long snouts and good occlusion. Although pigs are omnivorous, the diet of feral swine consists in large part of acorns and similar nuts, roots, and sometimes grasses (Henry and Conley, 1972; Pine and Gerdes, 1973), all resistant foods that must require forceful mastication. Thus pigs would seem an appropriate group of mammals in which to investigate the biomechanical aspects of chewing.

Although many models of mammalian skull function emphasize the teeth as the point of applied force (Badoux, 1966; Preuschoft et al., 1985), it is important to remember that in most mammals, the jaw approximates a third-class lever system (Hylander, 1975). Because the moment arm of the bite force exceeds that of the muscles, at equilibrium the muscle force must exceed the bite force. For this reason the studies described below pay particular attention to the effect of the two large adductor muscles that attach to the outer surfaces of the cranium and mandible, the temporalis and masseter. Both these muscles close the jaw, but they have opposite effects on transverse movements. The backward-pulling temporalis moves the mandible ipsilaterally, while the forward-pulling masseter moves it contralaterally; these muscles are thus active in opposite side pairs (‘diagonal couples’), e.g. right temporalis and left masseter are active when the mandible moves to the right (Herring and Scapino, 1973). The position of the bite point (‘working side’ of unilateral mastication, as opposed to the ‘balancing side’) is also significant for jaw mechanics, especially in setting up bending moments in the jaws. This creates some difficulties in the study of pigs. Pigs have unilateral mastication, to the extent that a working side can be identified by the direction of jaw movement. However, they have isognathous jaws and bilateral occlusion, so the bite location is never clear and may be bilateral (Herring and Scapino, 1973). In pig mastication, each cycle involves two transverse movements, first toward and then away from the working side (Herring, 1976). Thus, both diagonal couples are employed in series with every chew.

2. Materials and methods

This review draws on studies of the zygomatic arch (Herring and Mucci, 1991; Herring et al., 1996; Rafferty et al., 2000), jaw joint and mandibular body (Marks et al., 1997; Liu and Herring, 2000a,b), braincase (Herring and Teng, 2000), and facial sutures (Rafferty and Herring, 1999; Herring and Rafferty, 2000) that were published previously. The section below describes new experiments on the maxillary bone, using techniques similar to those of the previous studies. Fig. 1 summarizes the sutures and bones for which strain data are available.

A total of 11 miniature pigs of the Hanford strain (Charles River, Wilmington, MA), 3–5 months old and weighing 13–26 kg, were used for studies on the maxillary bone. All procedures were reviewed and approved by the University of Washington Animal Care and Use Committee. After acclimation to the laboratory environment, animals were anesthetized by mask with halothane/nitrous oxide. The skin and periosteum were incised over strain gage sites on the facial bones. The exposed bony surfaces were cauterized, smoothed, degreased, buffered and dried. Stacked 45° rosette gages (SK-06-030WR-120, Measurements Group, Raleigh, NC or FRA-1-11, Tokyo Sokki Kenkyujo Co., Tokyo), previously attached to lead wires and insulated, were attached using cyanoacrylate glue. The periosteum and skin were separately sutured closed with the lead wires exiting from one end of the incision. Most animals had additional strain gages or other transducers placed elsewhere on the head, but these results will be reported elsewhere.

For experiments involving mastication, fine-wire EMG electrodes were placed in up to six muscles of mastication, always including left and right

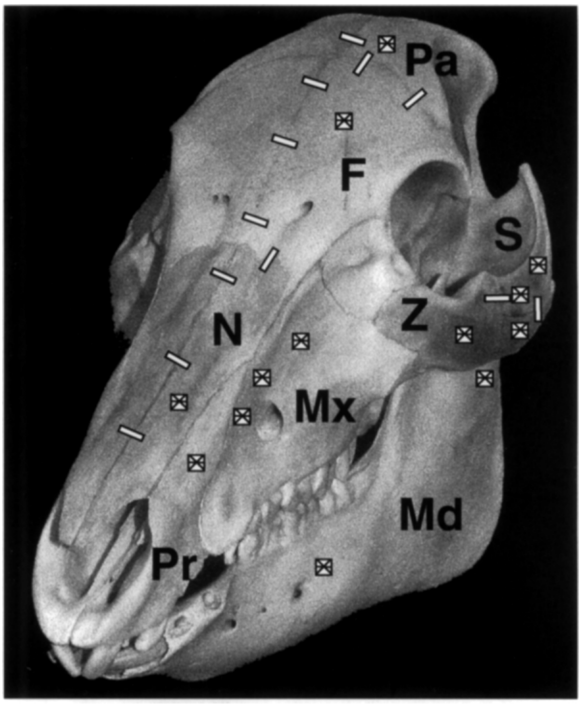

Fig. 1. Skull of miniature pig, *Sus scrofa*, showing sites of strain gage placement. Sutures were studied using uniaxial strain gages (rectangles) bonded to the bone on either side of the suture but not to the suture itself. Bones were instrumented with stacked rosette strain gages (squares with internal lines). F, frontal; Md, mandible; Mx, maxillary; N, nasal; Pa, parietal; Pr, premaxillary; S, squamosal; Z, zygomatic.

masseter muscles. A topical anesthetic (2% procaine) was infiltrated into the strain gage incisions and an analgesic (either buprenorphine 0.005 mg/kg or ketorolac 1 mg/kg) was administered IM. Animals were then allowed to recover from the anesthesia and were offered their normal diet of pig chow pellets. During feeding, EMG and strain signals were conditioned and amplified (Grass Polygraph, Quincy, MA and Measurements Group Model 2120, respectively) and the processed signals were digitized, sampled at 500 Hz, and stored to computer (Biopac Systems, Santa Barbara, CA). After approximately 15 min of mastication was recorded, animals were anesthetized again.

