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Deformation of Nasal Septal Cartilage During Mastication

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Abstract

The cartilaginous nasal septum plays a major role in structural integrity and growth of the face, but its internal location has made physiologic study difficult. By surgically implanting transducers in 10 miniature pigs (*Sus scrofa*), we recorded in vivo strains generated in the nasal septum during mastication and masseter stimulation. The goals were (1) to determine whether the cartilage should be considered as a vertical strut supporting the nasal cavity and preventing its collapse, or as a damper of stresses generated during mastication and (2) to shed light on the overall pattern of snout deformation during mastication. Strains were recorded simultaneously at the septo-ethmoid junction and nasofrontal suture during mastication. A third location in the anterior part of the cartilage was added during masseter stimulation and manipulation. Contraction of jaw closing muscles during mastication was accompanied by anteroposterior compressive strains (around $-1,000 \mu\epsilon$) in the septo-ethmoid junction. Both the orientation and the magnitude of the strain suggest that the septum does not act as a vertical strut but may act in absorbing loads generated during mastication. The results from masseter stimulation and manipulation further suggest that the masticatory strain pattern arises from a combination of dorsal bending and/or shearing and anteroposterior compression of the snout. *J. Morphol.*

Keywords

Nasal septum; cartilage; strain; skull; pig

INTRODUCTION

The nasal septal cartilage is a midline structure stretching from the perpendicular plate of the ethmoid to the external nose. In addition to a postulated ability to apply an antero-posterior growth pressure to the snout (Sarnat and Wexler, 1966, 1968; Kvinnsland, 1973, 1974a,b, 1977; Copray, 1986), the septal cartilage is hypothesized to play a major role in facial integrity. For example, Badoux conceptualized the bony rostrum as an imperfect framed structure and the septal cartilage as a midline vertical strut reinforcing the pentagonal rostrum, preventing its collapse during masticatory loading (Badoux, 1966, 1968). The finding that the nasal bones partially collapse after extirpation of nasal septal cartilage in young guinea pigs (Stenström and Thilander, 1970) and in rats (Moss et al., 1968) has been taken as evidence of the strut-

like role of the nasal septal cartilage. If this notion is correct, then the septal cartilage should bear compressive loading along the vertical axis during mastication.

The hypothesized strut role of the septal cartilage is, however, challenged by the mechanical weakness of most cartilages, especially in view of the heavy loading the snout probably receives from mastication. Cartilage in the body is usually thought to help protect the less flexible bones from overloading by shock absorption (storage of energy), load damping (absorption of energy) and/or by distributing loads over a greater area (Kobayashi et al., 2001; Ng et al., 2003; Poitout and Kotz, 2004). This belief is based on experimental comparison of the viscoelastic properties of bone and cartilage (Radin and Paul 1971; Røhl and Linde, 1997). Recently, it has been argued that despite the excellent energy absorption characteristics of cartilage, articular cartilage is too thinly layered to be the most important shock absorbing element in a typical joint (Martin et al., 1998). This argument does not apply to the septal cartilage, which comprises a large proportion of the height of the snout skeleton. Thus, the nasal cartilage might serve to store and/or absorb loads generated during mastication.

Mastication is a major source of loading of the mammalian skull, strongly influencing cranial morphology (Vilman et al., 1989; Varrela, 1990; Kiliaridis, 1995, 2006; Katsaros, 2001; Katsaros et al., 2002; Larsson et al., 2005). Masticatory strains in the facial bones and sutures have been studied in several species using strain gauges glued to the skull surface (Ross and Hylander, 1996; Hylander and Johnson, 1997; Rafferty and Herring, 1999; Herring et al., 2001; Thomason et al., 2001; Lieberman et al., 2004; Liu et al., 2004). At least in pigs, strains are much lower in facial bones (maximally a few hundred $\mu\epsilon$) compared with sutures (typically over 1,000 $\mu\epsilon$), suggesting that sutures are providing flexibility to the rostrum, damping loads by absorbing energy and perhaps protecting the bones from such loads (Jaslow and Biewener, 1995).

To date, there are no data on the in vivo strain levels in the nasal septum. Strain magnitudes similar to the sutures would suggest a damping function and the orientation of those strains could either support or refute the hypothesis that the septum is a vertically compressed strut during mastication. Information on patterns of strain in the septal cartilage could also help elucidate the overall nature of rostral deformation during chewing, specifically whether bending or torsion occurs during the power stroke (Ross and Hylander, 1996; Thomason et al., 2001; Rafferty et al., 2003; Lieberman et al., 2004).

