AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 112:553–574 (2000)

Elastic Properties and Masticatory Bone Stress in the Macaque Mandible

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KEY WORDS biomechanics; skeletal function; bone strain; craniofacial biology; bone adaptation

ABSTRACT One important limitation of mechanical analyses with strain gages is the difficulty in directly estimating patterns of stress or loading in skeletal elements from strain measurements. Because of the inherent anisotropy in cortical bone, orientation of principal strains and stresses do not necessarily coincide, and it has been demonstrated theoretically that such differences may be as great as 45° (Cowin and Hart, 1990). Likewise, relative proportions of stress and strain magnitudes may differ. This investigation measured the elastic properties of a region of cortical bone on both the buccal and lingual surfaces of the lower border of the macaque mandible. The elastic property data was then combined with macaque mandibular strain data from published and a new in vivo strain gage experiment to determine directions and magnitudes of maximum and minimum principal stresses. The goal was to compare the stresses and strains and assess the differences in orientation and relative magnitude between them. The main question was whether these differences might lead to different interpretations of mandibular function. Elastic and shear moduli, and Poisson's ratios were measured using an ultrasonic technique from buccal and lingual cortical surfaces in 12 macaque mandibles. Mandibular strain gage data were taken from a published set of experiments (Hylander, 1979), and from a new experiment in which rosette strain gauges were fixed to the buccal and lingual cortices of the mandibular corpus of an adult female *Macaca fascicularis*, after which bone strain was recorded during mastication. Averaged elastic properties were combined with strain data to calculate an estimate of stresses in the mandibular corpus. The elastic properties were similar to those of the human mandibular cortex. Near its lower border, the macaque mandible was most stiff in a longitudinal direction, less stiff in an inferosuperior direction, and least stiff in a direction normal to the bone's surface. The lingual aspect of the mandible was slightly stiffer than the buccal aspect. Magnitudes of stresses calculated from average strains ranged from a compressive stress of -16.00 GPa to a tensile stress of 8.84 GPa. The orientation of the principal stresses depended on whether the strain gage site was on the working or balancing side. On the balancing side of the mandibles,

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Grant sponsor: National Institute of Dental Research Merit Award; grant number DE04532; Grant sponsor: National Institute of Dental Research; Grant number: DE07761; Grant sponsor: National Science Foundation; Grant number: BNS-8711842.

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Received 19 June 1998; accepted 23 June 1999.

maximum principal stresses were oriented nearly perpendicular to the lower border of the mandible. On the working side of the mandibles, the orientation of the maximum principal stresses was more variable than on the balancing side, indicating a larger range of possible mechanisms of loading. Near the lower border of the mandible, differences between the orientation of stresses and strains were 12° or less. Compared to ratios between maximum and minimum strains, ratios between maximum and minimum stresses were more divergent from a ratio of 1.0. Results did not provide any major reinterpretations of mandibular function in macaques, but rather confirmed and extended existing work. The differences between stresses and strains on the balancing side of the mandible generally supported the view that during the power stroke the mandible was bent and slightly twisted both during mastication and transducer biting. The calculated stresses served to de-emphasize the relative importance of torsion. On the working side, the greater range of variability in the stress analysis compared to the strain analysis suggested that a more detailed examination of loadings and stress patterns in each individual experiment would be useful to interpret the results. Torsion was evident on the working side; but in a number of experiments, further information was needed to interpret other superimposed regional loading patterns, which may have included parasagittal bending and reverse parasagittal bending. Am J Phys Anthropol 112:553–574, 2000.

One of the most productive methods for determining the functional properties of the skeleton is strain gage technology. Strain gages can directly measure skeletal deformation. This information can be coupled with data on morphology to better understand how skeletal elements function, what sorts of loading patterns result from diverse loads induced by muscles and external forces, and how function affects skeletal modeling and remodeling. Yet mechanical analyses with strain gages have several limitations; most notable is the difficulty in directly estimating patterns of stress or loading in skeletal elements from strain measurements.

Another approach to mechanical analysis of the skeleton is to study the material properties of the bone itself (Dechow et al., 1993). Such studies, which determine features such as cortical thickness, bone density, and elastic properties, tell us about the structure of the skeleton but do little to reveal how skeletal elements may actually function. Indeed, much of the literature of functional morphology seeks to determine the relationship between the form and structure of tissue and its possible functional adaptation. The often apparent reality is that form and function do not appear to correspond in the skeletal system in a consistent way. Such discrepancies as the apparent differences in adaptation between the cranial vault and the midcortex of bones, such as the femur or mandible, lead to considerable speculation about mechanisms that have led to the development and maintenance of skeletal adaptations in different parts of the skeleton.