The purpose of the procedures on anesthetized animals was to elucidate the loads most likely to have caused the strains. We reasoned that if the feeding strain pattern could be mimicked by an isolated, known load, then that load was probably responsible for the masticatory pattern. Pigs were placed on a table, usually prone with the teeth in occlusion or with a bite block placed at the incisors or molars. Bite force was simulated by pressing on the teeth. Pairs of stimulating needle electrodes were placed bilaterally in the masseter and sometimes in the temporalis muscles. Muscles were tetanized at 0.5 Hz singly and together by 600-ms trains of 5 ms pulses delivered at 60 pps. Voltage was set as high as possible (supramaximal) without spreading to adjacent muscles. Bone strain was recorded as for mastication.

The raw EMG signals were used to determine chewing side (Herring and Scapino, 1973). The strain signals were analyzed by subtracting baseline values from each element of the rosette and calculating principal strain magnitudes and orientations (TechNote 515, Measurements Group). Following Hylander and Johnson (1989), peak masticatory strains were defined as those coinciding with the maximum shear strain (sum of the absolute values of principal strains) for each chewing cycle. Tensile strains were expressed as positive and compressive strains as negative values.

3. Results and discussion

3.1. Generalizations

Average magnitudes of peak principal strains during mastication are summarized in Table 1, and strain orientations are illustrated in Figs. 2–5. There are two surprising generalizations. First, strain patterns, although generally consistent at different locations on the same bone surface, were often strikingly different between adjacent bones. The second surprise was that for most locations, chewing side was immaterial for either strain magnitude or orientation. Although individual gauges often gave different results depending on the side of mastication, these differences were not consistent among or even within pigs. Because the strains were bone-specific, cranial regions are treated separately below for description.

3.2. Zygomatic arch

The cheekbone of pigs is formed by the zygomatic bone and the zygomatic process of the squamosal bone, joined by the L-shaped zygo-

Table 1
Magnitudes of principal strains during mastication (mean ± S.D.)

Gage site	Sample size (# pigs)	Total cycles analyzed	Tension ($\mu\varepsilon$)	Compression ($\mu\varepsilon$)
Zygomatic arch				
Zygomatic bone				
Body[a]	9	101	174 ± 91	−124 ± 106
Ventral flange[b]	8	151	142 ± 69	−168 ± 85
Squamosal bone				
Lateral to joint[c]	12	90	212 ± 138	−84 ± 76
Zygomatic process, lateral[a,b]	9	158	494 ± 22	−140 ± 160
Zygomatic process, medial[b]	6	169	220 ± 109	−572 ± 238
Braincase				
Parietal bone[d]	6	109	43 ± 25	−23 ± 8
Frontal bone[d]	8	190	43 ± 35	−28 ± 23
Mandible				
Condylar process[c,e]	16	190	152 ± 80	−223 ± 135
Body[c]	4	30	77 ± 32	−136 ± 100
Snout				
Maxillary bone	7	186	232 ± 75	−147 ± 117

[a] Herring et al. (1996).
[b] Rafferty et al. (2000).
[c] Liu and Herring (2000b).
[d] Herring and Teng (2000).
[e] Marks et al. (1997).

matic suture. In various studies we have instrumented six lateral (two on each bone and both the vertical and horizontal parts of the suture) and one medial location. During mastication, the arch is distorted as follows on both sides of the skull (Fig. 2): (1) the largest strains are in the suture, compressive in the vertical part and tensile in the horizontal part (Herring and Mucci, 1991); (2) all parts of the zygomatic bone show tension aligned with the pull of the masseter muscle (rostrodorsal); the body is bent in-plane such that the inferior border becomes more convex (Herring et al., 1996); and (3) the squamosal is bent out-of-plane with the lateral surface becoming more convex; the axis of tension on the lateral surface is caudodorsal (Rafferty et al., 2000).

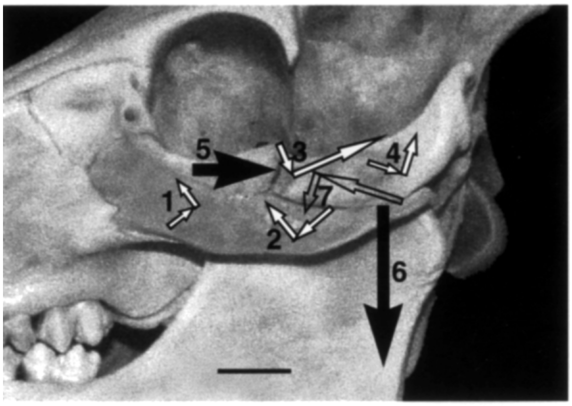

Fig. 2. Average strains on the zygomatic arch during mastication. For sutures (large black arrows), only polarity and approximate magnitude of strain are known. For bones (pairs of open arrows), the magnitudes and orientations of both principal strains are shown. Arrows pointing away from the gage sites indicate tensile strain, whereas arrows pointing toward gage sites indicate compressive strain. The scale bar equals 200 $\mu\varepsilon$ for the bone locations (open arrows) and 400 $\mu\varepsilon$ for the sutures (black arrows). 1 and 2, zygomatic bone body and flange; 3 and 4, lateral surface of squamosal; 5 and 6, vertical and horizontal segments of suture; 7, medial surface of squamosal.