Because strain gauges cannot be glued to cartilage, an alternative method must be used to assess septal strain. In this study, we employed differential variable reluctance transducers (DVRTs), which rely on barbed broaches for attachment. These transducers were developed to measure linear displacement of soft tissues (Beynon and Fleming, 1998; Fleming et al., 1999; Byl et al., 2002; Cerulli et al., 2003). Pigs were used to build on the body of literature already gathered, and also because their large snouts facilitate surgical access and implantation. Because of the difficult access to the nasal cavity, we were restricted to anteroposterior measurements of the dorsal portion of the septum. Our masticatory measurements were made at the septoethmoid junction, where the bony ethmoid joins the cartilaginous septum, and from the nearby nasofrontal suture. To ensure that the DVRT data were comparable with the strain gauge measurements of our previous study (Rafferty and Herring, 1999), a strain gauge was also installed across the nasofrontal suture. Although the septo-ethmoid junction was the least invasive site for instrumentation, it is probably not representative of the whole septum, because the DVRT span included ethmoid bone and septal cartilage. Therefore, we supplemented the observations by instrumenting a more anterior location, but only in anesthetized animals.

The main goal of this study was to establish the pattern and magnitude of masticatory strain in the nasal septum, to shed light on whether this structure should be considered more as a strut

or more as a load damper. A secondary goal was to use the data to understand how the rostrum as a whole deforms during mastication.

MATERIALS AND METHODS

The subjects used for this study were 10 Hanford pigs (*Sus scrofa*), both sexes, ranging in age from 4 to 6 months and weighing 19–32 kg. All the procedures were approved by the Institutional Animal Care and Use Committee of the University of Washington, and were carried out in Seattle in 2005–2007. The animals were trained to eat their normal diet of pelleted pig chow in the lab environment. Experiments were performed when the animals showed normal feeding behavior under experimental conditions.

On the day of the experiment, the pigs were mask-anesthetized using isoflurane/nitrous oxide and then intubated. A 3.5-cm midline incision was made to expose the frontal and nasal bones, and then a window was cut through the frontal bone just posterior to the nasofrontal suture, to reach the floor of the frontal sinus, which was removed to gain access to the posterior part of the nasal septal cartilage at the septo-ethmoid junction. A 25-gauge vertical hole was drilled in the ethmoid bone, and a DVRT (Microstrain, Williston, VT) was implanted in an anteroposterior orientation with approximately half its length on the ethmoid and half on the cartilage (Fig. 1). The distance between the barbs, typically 1.0–1.5 cm, was recorded. The bony window was replaced and fixed using mini-plates and screws (Mandible Trauma, SYNTHES Maxillofacial, West Chester, PA). The nasofrontal suture was instrumented lateral to the window (see Fig. 2). A second DVRT was placed on one side and on the other the bone was cleaned, dried and prepared (M-Bond 200 catalyst, Vishay Micro-Measurements, Raleigh, NC) and then a single element strain gauge (EP-08-125BT-120, Vishay) was glued (M-Bond 200, Vishay) across the suture. Fine wire electrodes for electromyography (EMG) were inserted in the masseter and temporalis bilaterally. The strain gauge and DVRT signals were conditioned (Model 2120A, Vishay and MB-STD-4, Microstrain, respectively), and with the EMG signals (MEC 100, BIOPAC Systems, Santa Barbara, CA), digitized (MP100A, BIOPAC) and recorded using AcqKnowledge software (BIOPAC).

Intramuscular analgesics, buprenorphine (0.5 mg/kg, Reckitt Benckiser, Berkshire, UK) and/or ketorolac (1 mg/kg, Hospira, Lake Forest, IL) were injected and the animals were allowed to recover from anesthesia. Regular pig chow was offered and animals were permitted to eat for 15 min while signals were captured. Following that, animals were reanesthetized; an anterior incision was made and a 4-cm window through the anterior part of one nasal bone was cut to gain access to a more anterior part of the septal cartilage (see Fig. 2). A third DVRT was placed horizontally in the dorsal part of the cartilage. Pairs of stimulating electrodes were placed in the masseters on opposite sides of the motor nerve entry point to assure stimulation of the whole muscle. The muscles were tetanized (60 pps, 600 ms trains, 2 trains/sec) with increasing voltage until visible spread of the contraction to neighboring muscles, typically 20–60 V (S48, Grass Instruments, Warwick, RI) in the following order: left, right and both masseters. In some subjects, a bite block was placed between the anterior teeth, and the above stimulation was repeated. The signals were captured as before. Finally, the snout was gripped around the anterior teeth and manually manipulated: pushed anteroposteriorly and bent dorsoventrally. Lateral bending was also attempted but could not be performed consistently. After finishing the procedure, the animals were killed by perfusion or by a lethal dose of pentobarbital in the ear vein. After killing, the DVRTs and strain gauge were visually inspected to check for positioning.

The DVRT and strain gauge data were analyzed using Acq-Knowledge. DVRT voltage was converted to displacement using a calibration procedure conducted before each experiment.

DVRT strain was then calculated by dividing displacement by the measured length of the DVRT as initially placed in the tissue. Negative numbers are used to indicate compression.