Because the material properties of the bone do not consistently correlate with the function of individual skeletal elements, there is a potential danger in making functional inferences based on strain gage studies alone. A series of studies have pointed out the possible theoretical discrepancies between bone strain and stress, if bone properties are regarded as isotropic (Carter, 1978; Cowin and Hart, 1990). One of the largest dangers is due to the misalignment of the principal axes of strain and stress in anisotropic materials. If functional interpretations rely on a correspondence of the directions of these axes, as they do in isotropic materials, the potential discrepancies between them may result in misinterpretations of strain data. While the theoretical studies have shown that discrepancies in axis orientation in bone may be as large as 45° (Cowin and Hart, 1990), the degree of differences actually depend on the degree of anisotropy of the skeletal element under study and the pattern of loading (Ricos et al., 1996).

In a series of studies, one of us (WLH) has used strain gage techniques to define patterns of loading and function in the craniofacial skeleton of several species of primates (Hylander, 1979, 1981, 1984, 1985, 1986, 1987; Hylander and Johnson, 1989, 1997; Hylander et al., 1991). Likewise, one of us (PCD) has conducted a series of studies to define the material properties of the facial skeleton in humans (Dechow et al., 1992, 1993; Schwartz-Dabney and Dechow, 1997). In this investigation, we combined approaches to study the relationship between patterns of stress and strain in the mandible of macaque monkeys during function. Specifically, we asked (1) what are the elastic properties of the mandibular corpus, (2) what are the magnitudes and directions of stress in the macaque mandible during function, (3) how well do directions and relative magnitudes of principal stresses and strains correspond, and (4) do differences between these axes result in any reinterpretation of our understanding of mandibular function in macaques. Our hypothesis was that although there are significant differences by direction in the elastic properties of the mandibular corpus in macaques, as in the human mandible, the impact of these differences was small compared to the full range of theoretical differences, resulting in minor reinterpretations of studies of function of the mandible based on strain gage techniques.

Several approaches are taken to this research. First, elastic properties of the corpus of the macaque mandible are determined. Second, these data are used with published data on strains in the macaque mandible during function to determine directions and magnitudes of stress. These values are compared with directions and magnitudes of strain. Third, elastic property data are applied to the results of an experiment that measured mandibular bone strain on both the facial and lingual aspects of an adult female macaque during function. As in the second experimental approach, the principal directions and magnitudes of strain and the calculated values of stress are compared. Possible differences in interpretation of the data with and without the inclusion of the information on bone elastic properties are considered.

Dechow et al. (1993) showed that the human mandible is about 40% stiffer in the longitudinal direction than in the inferosuperior direction. As the discussion of strain gage experiments in the mandible of macaques (Hylander, 1979, 1981) did not take this inherent anisotropy into consideration, it is possible that reexamination of results might lead to additional insights and reinterpretation. Dechow et al. (1993:300) speculated that the combination of elastic property and strain data would “strengthen the assessment of the importance of bending along the lower border of the corpus, and de-emphasize the importance of torsion during mastication and incision.” The strain gage experiment described in this paper was meant to address this question directly by looking at strain on both the lingual and buccal aspects of the mandible. As will be subsequently described, predictable patterns should be found simultaneously on the buccal and lingual aspects of the mandible depending on the pattern of loading (twisting, bending, or some combination thereof) during function.

MATERIALS AND METHODS

Measurement of elastic properties

Cortical bone samples from the mandibles of 12 adult female rhesus monkeys (*Macaca mulatta*) were used to measure elastic properties. All monkeys had third molars in occlusion prior to death. Mandibles were obtained from monkeys sacrificed for research projects unrelated to the current investigation; no animals were known to have been exposed to any medication or treatment with recognized effects on bone structure. In life, all animals had been fed a diet of hard monkey chow supplemented with fruit. Mandibles were obtained fresh at sacrifice. They were dissected free of surrounding tissues, tightly wrapped in cloth and plastic to