This strain pattern could be duplicated but with larger magnitudes in anesthetized animals by stimulating a single muscle, the ipsilateral masseter (Herring et al., 1996). Changing the occlusion with a bite block had no effect. No other muscles or manipulations produced significant strain anywhere in the zygomatic arch, with the interesting exception of the zygomatic ventral flange. Masticatory-like strain in this region could also be simulated by contraction of the opposite masseter or by simply moving the jaw toward the instrumented arch (Rafferty et al., 2000).

As complex as these strains may seem, they can

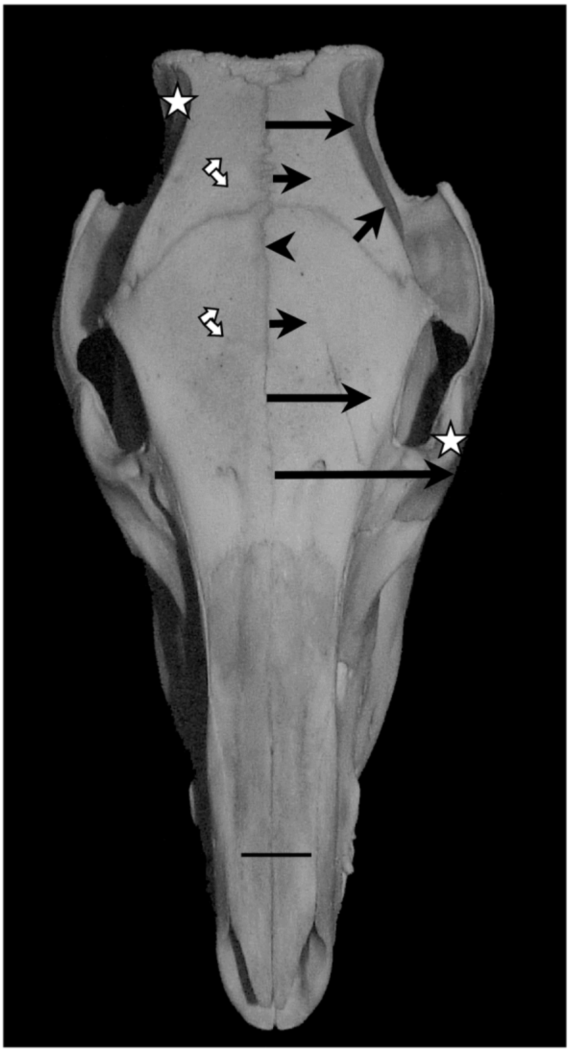

Fig. 3. Average strains on the braincase during mastication. A left chewing cycle is depicted; the mandible would be moving from left to right, with the most active muscles being the left masseter and right temporalis (white stars). Sutural strains (black arrows) are not affected by chewing side, but the orientation of principal bone strains (open arrows) alternates between +45° and −45°. The scale bar is 400 $\mu\varepsilon$ for sutural strain and 200 $\mu\varepsilon$ for bone strain.

be explained simply as a result of the masseter's backward and downward pull on the zygomatic bone, which is braced at its sutures with the maxillary and squamosal bones. The muscle force vector is directly responsible for the orientation of the tensile strain and the in-plane bending of the zygomatic bone, and for the sutural strains. The medial pull of the masseter on the zygomatic bone indirectly causes the out-of-plane bending of the squamosal because of the beveled shape of the sutural interface (Rafferty et al., 2000). The opposite-side masseter indirectly causes the strain on the zygomatic flange by driving the condyle against it. The similarity of working- and balancing-side strains in the zygomatic arch is clearly due to the fact that during pig mastication, the masseters are almost equally activated (Herring and Scapino, 1973).

3.3. Braincase

The pig is well known for the thickness of its vault bones. Although air sinuses eventually hollow them, the frontal and parietal bones of our young study animals were still composed of dense fine trabecular bone. In addition to these two paired bones, our data include the interparietal, interfrontal and coronal sutures (Fig. 3, Herring and Teng, 2000).

Even more than in the zygomatic arch, masticatory strains in the braincase sutures were far greater than those of the bones (Herring and Teng, 2000). Indeed, braincase bone strains were the lowest anywhere in the skull (Table 1). During mastication the ectocranial bone surfaces showed a pattern of simple torsion; strains were identical in all four bones (parietal and frontal pairs) and were oriented at +45° or −45° to the sagittal plane (Fig. 3). The direction of the tensile axis corresponded to the diagonal couple active at the moment. For example, when the jaw was moving to the left, the tensile strain seemed to connect the active muscles, right masseter and left temporalis. Sutural strains were more complex, but peak strains were usually tensile (Fig. 3). The coronal suture was unique in being the only location on the skull that consistently showed strain during jaw opening as well as jaw closing (Herring and Teng, 2000).