To assess the anatomy of the septum and the histological nature of its attachment to the bony skeleton of the snout, additional skulls and heads of Hanford pigs of similar size were examined. Three skulls were cut parasagittally for gross examination and four heads were cut into 5–7 coronal blocks using a band saw. Blocks were decalcified in 10% formic acid/sodium formate, embedded in paraffin and cut at 7 μ m. The sections were stained with hematoxylin and eosin, and observed by light microscopy (Nikon Eclipse E400, Tokyo, Japan); images were captured digitally (Coolsnap FX, Image Processing Solutions, North Reading, MA). Histological measurements of septal cartilage width and height were made using MetaVue (Universal Imaging, Downingtown, PA)

Statistical testing (ANOVA, paired and two-sample *t* tests) was performed using Excel, GraphPad and SPSS (version 13.0) software.

RESULTS

Anatomy

The nasal septum is composed of an osseous and a cartilaginous part (Figs. 1, 3). The osseous portion consists of the perpendicular plate of the ethmoid posteriorly and the vomer inferiorly. The vomer, representing a fused pair of dermal bones, extends from the anterior border of the presphenoid bone to the nasal surface of the premaxillary bone; its superior surface is split to form the vomerine groove. This groove houses the inferior aspect of the nasal septal cartilage, including complete enclosure of a cylindrical posterior extension that joins the presphenoid bone (see Fig. 1). The sides of the septal cartilage are covered by an adherent perichondrium and coated with epithelium (see Fig. 3). The cartilage tapers anteriorly, with height decreasing from 20 ± 3 mm posteriorly to 12 ± 1 mm anteriorly ($n = 4$). Cartilage thickness varies as well (Fig. 3A, B), with the anterior area being thicker (4.0 ± 0.7 mm) compared with the rest of the cartilage (2.9 ± 0.2 mm; $P = 0.01$, paired *t* test). The posterior abutment of the cartilage with the perpendicular plate of the ethmoid separates easily, and its articulation with the vomerine groove is loose. However, anterior to the groove the cartilage strongly adheres to the nasal surface of the premaxillary bone. Superiorly (dorsally), the septum divides into the parietotectal cartilages, which are in tight contact with the inferior surface of the frontal and nasal bones. The septal cartilage extends 3–4 mm anterior to the tip of the nasal bones and 5–10 mm anterior to the premaxillary bones. The most anterior part of the cartilage expands to form a wedge in which the *os rostri* ossifies (see Fig. 1).

Microscopically, the perichondrium is composed of two layers, an outer fibrous and an inner cellular layer containing flattened cells assumed to be chondroblasts. Within the cartilage matrix, chondrocytes are often arranged in nests of 2–3 cells. A few blood vessels run anteroposteriorly through the lower part of the septum, but the matrix itself is avascular. The tight superior connection of the septum and its parietotectal extensions to the nasal dorsum consists of a fibrous articulation with the frontal and nasal bones (Fig. 3C). The tight connection of the inferior septum to the premaxillary bones is also fibrous. The loose inferior connection with the vomerine groove consists of a pad of loose connective tissue (Fig. 3D).

Strain Experiments

The instrumentation created no problems for mastication. All animals recovered quickly from anesthesia and ate normally (Table 1), except for one (#415) which refused food but chewed on a rubber tube. Most instruments functioned well during mastication and muscle stimulation, but some failed sporadically during manipulation (Tables 2, 3). Although these failures might

simply reflect the fact that manipulations were performed last, we think it likely that gripping the head and distorting the soft tissues affected the instruments, for example by preventing the DVRTs from sliding freely. We, therefore, have less confidence in the manipulation results.

In awake pigs, measurable displacements and strains were only seen during mastication, not during food gathering or investigative activities. During mastication, the septo-ethmoid and nasofrontal DVRTs and the nasofrontal strain gauge showed peaks of displacement/strain that coincided with the end of each power stroke (see Fig. 4). The two DVRTs were usually in synchrony and their peak displacement was slightly delayed relative to the peak measured by the sutural strain gauge (53 ± 12 msec, $n = 5$; see Fig. 4).

Septo-ethmoid junction DVRT—Antero-posterior strains generated during mastication at the septo-ethmoid junction were consistently compressive, averaging about $-1,000 \mu\epsilon$ (Table 1, Fig. 4). Not surprisingly for a midline recording, side of chewing made no difference in the seven experiments with sufficiently good EMG to determine the direction of jaw movement ($P > 0.2$, paired t test).

Although masseter stimulation was intended to mimic mastication on anesthetized animals, the results were different at the septo-ethmoid junction. Strain values were still compressive but were much lower, averaging only $-73 \mu\epsilon$ (Table 1). One individual had no measurable strain (#399) and one was slightly tensed (#405, Table 1). There was no significant difference between bilateral, right or left masseter stimulation ($P > 0.5$, ANOVA). Insertion of a bite block between the anterior teeth in four animals did not cause any significant change ($P > 0.6$, paired t test).