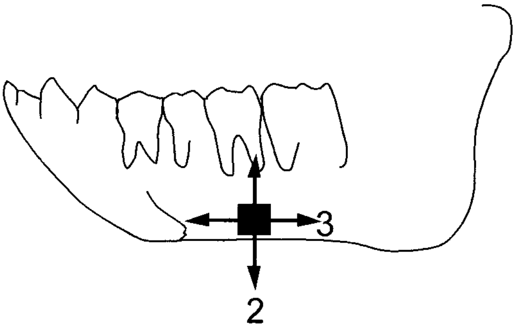


Fig. 1. Area and directions for bone sample site. Bone samples, approximately 5 × 5 mm and the thickness of the cortical plate (1.5–2.5 mm), were taken from macaque mandibles on both the lingual and facial cortices at the site indicated. The 1 direction was approximately mediolaterally oriented or normal to the surface of the bone; this direction is not shown in the illustration. The 2 direction was inferosuperior along the bone surface. The 3 direction was oriented along the long axis of the lower border of the mandible (longitudinal).

prevent desiccation, and stored in a freezer at −20°F.

Bone samples were removed from the facial and lingual corpora below the second molar in the mandibles. After the mandibles were thawed, low-speed dental drills were used to remove the bone in cubes of 5 × 5 mm with a thickness of 1.5–2.5 mm. A Unimat miniature lathe was used to grind specimens where necessary to make sure that the opposite sides of the cubes were parallel. Specimens were cooled with water during grinding. In the initial three specimens, bone cubes were only removed on the facial side prior to discarding the mandibles. Thus the sample size consisted of 12 facial samples and 9 lingual samples.

Studies on the effects of storing bone samples in preservative media such as formalin suggested that such media altered the collagen fibers comprising the organic matrix of bone affecting the elastic properties of the bone (Reilly and Burstein, 1974). Likewise, work in our laboratory suggested that preservation in formalin decreased bone stiffness (Dechow and Huynh, 1994). Accordingly, samples were stored in a solution consisting of 95% ethanol and isotonic saline in equal proportions; this medium maintained the elastic properties of cortical bone for extended periods (Ashman et al., 1984, Dechow and Huynh, 1994).

Bone specimens were prepared for testing from each of the following locations (Fig. 1): (1) on the facial aspect of the mandibular corpus, 1–2 mm above the lower border, and inferior to the second molar, and (2) on the lingual aspect on the mandibular corpus in a similar position as the first sample. Bone specimens were labeled with an arrow to indicate orientation. For each sample, densities were determined according to Archimedes principle of buoyancy (Ashman, 1989) using a Mettler PM 460 balance equipped with a densitometry kit.

Samples were tested with an ultrasonic pulse transmission technique in three mutually perpendicular directions, using methods described by Ashman et al. (1984) for postcranial cortical bone and modified by Dechow et al. (1993) for use in bone samples from the cortex of human mandibles. The ultrasonic waves were generated by piezoelectric transducers resonating at 2.25 MHz. Directions were labeled on each sample such that 1 represented a direction normal (radial) to the bone surface, 2 was inferosuperior to the bone surface, and 3 (the reference axis) was parallel to the longitudinal axis of the mandible (Fig. 1). Pretests using histological sections and longitudinal ultrasonic waves confirmed that, like human mandibles (Dechow et al., 1993), macaque mandibles can be modeled as orthotropic with their stiffest axis oriented along the long axis of the bone. In macaque mandibles, Haversian canals and most collagen fibrils are oriented parallel to the long axis (Bromage, 1993). In human mandibles, the apatite crystals are also primarily oriented in this direction in the corpus (Bacon et al., 1980); this is most likely also true for macaque mandibles.

Ultrasonic measurements were made by using two mounted piezoelectric transducers to propagate longitudinal and transverse ultrasonic waves through the bone samples in the directions under test. The time delay of wave propagation was read from an oscilloscope connected to the transducer. The time delay and width of the specimen were used to calculate ultrasonic velocities. These velocities and data on the density of the bone samples were used to generate a matrix of elastic coefficients, or

"C" matrix, defined by Hooke's law. Technical elastic constants were calculated from the matrix. The computational techniques are more fully described in the literature (Ashman, 1982; Ashman et al., 1984; Ashman and Van Buskirk, 1987; Carter, 1989). The technical elastic constants included the elastic modulus, shear modulus, and Poisson's ratio.