As in the case of the zygomatic arch, masticatory strains could easily be reproduced by stimulating muscles, but in the braincase the masseter was not sufficient. The torsional strain on the braincase bones was the same whether it was caused by unilateral masseter stimulation or by stimulation of the masseter's diagonal partner, the opposite-side temporalis. Of course, both muscles contract simultaneously during chewing. The masseter was found to be responsible for tension in the interfrontal suture and in the coronal suture (during jaw closing), but the temporalis accounted for the tension in the interparietal

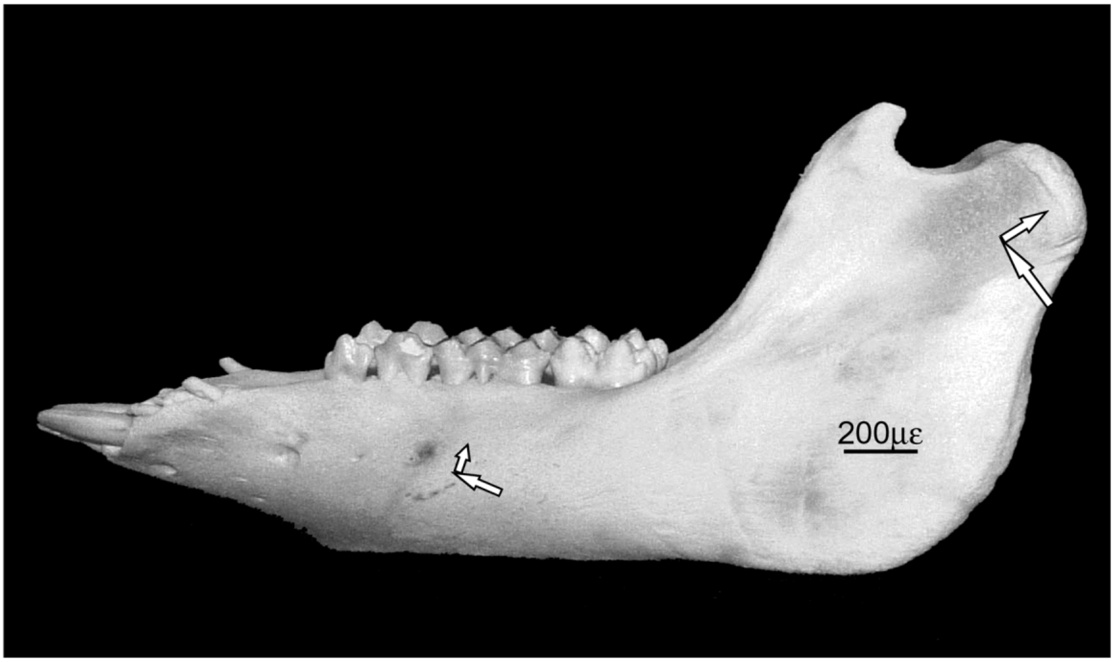

Fig. 4. Average principal strains on the mandibular condyle and body during mastication. Working and balancing side strains are the same.

suture. The tensile strain observed during jaw opening in the coronal suture could be mimicked by stimulating the neck extensor musculature. The braincase sutural strains were independent of bite force and could all be interpreted as the direct result of muscular pull on bony attachments (Herring and Teng, 2000). In general, muscle stimulations and mastication produced similar magnitudes of strain in the braincase bones. In the sutures, however, stimulated strains were larger than those observed in vivo. This phenomenon probably occurs because the masseter and temporalis produce strains of opposite polarity in the braincase sutures. During mastication but not stimulation, both muscles are active and thus the sutural strains partially cancel each other. In summary, braincase strains are produced by the musculature. No other muscles than masseter, temporalis and the neck extensors are involved, nor is a bite point necessary for these effects.

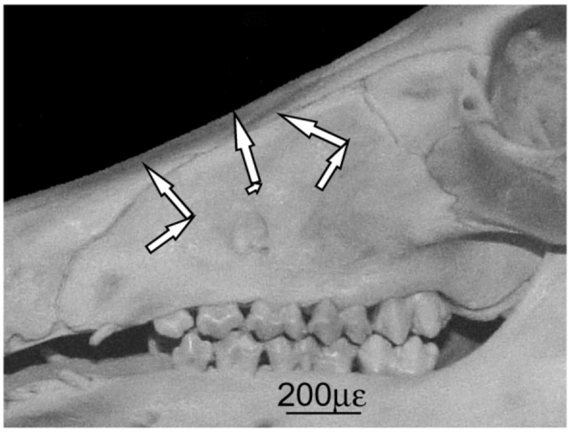

Fig. 5. Average principal strains on three locations of the maxillary bone during mastication. As in the mandible, working and balancing side strains are the same. Tensile strain is oriented rostrodorsally, in contrast to the mandible, in which tensile strain is oriented caudodorsally (Fig. 4).