Strains at the septo-ethmoid junction were also usually low when the snout was manipulated (Tables 2 and 3). Most measurements were compressive when the snout was forced posteriorly, with two individuals (#400 and #404) having magnitudes comparable to mastication. Pulling the snout anteriorly had either no effect or caused low-tensile strain. Bending the snout dorsally gave very inconsistent results, whereas bending it ventrally usually caused low tension.

Anterior septal cartilage DVRT—The anterior septal DVRT was inserted after the chewing portion of the experiment, so only masseter stimulation and snout manipulation were recorded. Masseter stimulation consistently resulted in antero-posterior compression of the anterior cartilage with magnitudes greatly exceeding those of the septo-ethmoid junction even during mastication (Table 1). Higher compressive strains were obtained when the masseter was bilaterally stimulated ($-11,271 \pm 5162 \mu\epsilon$, Table 1) than either contralateral ($-6512 \pm 4560 \mu\epsilon$, $n = 9$) or ipsilateral ($-5278 \pm 4684 \mu\epsilon$) stimulation; however, this difference did not reach statistical significance ($P = 0.1$, ANOVA). Block placement during bilateral stimulation resulted in a nonsignificant increase in strain ($P > 0.2$, paired t test).

Pushing the snout posteriorly and pulling it anteriorly produced high magnitudes of compression and tension, respectively (Table 2). Strong compression was recorded when the snout was bent dorsally. Only four successful recordings were made during ventral bending, but these were all strongly tensile (Table 3).

Nasofrontal suture—Recorded by strain gauge, masticatory strain at the nasofrontal suture was consistently and strongly compressive, averaging over $-2,000 \mu\epsilon$ (Table 1), with no significant effect of side of chewing. Recorded by DVRT, masticatory strain was still compressive, but usually less than that recorded by the strain gauge (approximately $-1,000 \mu\epsilon$, Table 1) and considerably more variable, owing to very low strains in two pigs (#403 and #405).

Masseter stimulation resulted in similar sutural strain values to those recorded during mastication. Strains were usually higher for bilateral ($-2,666 \pm 750 \mu\epsilon$ and $-910 \pm 1,019 \mu\epsilon$ for strain gauge and DVRT respectively, Table 1) followed by ipsilateral ($-2,059 \pm 611 \mu\epsilon$ for strain gauge and $-739 \pm 897 \mu\epsilon$ for DVRT) and contralateral ($21,272 \pm 505 \mu\epsilon$ and $-202 \pm 270 \mu\epsilon$, respectively). ANOVA on the strain gauge results showed that contralateral stimulation was significantly less than bilateral and ipsilateral ($P = 0.002$), but the difference was not significant for the DVRT data ($P > 0.6$). Bite block placement did not cause any significant increase in strain with either instrument.

During manipulations, the gauge and DVRT gave similar results: compression for posterior pushing and dorsal bending, and tension for anterior pulling (except the anomalous #401 DVRT) and ventral bending (Tables 2, 3).

DISCUSSION

Functional Morphology of the Septum

The septal cartilage tightly adheres to the roof of the nasal cavity, implying that deformations should be comparable with those of the nasal dorsum. In contrast, the ventral border is tightly attached only at its anterior (premaxillary) extremity. Although the vomerine groove constrains the septal cartilage to the midline, the cartilage seems to be capable of some antero-posterior sliding within the groove. The placement of the DVRT at the anterior septum coincided (unintentionally) with the area in which the cartilage is firmly attached to its ventral boundary.

Another pertinent feature of cartilage anatomy is the fact that it is thicker anteriorly and thinner posteriorly, implying a greater ability to resist loading anteriorly. The anteroposteriorly oriented bulge in the middle (Fig. 3A, B) also suggests the possibility of horizontal loading.

Pattern and Magnitude of Masticatory Strain in the Nasal Septum

During mastication the septo-ethmoid junction showed clear evidence of loading. Strain at the septo-ethmoid junction occurred at the end of each power stroke and was simultaneous with strain in the nasofrontal suture. Because the onset of strain occurred after the onset of muscle contraction, it was likely caused by occlusal force rather than being a direct result of muscle pull on the skull.

Notably, however, the compressive strain recorded was anteroposterior. If the septum behaved as a compressive strut under an idealized axial load, compression would have been dorsoventral and, based on a Poisson ratio of 0.32 in septal cartilage (Grellmann et al., 2006), we should have seen tensile strain in the anteroposterior direction. Thus, our results indicate that the septal cartilage is not under simple vertical compression during mastication, as envisioned by the idealized compressive strut model. Rather, the septo-ethmoid junction is under anteroposterior compression caused by some aspect of occlusal loading. It is, of course, possible that the septo-ethmoid junction is not representative of the septum as a whole. However, anteroposterior compression was also the pattern of strain observed in the anterior septum during masseter muscle stimulation. In fact, the only loading regimes that produced the expected anteroposterior tension in either septal location were nonphysiological manipulations that pulled the snout anteriorly (an axial tension) or bent it ventrally (placing the dorsum of the entire skull under tensile strain). We conclude that the septum does not function as a vertical strut during mastication.

It is also notable that the magnitude of strain recorded by the septo-ethmoid DVRT during mastication was essentially the same as that recorded by the sutural DVRT, roughly $-1,000 \mu\epsilon$. Both recordings probably underestimated the true magnitude of strain, because part of the instrument was over bone (about 50% of the septo-ethmoid DVRT and much more of the sutural

DVRT). Underestimations as they may be, these strains are far higher than the largest principal strains observed during mastication in the nearby bones: $-85 \pm 12 \mu\epsilon$ for the nasal bone (Rafferty et al., 2003) and $-53 \pm 23 \mu\epsilon$ for the frontal bone (Herring and Teng, 2000). Therefore, strain at the septo-ethmoid junction is at least an order of magnitude greater than the bones. This differential suggests that the septal cartilage, like sutures, may serve to absorb energy and hence damp the forces transmitted through the skull.

Overall Deformation: Why was the Septo-ethmoid Junction Deformed Less by Stimulation and Manipulation than by Mastication?

Masseter stimulation was intended to mimic the power stroke of mastication in unconscious animals. In our previous studies, on other parts of the skull, such stimulations have typically produced similar or larger strains than mastication (larger strains are explained by the more complete contraction of the muscles). Even in the present study, the instruments over the nasofrontal suture recorded higher but comparable strains to those of mastication and the DVRT in the anterior septal cartilage registered very large compressive strains. Thus, it does not seem likely that the additional surgery (cutting an anterior window in the nasal bones) somehow destroyed force transmission in the skull. Nevertheless, although strains were still compressive, the septo-ethmoid junction showed much smaller values during stimulation than during mastication (Table 1). Thus, masseter stimulation may mimic masticatory loading of the naso-frontal suture, but it does not do so for the septoethmoid junction.

The discrepancy for the septo-ethmoid junction means that the skull is deformed differently during mastication and during masseter stimulation. As a working hypothesis, we propose that during masseter stimulation the snout is primarily bent and/or sheared dorsally, and that these loading regimes have minimal effects on the septo-ethmoid junction while deforming the other parts of the snout. During mastication, we propose that, additionally, the septo-ethmoid junction is axially compressed. Our reasoning is as follows. Two important variables are different for these activities (mastication and masseter stimulation), the point of occlusal contact and the direction of occlusal force. Masseter stimulation applies an antero-superior force to the whole dentition, especially the anterior teeth. This occlusal force at the incisors should bend and/or shear the snout dorsally. Dorsal bending will compress the dorsum, including the nasofrontal suture and the anterior septal cartilage, but not the septo-ethmoid junction, which is located centrally in the skull, close to the presumed neutral plane (see Fig. 1). Dorsal shearing, on the other hand, will cause tensile strain along the anterodorsal-posteroventral diagonal and compressive strain along the anteroventral-poster-odorsal diagonal. These opposite strains will tend to cancel out for the anteroposteriorly oriented septo-ethmoid DVRT, but not for the sutural and the anterior septal DVRTs, which were more aligned with the compressive diagonal (see Fig. 1). Thus, both dorsal bending and dorsal shear would compress the nasofrontal suture and the anterior septum but have little effect on strain at the septoethmoid junction. In contrast, mastication occurs especially at the molar teeth with only fleeting contact of the premolars and incisors; further, it recruits all major jaw closing muscles, not just the anteriorly directed masseters. Molar root anatomy suggests that maxillary occlusal loads are slightly posterior in pigs (Ferrari and Herring, 1995). Thus, mastication would apply a posterior force to the molar teeth, compressing the septo-ethmoid junction, which is located at the level of the second molar (see Fig. 1).

The manipulation data should have tested this operating hypothesis, which predicts that posterior pushing, an axial load, will compress the septoethmoid junction, whereas dorsal bending/shear will have little effect. Unfortunately, the septo-ethmoid manipulation results were too poor to provide an adequate test. However, the other locations recorded confirm that anteroposterior axial forces and dorsoventral bending/shear are capable of producing large strains on the anterior septum and the nasofrontal suture, and the strains are in the expected

directions. Thus, the hypothesis that during mastication the snout is axially compressed as well as bent or sheared dorsally is plausible but still lacks a definitive test.

High Strain Magnitudes in the Anterior Septal Cartilage: Flexibility or Loading?

The pattern of strain recorded in the anterior cartilage during masseter stimulation was antero-posterior compression, the same as for the septoethmoid junction and the nasofrontal suture. Interestingly, the magnitude of strain (over 11,000 $\mu\epsilon$, Table 1) was much higher even than that recorded by the sutural strain gauge ($P = 0.0008$, two-sample t test) and vastly greater than that at the septo-ethmoidal junction, even when compared to masticatory values ($P < 0.0001$, two-sample t test). Even if the bone portion of the septo-ethmoid junction is accounted for by doubling the observed values, the significance level does not change. Clearly, strain distribution in the cartilage is not uniform.