3.4. Mandible

The pig mandible is elongate, with a fused symphysis and condylar processes elevated above the occlusal plane (Fig. 4). The jaw joint area is one of special interest from both an evolutionary and a clinical point of view. Strain gages placed close to the lateral side of the condyle showed a predominance of compression over tension (Table 1), with the compressive axis oriented dorsally or rostrodorsally (Marks et al., 1997; Liu and Herring, 2000b). The same compressive pattern was found on both the working and balancing sides of the jaw. Net compression is indeed expected at this location because the third-class lever nature of jaw mechanics implies a compressive reaction force at one or both jaw joints (Hylander, 1975). Furthermore, the orientation of the compressive axis is similar to the vector of the masseter muscle, suggesting that the masseter muscle might be particularly important in engendering the reaction force. This was confirmed in anesthetized animals, where maximum stimulation of the ipsilateral masseter produced similar but larger strains than mastication (Liu and Herring, 2000a,b), but the temporalis and contralateral masseter produced much smaller and differently oriented strains (Marks et al., 1997; Liu and Herring, 2000a).

Although the compressive condylar strains fit neatly into the expectations of the lever model, attentive readers may have already noticed a problem with this discussion of the jaw joint. The reaction force must act equally on the condyle and the squamosal bone. Yet as explained above, strains on the squamosal lateral to the joint are quite different; not only is the strain predominantly tensile, but the compressive axis is rotated approximately 90° relative to that of the condyle (compare Figs. 2 and 4). This surprising result does not mean that the third-class lever model is flawed. It is more likely that the articular eminence (the actual contact surface of the squamosal) is indeed loaded by the same reaction force as the condyle, but that its irregular shape leads to cantilever bending rather than axial compression. This bending and the out-of-plane bending experienced by the entire squamosal may dominate the lateral surface of the bone to the exclusion of the reaction force. The remarkable difference between these two bony elements of the same joint emphasizes that strains are as much a result of geometry as of applied loads.

In preliminary experiments on the mandibular body, we used a simple uniaxial strain gage placed vertically beneath a mandibular molar, thinking that strain here could serve as a surrogate for bite force (Hylander, 1986). We were disappointed to find that strains in the dorsoventral direction were tensile, not compressive. The results from stacked rosette gages (Fig. 4) explain why. Although the body of the mandible showed a predominance of compression over tension (Table 1), the compressive orientation was closer to the rostrocaudal than to the dorsoventral axis, suggesting that bending or torsion of the corpus more strongly influences strain than the vertical component of bite force. Unexpectedly, especially considering studies on other species (Weijs and de Jongh, 1977; Crompton, 1995; Hylander et al., 1998), working and balancing side strains were indistinguishable in magnitude or orientation.

Unlike the previously discussed regions and even unlike the mandibular condyle, ipsilateral masseter stimulation could not completely reproduce the masticatory strain pattern on the mandibular body. Although far better than the contralateral masseter, the strains resulting from ipsilateral masseter differed from chewing strains in two ways: (1) compression no longer exceeded tension; and (2) the principal strains were approximately 45° to the rostrocaudal axis of the mandible (Liu and Herring, 2000a). The strain pattern caused by masseteric stimulation suggests torsion, a mode of loading for which the mandibular body with its thick cortex and large marrow cavity seems especially suited. It seems likely that torsion is produced, as described by Hylander and colleagues in primates (e.g. Hylander, 1979) by the fact that the caudally placed masseter and the rostrally placed occlusal contact tend to rotate the mandible in opposite directions around its long axis. We have not been able to determine what additional muscular or occlusal loads account for the differences between masseter stimulation and mastication.

3.5. Snout

The maxillary bone was investigated with gages placed in the dorsal (non-alveolar) part of the bone, either anterior, directly above ('middle'), or posterior to the infraorbital foramen (Fig. 5). A comparison of the strains recorded during mastication in these three locations (Table 2a) reveals similar patterns. The only significant difference among locations was a minor variation in orientation; all locations showed tensile strain oriented rostrodorsally, but the posterior location was more rostrally inclined than the middle location ($P < 0.05$, Bonferroni-corrected t-test). All locations showed a predominance of tension over compression (17/20 total comparisons). In fact, the minimum principal strain was 0 or a positive value (i.e. tension) for two of the middle gages and one of the posterior gages, accounting for the unusually large standard deviations.

Table 2
Peak maxillary principal strains during mastication (mean ± S.D.)

Gage location	Sample size (# gages)	Total cycles analyzed	Tension ($\mu\varepsilon$)	Compression ($\mu\varepsilon$)	Orientation of tensile strain
A. Effect of location (combined working and balancing sides)					
Anterior	3	97	206 ± 64	−160 ± 156	53° ± 20
Middle	4	73	227 ± 15	−18 ± 95	76° ± 15*
Posterior	4	89	232 ± 99	−155 ± 86	22° ± 20*
B. Effect of the side of chewing (all gage positions)					
Working side	9	56	212 ± 131	−92 ± 181	54° ± 36
Balancing side	9	70	213 ± 76	−73 ± 76	62° ± 28

*$P < 0.05$.

To achieve an adequate sample size, maxillary locations were grouped to compare working- vs. balancing-side strains. Table 2b shows clearly that working and balancing strains were identical. Because this conclusion was unexpected, individual gages were surveyed. This examination revealed that working side strain magnitudes were larger for 5/9 gages and smaller for 4/9 gages, and that the orientation of strain was more rostral in 3/9, more dorsal in 1/9, and unchanged in 4/9. These very inconsistent differences, which were independent of gage placement, reinforce the conclusion that working and balancing side peak strains are similar.