The load responsible for the deformation of the anterior septal cartilage is not obvious. The anterior septum also showed high-strain magnitudes with very consistent directionality when the snout was manipulated (Table 2). Compression due to posterior pushing was not significantly different from that seen during masseter stimulation ($P = 0.34$, paired t test) but both were greater than that seen for dorsal bending ($P = 0.01$ and 0.008 , paired t tests). This suggests (but does not prove) that masseter stimulation includes a component of anteroposterior axial compression on the anterior septum (but not the septo-ethmoid junction, as discussed above). One possible source is from contraction of the robust facial muscles which move the rhinarium in pigs; stimulation of the facial nerve could not be avoided during masseter tetanus because the nerve overlies the muscle. If this scenario is correct, then the facial muscles compress the cartilage axially rather than bending it laterally, because right and left masseter stimulations resulted in similar compressive values rather than causing compression on one side and tension on the other. However, it is unlikely that this particular strain pattern would have been seen during natural mastication, which does not involve the rhinarial muscles.

Regardless of the source of load to the anterior cartilage, the question remains as to why the observed strains were so large. This part of the septum is actually relatively thick (see Fig. 3), and preliminary mechanical testing indicates that its elastic moduli in compression and tension are at least as high as other regions of the cartilage (unpublished data). Therefore, the larger strains in the anterior cartilage do not arise from greater flexibility of this region. A possible explanation is that this area was still firmly attached to surrounding tissue and would have to follow all snout deformations. The anterior surgical window was unilateral and the cartilage retained a part of its dorsal attachment. The anterior septum is the only part of the cartilage that is firmly attached by fibrous tissue to both the nasal dorsum and the nasal floor at the premaxillary bone. In contrast, the septo-ethmoid junction DVRT location is less well moored to the skull. First, the symmetrical access window removed the dorsal attachment entirely. Second, more posterior areas of the cartilage (including the septo-ethmoid junction) sit on a pad of loose connective tissue in the vomerine groove which may partially insulate them from masticatory strains. In addition, as mentioned above, both ends of the anterior DVRT were anchored in the cartilage, and the device was located near the nasal dorsum, and thus would be strongly affected by dorsoventral bending as well as antero-posterior axial loads. Finally, inasmuch as the snout tapers anteriorly, higher stress concentrations may occur anteriorly. In summary, high strains in the anterior septum are probably related to its anatomical position, not to a low modulus of elasticity. The particularly high compression seen during masseter stimulation was partially due to facial muscle contraction.

Nasofrontal Suture and the Relative Performance of DVRT and Strain Gauge

In a previous study on intact pigs (Rafferty and Herring, 1999), strain gauge readings from the nasofrontal suture were similar in pattern but somewhat smaller in magnitude (masticatory

strain $-1,583 \pm 506 \mu\epsilon$) than in the present work ($-2,252 \pm 826 \mu\epsilon$). The difference is statistically insignificant ($P = 0.11$), but if real, can probably be ascribed to the presence of the bone window in the present study, which would have reduced the stiffness of the region.

In theory, DVRTs and strain gauges should give the same results for the nasofrontal suture, and this comparison was intended as a validation test for the DVRT. However, the DVRT projected several millimeters above the skull surface, a position that could accentuate its response to dorsoventral bending, but which was also vulnerable to interference from overlying skin. This is the most likely explanation for the fact that the DVRT measurements of the nasofrontal suture were more variable than those of the strain gauge. The DVRT strain magnitudes were also significantly less than those measured by strain gauges (paired t test for mastication data, $P = 0.024$). Likely causes for the difference in magnitude include (1) several extremely low DVRT values that probably indicate the device was hung up (for example, #403, Tables 1–3) and (2) a relatively greater amount of bone included in the span of the DVRT compared with the strain gauge.

The short lag of about 50 msec in the peak of DVRT displacement relative to the peak of strain measured by the strain gauge (see Fig. 4) must have been due to the instrumentation, since placement on the suture was similar. The frequency response for DVRT is reported as 7 kHz by the manufacturer (vs. 100 kHz for the strain gauge conditioners), and thus is not likely to have caused a lag of this magnitude. Rather, the lag of the DVRT may relate to the time taken for the barbs of the DVRT, sitting in drilled holes, to engage the tissue, i.e. a compliance issue. Although the DVRT is a less exact instrument than the strain gauge, in the context of the present study it was useful to have both on the suture, because this comparison enabled us to determine that the septo-ethmoid junction and the suture deformed simultaneously.

Mastication in Pigs and Bilateral Symmetry of strain

Because the septo-ethmoid junction was instrumented in the midline, no differences due to side of chewing or stimulation were expected, and none were seen. The nasofrontal suture is bilateral, but as in previous studies it did not show an effect of chewing side, presumably because chewing in pigs involves muscles of both sides and possibly bilateral tooth contact (Herring et al., 2001; Rafferty et al., 2003). Asymmetry of sutural strain was seen for unilateral masseter stimulations; whereas bilateral and ipsilateral masseter stimulations produced similar levels of compression, levels were decreased 50% or more for contralateral stimulations. This suggests that in addition to the dorsal bending produced by the masseter, unilateral contraction adds an element of lateral bending or twisting.

The anterior septal cartilage was instrumented from the side, so it should also have reflected lateral bending caused by unilateral muscle contraction. However, identical strong compressive strains of the anterior septum were observed for contralateral and ipsilateral stimulations. Notably, the anterior origin of the masseter muscle is at the same level as the nasofrontal suture, whereas the anterior septum is far anterior to this location. Probably the lateral deviation toward the contracting masseter is a local effect that does not impinge on the anterior snout.

CONCLUSIONS

The finding of anteroposterior compression in the nasal septum is inconsistent with the expectations for an idealized compressive strut, and we conclude that the septum does not function in this manner during mastication. Strain magnitudes in the septum are at least an order of magnitude higher than local bone strain, suggesting that the septal cartilage may help to absorb energy and dampen masticatory loads. The septum is probably capable of some limited sliding movement in the vomerine groove but is elsewhere firmly attached to the

rostrum. The strain patterns observed suggest that during the power stroke, axial compression is superimposed on dorsal bending and/or shearing of the snout.

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Fig. 1.

Sagittal section of a pig skull illustrating location of nasal septal cartilage, its relations to surrounding structures, and the location of the DVRTs. E, perpendicular plate of ethmoid bone; F, frontal bone; FS, frontal sinus; M, maxilla; N, nasal bone; OR, rostral bone (*os rostri*); PM, premaxilla; PS, presphenoid bone; SC, septal cartilage; V, vomer; VG, vomeric groove which contains the lower portion of the septal cartilage. The DVRTs were implanted in the anterior cartilage (Ant DVRT), nasofrontal suture (NF DVRT) and the septo-ethmoid junction (SE DVRT). Note that the anterior DVRT was inserted after the pig was reanesthetized.

Fig. 2. Dorsal view of a pig skull illustrating surgical access windows (dashed boxes) and sensor locations. Ant, anterior; NF SG, nasofrontal suture strain gauge. Other abbreviations are as in Figure 1.

Fig. 3.

Coronal sections of the snout (hematoxylin and eosin stain) showing the nasal septal cartilage (**A**) at the location where the anterior DVRT was implanted and (**B**) close to the septo-ethmoid junction where the posterior DVRT was implanted. Dorsally the cartilage splits into two parietotectal cartilages that underlie the nasal and frontal bones. (**C,D**) Enlargements of the boxed areas in B. The parietotectal cartilages are tightly connected to the overlying bones by fibrous tissue as seen in C. The ventral part of the cartilage lies on a pad of loose connective tissue in the vomerine groove as seen in D. The vomerine groove depth increases posteriorly (compare A and B). The break between the palate and the palatal mucosa in both A and B is artifactual.

Fig. 4.

Recording from subject 401 during mastication illustrating EMG of right and left masseter and temporalis synchronized with the nasofrontal and septo-ethmoid DVRTs and nasofrontal strain gauge. The side of chewing is indicated at the top. Scale bars correspond to 30 mV for masseter and 100 mV for temporalis, 500 μ e for the DVRTs and strain gauge.

TABLE I

Peak antero-posterior strain during mastication and masseter stimulation ($\mu\epsilon$)