Even though peak strains were the same on working and balancing sides, this is not the whole story. Several gages, including most posterior gages, showed dynamic changes during the course of the power stroke. One example is shown in Fig. 6. Channel 2 of this rosette gage, which sloped caudodorsally, shows a double peak; when the instrumented left maxilla was on the working side, both peaks were tensile, otherwise, the first peak was compressive. This indicates that either the changing occlusion or the switching from one muscular diagonal couple to the other has altered the strain orientation.

Maxillary strains resulting from masseter muscle stimulations are given in Table 3. Strains from stimulation resembled masticatory strains in that (1) tension greatly exceeded compression, and in one case the minimum principal strain was slightly tensile; and (2) the orientation of the tensile strain was the same, 50–60° rostrodorsal from the occlusal plane. The opposite-side masseter produced larger (but not statistically different) strains than the same-side muscle. Although the pattern of stimulated strain was similar to masticatory strain, the maxillary bone was unique in the skull in that strain magnitudes were generally smaller during stimulation than during chewing (Tables 2 and 3). This was true not only for average values but also in each of the four animals for which both chewing and stimulation data were available. This surprising finding means that the masseter muscle is not the sole source of maxillary strain. Yet no other muscle appeared to play a significant role. Some insight into the situation was afforded by inserting a tongue depressor between the teeth during one experiment; this had the effect of making stimulation strain the same as masticatory strain. We conclude that maxillary strain involves tooth contact.

Our information on the other elements of the snout, the nasal and premaxillary bones, is very preliminary (Rafferty, Marshall and Herring, unpublished data). The premaxillary was tensed dorsoventrally and compressed rostrocaudally. Strains were larger on the balancing side and when the contralateral masseter was stimulated. Furthermore, strains were greatly increased when an anterior bite block was present. These findings are reminiscent of the ventral flange of the zygomatic bone and thus suggest that movement of the mandible toward the instrumented premaxillary bone, occluding the anterior teeth, is a major source of strain. The nasal bone was also under rostrocaudal compression, but was relatively unaffected by the side of chewing or stimulation. When the masseters were stimulated in the presence of anterior occlusal contact, the nasals were compressed biaxially (that is, both principal strains were negative).

Finally, recordings from the internasal and na-

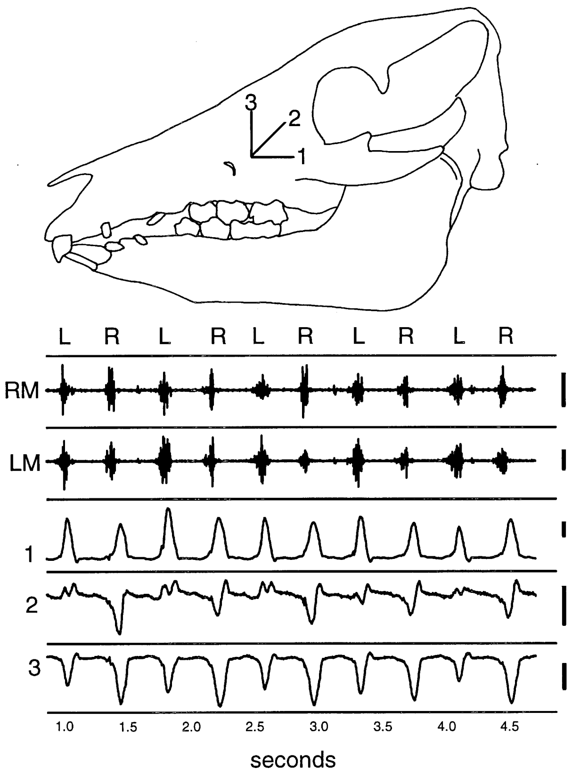

Fig. 6. Example of EMG and strain recorded during mastication. The stacked rosette gage was posteriorly positioned on the left maxillary bone; the orientations of its elements are indicated by lines 1–3. The recording shows a series of chewing cycles that alternate between right (R) and left (L) working sides. The top two channels are EMG from right and left masseter muscles (RM and LM). The bottom three channels are raw strain signals from each of the gage elements (1, 2, 3). Although element 1 is consistently tensile and element 3 is consistently compressive, element 2 shows a double strain peak. Both peaks are tensile when the left side is the working side, but the first peak is compressive when the left side is the balancing side.

sofrontal sutures again showed much higher strains than those on the neighboring nasal and frontal bones. During mastication both these sutures were strongly compressed (Rafferty and Herring, 1999). In fact the compressive strains at the nasofrontal suture, which averaged -1583 $\mu\varepsilon$, were the highest observed anywhere in the skull during quiet chewing. Masseter stimulation, regardless of side, reproduced the compressive pattern but at somewhat lower magnitude than mastication, while temporalis stimulation produced an opposite pattern of tension (Herring and Rafferty, 1999).

It is possible that the maxillary strain pattern, which is very similar to that of the neighboring zygomatic bone, directly reflects the pull of the masseter muscle transmitted through the zygomatico-maxillary suture. In fact, the pull of the masseter coupled with bite force could create torsion or shear, analogous to the twisted mandible. But these explanations do not account for the large strains seen when only the contralateral masseter is active, nor for the strain patterns elsewhere in the snout. Also, a direct effect of the occlusal load, at least at the non-alveolar locations studied, seems unlikely. Occlusal loads should put equal and opposite strains on these two tooth-bearing bones, but in fact the patterns are orthogonal, rostrodorsal tension in the maxilla and caudodorsal tension in the mandibular body. Instead, the dominant loading regime for the snout as a whole is probably bending in response to the bite force, the role of the masseter primarily being to produce occlusal contact. An upward bending of the snout from the applied load would explain not only the direction, but also the predominance of tensile strain in the maxillary bone. Furthermore, such bending would lead to compression throughout the dorsum of the snout (nasal bone and its sutures) and explain the equal effect of ipsilateral and contralateral muscle contraction on all the bones and sutures of the face.

Table 3
Maxillary principal strains resulting from stimulation of the masseter muscles (all locations, mean ± S.D.)

	Ipsilateral masseter	Contralateral masseter	Bilateral masseters
Sample size (# gages)	6	7	7
Total contractions analyzed	51	50	55
Tension ($\mu\varepsilon$)	87 ± 35	146 ± 87	181 ± 94
Compression ($\mu\varepsilon$)	-60 ± 30	-50 ± 36	-66 ± 71
Orientation of tensile strain	$48° \pm 37$	$59° \pm 31$	$63° \pm 43$

3.6. Overall patterns of strain

Perhaps the most important conclusion from this work is that there is no ‘overall pattern’ of strain in the skull. Although there are many theoretical analyses of the mammalian skull that treat the skull as a unitary structure such as a beam (summarized by Russell and Thomason, 1993; Weishampel, 1993), this is not how it works. Rather, different regions of the skull are differentially distorted by loads arising variously from muscles, the jaw joint, and the occlusion.

If there is a unifying theme in this analysis of masticatory biomechanics, it is the masseter muscle. The masseter muscle is directly responsible for bending the zygomatic bone in-plane, and the load transmitted from the zygomatic bone to the squamosal bone is responsible for the out-of-plane bending of the squamosal. By moving the mandible to the opposite side, the masseter is indirectly responsible for the strain patterns in the zygomatic flange and probably the premaxillary bone. In conjunction with the temporalis muscle, the masseter twists the braincase and tenses the braincase sutures. Reaction forces from masseteric contraction compress the mandibular condyle, and occlusal forces produced by masseteric contraction bend the snout dorsally. The pull of the masseter, in combination with the bite force, twists the body of the mandible. These suggestions are illustrated in Fig. 7.

The variant strain regimes of different regions of the skull beg the question of whether the mammalian skull is akinetic after all. The difference between ‘rigid’ mammals and ‘flexible’ other vertebrates begins to look more quantitative than qualitative. In the pig skull, the sutures are the key elements of flexibility. They are the loci of the greatest strains, and they separate the regions of the cranium that are differentially strained. Of course, sutures are often considered temporary structures. In many species including *Sus scrofa*, suture fusion is a gradual process that is never completed even in the oldest animals (Herring, 1972). The animals investigated in our experiments were juveniles. It would be extremely interesting to investigate bone strain in elderly, mostly fused individuals, but unfortunately this is not practicable. Certainly, one would expect to find a more unified strain pattern in a completely synostosed skull.

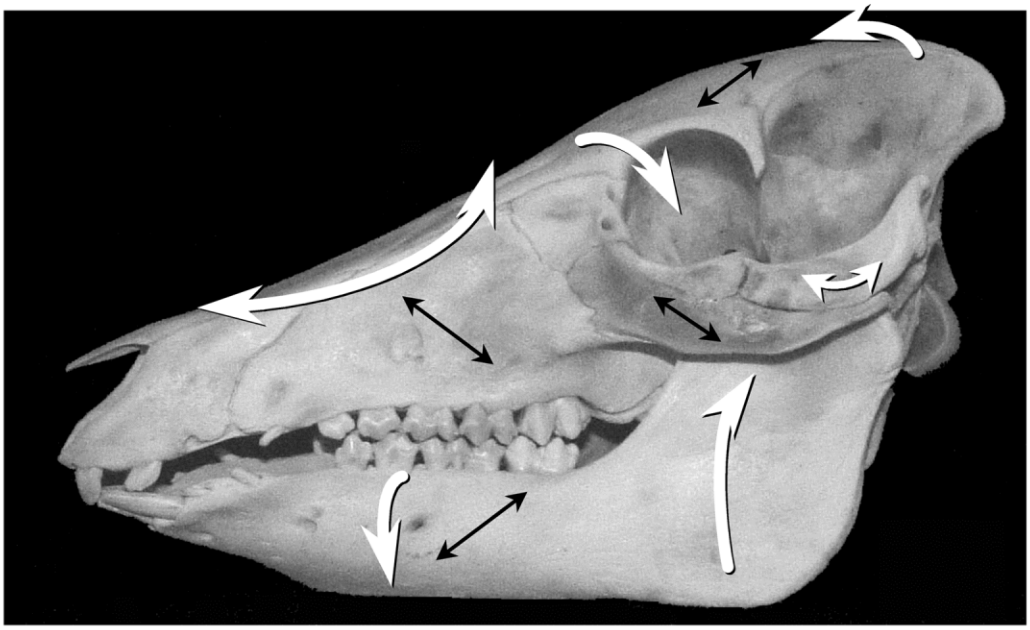

Fig. 7. Proposed overall loading patterns in the skull of the pig. Bending (squamosal bone and snout) is indicated by white, curved double-headed arrows. Torsion (braincase and mandible) is represented by pairs of white single-headed arrows. Straight black double-headed arrows show the orientation of principal tensile strain in selected regions. The direction of torsion and tension in the braincase are those associated with contraction of the left masseter and right temporalis.