Pig#	Septo-ethmoid junction DVRT		Anterior cartilage DVRT		Nasofrontal suture DVRT		Nasofrontal suture strain gauge	
	Mastication	Stimulation ^d	Stimulation ^d	Mastication	Stimulation ^d	Mastication	Stimulation ^d	
398	-1,224 ± 132 (n = 18)	-216 ± 61 (B)	-4,291 ± 124 (B)	-2,168 ± 166 (n = 6)	ND	-2,257 ± 779 (n = 24)	-1,915 ± 61 (B)	
399	-1,815 ± 195 (n = 18)	0	ND	-1,671 ± 94 (n = 24)	-757 ± 71 (B)	-1,650 ± 392 (n = 24)	-2,157 ± 59 (B)	
400	-301 ± 57 (n = 9)	-119 ± 7(R)	ND	-743 ± 182 (n = 24)	-1,354 ± 184 (B)	-2,892 ± 737 (n = 24)	-2,093 ± 51 (B)	
401	-1,031 ± 215 (n = 24)	-111 ± 23 (B)	-6,411 ± 662 (B)	-1,052 ± 224 (n = 24)	-3,239 ± 227 (B)	-2,533 ± 251 (n = 30)	-3,086 ± 265 (B)	
402	-1,194 ± 234 (n = 24)	-109 ± 13 (R)	-10,215 ± 101 (B)	-1,434 ± 399 (n = 24)	-788 ± 37 (B)	ND	-3,880 ± 28 (B)	
403	-196 ± 12 (n = 3)	-24 ± 2 (B)	-7,307 ± 890 (B)	-79 ± 6 (n = 18)	-12 ± 6 (C)	-2,866 ± 389 (n = 24)	-2,240 ± 595 (B)	
404	-877 ± 145 (n = 12)	-132 ± 40 (B)	-17,480 ± 372 (B)	-213 ± 4 (n = 12)	-1,439 ± 188 (I)	-682 ± 73 (n = 18)	ND	
405	-52 ± 5 (n = 12)	18 ± 3 (R)	-11,325 ± 1,250 (B)	-81 ± 20 (n = 24)	-273 ± 22 (I)	-2,885 ± 668 (n = 24)	-3,295 ± 193 (B)	
414	-992 ± 392 (n = 24)	-20 ± 6 (L)	-17,711 ± 136 (B)	-566 ± 200 (n = 18)	-242 ± 45 (B)	ND	ND	
415	-2,150 ± 140 (n = 3) ^b	-19 ± 3 (R)	-15,430 ± 1,041 (B)	-2,005 ± 156 (n = 6) ^b	-427 ± 137 (B)	ND	ND	
Grand mean	-983 ± 677	-73 ± 75	-11,271 ± 5,162	-1,001 ± 788	-948 ± 988	-2,252 ± 826	-2,666 ± 750	

Mean $\pm$ standard deviation; n, number of chewing strokes; negative values indicate compressive strain; ND, no data.

^aThe values listed are the maximum strain recorded during masseter stimulation regardless of side stimulated. The letter in parentheses indicates the stimulation condition producing this maximum: B, bilateral; R, right; L, left; C, contralateral; I, ipsilateral masseter stimulation. Stimulation averages are for three repetitions at supramaximal tetanus.

^bChewing on a rubber tube.

TABLE 2

Antero-posterior strain recorded during anterior (axial tension) and posterior (axial compression) manipulations ($\mu\epsilon$)

Pig#	Septo-ethmoid DVRT		Anterior cartilage DVRT		Nasofrontal suture DVRT		Nasofrontal suture strain gauge	
	Posterior	Anterior	Posterior	Anterior	Posterior	Anterior	Posterior	Anterior
398	-27	0	-3,818	1,296	ND	ND	-431	547
399	ND	0	ND	ND	ND	538	ND	943
400	-408	0	-1,860	716	-1,209	716	-1,376	995
401	0	16	-8,734	4,512	-2,957	-1,177	-1,449	710
402	ND	ND	-12,911	340	-159	223	-2,236	1,455
403	-21	23	-6,132	1,670	ND	70	-1,639	994
404	-985	ND	-14,170	1,135	-1,028	1,490	ND	ND
405	-15	10	-15,407	318	-603	9,700	-3,298	ND
414	0	0	-7,376	5,213	-1,044	75	ND	ND
415	ND	ND	-5,363	ND	ND	60	ND	ND
Grand mean	-208 $\pm$ 373	7 $\pm$ 10	-8,419 $\pm$ 4,770	1,900 $\pm$ 1,895	-1,167 $\pm$ 957	1,299 $\pm$ 3,228	-1,738 $\pm$ 961	941 $\pm$ 309

Three identical strokes were analyzed for each manipulation. ND, no data.

TABLE 3

Antero-posterior strain recorded during manipulated dorsal and ventral bending of the snout ($\mu\epsilon$)

Pig #	Septo-ethmoid DVRT		Anterior cartilage DVRT		Nasofrontal suture DVRT		Nasofrontal suture strain gauge	
	Dorsal	Ventral	Dorsal	Ventral	Dorsal	Ventral	Dorsal	Ventral
398	-30	-29	-3,314	1,470	ND	ND	-1,300	1,800
399	ND	ND	ND	ND	-1,550	ND	-2,300	2,200
400	70	0	ND	ND	-2,340	1,460	-1,800	2,900
401	7	50	-2,985	1,480	-4,560	2,280	-1,700	1,000
402	500	ND	-1,750	2,290	-1,416	1,770	-1,400	2,500
403	-7	34	-3,600	1,090	ND	ND	-2,000	3,500
404	1,370	0	-2,300	ND	-3,820	1,620	ND	ND
405	-30	10	-3,360	ND	-1,430	ND	-3,500	4,000
414	0	10	ND	ND	-93	800	ND	ND
415	-140	221	-518	ND	-270	690	ND	ND
Grand mean	193 $\pm$ 477	37 $\pm$ 78	-2,547 $\pm$ 1,108	1,583 $\pm$ 505	-1,935 $\pm$ 1,579	1,437 $\pm$ 603	-2,000 $\pm$ 744	2,557 $\pm$ 1,018

Three identical strokes were analyzed for each manipulation. ND, no data.