3.7. Is the pig a typical mammal?

In vivo strain gage recording has been used to assess cranial biomechanics for several decades, but the number of species investigated is still very small, especially for bones other than the mandible. The richest data are those for primates (Oyen et al., 1996; Ross and Hylander, 1996; Hylander et al., 1998, 2000 and earlier papers; Ravosa et al., 2000). Unfortunately, higher primates and pigs have very similar masticatory mechanisms (Herring, 1976), and so biomechanical similarities between them cannot be taken as evidence for mammalian homogeneity.

Two of the most general findings of the present survey are (1) the pre-eminence of the masseter muscle as a source of load; and (2) the characterization of sutures as highly strained, movable joints. Both seem to be supported by studies on other species. The role of the jaw muscles, particularly the masseter, has not been well investigated. However, Buckland-Wright's (1978) path-breaking study on cats (*Felis catus*) also found the masseter to be a more important influence on cranial strain than the temporalis. This is particularly interesting, because as in other carnivorans, the cat temporalis is larger than the masseter (Turnbull, 1970). There is also support from cats (Buckland-Wright, 1978) and goats (Jaslow and Biewener, 1995) for the commonality of the finding that sutures are zones of flexibility compared to the rigid skull bones.

Strain magnitudes in pigs are typical of those reported from other species, but there are some differences in strain gradients. As Table 1 indicates, most bones had total shear strains (maximum strain plus the absolute value of minimum strain) of 200–400 $\mu\varepsilon$. The exceptions were the zygomatic process of the squamosal (much higher strains) and the braincase bones (much lower strains). Strain information from the bones of the zygomatic arch is available from cats (Buckland-Wright, 1978) and macaque monkeys (*Macaca*, Hylander and Johnson, 1997). Cats, like pigs, show much higher strains in the squamosal part of the zygomatic arch than in the zygomatic part, but macaques show the reverse strain gradient. This difference is most likely due to a real difference in the nature of deformation. In pigs, high squamosal strains are the result of out-of-plane bending (Rafferty et al., 2000), which probably does not occur in the macaque squamosal (Hylander and Johnson, 1997). A possible morphological correlate is the postorbital bar or septum, lacking in pigs and cats but present in monkeys.

The surprisingly low strains in braincase bones (Table 1) have also been found in rats (*Rattus*, Rawlinson et al., 1995), dogs (*Canis*, Sugimura et al., 1984), galagos (*Otolemur*, Ravosa et al., 2000), and anthropoid primates (Hylander et al., 1991; Ross and Hylander, 1996), although apparently not in cats (Buckland-Wright, 1978) or sheep (*Ovis*, Thomason, personal communication). Where present, the low braincase bone strains are associated with thick, stiff calvarial bones. These bones are unique in the skull in that their inner periosteum is the dura mater, which produces growth factors that may promote osteogenesis beyond what is required to resist the forces of mastication (Opperman, 1997).

Like strain magnitudes, strain orientations show many similarities and some differences across species. The contrasting orientations of strains in the zygomatic and squamosal elements of the zygomatic arch are the same in pigs and in macaques (Hylander and Johnson, 1997). Although braincase torsion is a common finding, the direction of twisting varies. In pigs the axis of tension runs from the working side anteriorly to the balancing side posteriorly, as is also found in macaques (Hylander et al., 1991) and probably dogs (Sugimura et al., 1984), but the opposite orientation is found in sheep (Thomason, personal communication), galagos (Ravosa et al., 2000), and owl monkeys (*Aotus*, Ross and Hylander, 1996). The pig pattern, as we have shown, results from the coordination of muscle activity, which may not be the same in all the above species. The opposite pattern is thought to arise from torsion set up by the bite point on the working side and the jaw joint reaction force on the balancing side (Greaves, 1985).

Strain orientations in the jaws appear to be more uniform among different taxa. Tensile strain in the maxilla is oriented rostrodorsally not only in pigs, but also in sheep (Thomason, personal communication) and dogs (Sugimura et al., 1984). In the mandible, a rostrocaudal direction for tensile strain is found in pigs, dogs (Sugimura et al., 1984), rabbits (*Oryctolagus*, Weijs and de Jongh, 1977), galagos (Hylander, 1979) and macaques (Dechow and Hylander, 2000), at least on the working side. However, unlike the pigs, all these species show considerable differences between strains on the working and balancing sides. In general, the strains observed bilaterally in pigs look most similar to working side strains in other species. The simple explanation for this is probably the fact that pigs are isognathous. Both sides of the dentition are in occlusal contact for most of each chewing cycle, and it is even possible that the bolus is bilateral. Thus, the balancing side of pigs has a bite force and undergoes the same loading regime as the working side.

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