Directions in technical constants were indicated with the following convention, as defined in Figure 1. Elastic moduli E are followed by a subscript indicating direction. Shear moduli are followed by a double subscript indicating the plane of shear. Poisson's ratios are followed by a double subscript in which the first number indicates the direction of the primary strain and the second number indicates the direction of the secondary strain (for further explanations, see Ashman et al., 1984, Cowin, 1989a, b, or Martin and Burr, 1989).

One-way analysis of variance was used to test for significant differences in bone density among locations. Two-way analysis of variance was used to test for significant differences between directions and locations for the elastic moduli, shear moduli, and Poisson's ratios. Significant differences between individual cells were determined with post hoc Tukey tests.

Calculation of stress in macaque mandibles

Mean elastic properties of the macaque mandibular corpus, as presented in Tables 2–4, were combined with macaque bone strain data to calculate the magnitude and direction of principal stresses in the macaque mandible during function. As a sample of macaque mandibular strain values, data were taken from Hylander (1979). The data consisted of mean balancing and working side strains during transducer biting (Table 3 and Fig. 8 in Hylander, 1979) and during mastication of apples (Table 8 and Fig. 13 in Hylander, 1979).

Several computational steps were needed to calculate the magnitude and direction of stress from these data. First, it was necessary to compute the magnitude of bone strain in the direction of the primary axes of stiffness of the mandibular corpus, namely the directions shown in Figure 1. These directions were along the longitudinal axis of the mandibular corpus (3 direction) and at 90° to this in the inferosuperior direction (2 direction). Equations to transform strain values from maximum and minimum strains (as given in Hylander, 1979) to those along these designated axes were:

$$\epsilon_2 = \epsilon_p \times \sin(\alpha_r)^2 + \epsilon_q \times \cos(\alpha_r)^2$$

$$\epsilon_3 = \epsilon_p \times \cos(\alpha_r)^2 + \epsilon_q \times \sin(\alpha_r)^2$$

$$\tau = 2 \times \cos(\alpha_r) \times \sin(\alpha_r) \times (\epsilon_p + \epsilon_q),$$

where ξ_p and ξ_q were maximum and minimum principal strains; ξ_2 and ξ_3 were strains in the 2 (inferosuperior) and 3 (longitudinal) directions; α_r was the angle between the 3 (longitudinal) direction and the direction of the maximum principal strain; and τ was the shear strain.

Given the strains along orthotropic axes (directions 2 and 3), stresses in these directions were calculated from the following equations:

$$\sigma_3 = \frac{E_3}{1 - v_{32} \times v_{23}} \times (\epsilon_3 + v_{23} \times \epsilon_2)$$

$$\sigma_2 = \frac{E_2}{1 - v_{32} \times v_{23}} \times (\epsilon_2 + v_{23} \times \epsilon_3)$$

$$\gamma = \tau \times G_{32}$$

where σ_2 and σ_3 were normal stresses in the 2 and 3 directions respectively; E_2 and E_3 were elastic moduli of the cortical bone in the 2 and 3 directions; G_{32} was the shear modulus in the plane formed by the 2 and 3 directions; ν_{23} and ν_{32} were the Poisson's ratios in the directions indicated by their respective subscripts; and γ was shear stress.

Given the normal stresses in the 2 and 3 directions and the shear stress in that plane, maximum and minimum principal stresses and their orientations were calculated as follows:

$$\sigma_p = \frac{\sigma_3 + \sigma_2}{2} + \sqrt{\frac{\sigma_3 + \sigma_2}{2} + \gamma^2}$$

$$\sigma_q = \frac{\sigma_3 + \sigma_2}{2} - \sqrt{\frac{\sigma_3 + \sigma_2}{2} + \gamma^2}$$

$$\Phi_\sigma = \frac{1}{2} \times \mathrm{a\ tan}\left(\frac{\gamma}{\sigma_2 - \sigma_3}\right),$$

where σ_p and σ_q were the maximum and minimum principal (normal) stresses; and Φ_σ was the angle of the maximum normal stress.

From these data, the ratio of the maximum to the minimum principal strain (ξ_q/ξ_p) was compared with that of the maximum to the minimum principal stress (σ_q/σ_p). Also compared was the orientation or angle of the maximum principal strain (Φ_ξ) with the maximum principal stress (Φ_σ).

Strain gage experiment

One adult female macaque (*Macaca fascicularis*) served as a subject for this experiment. This animal had a Class I molar relationship and full adult dentition with all molars in occlusion. Two rosette strain gages were bonded on the right corpus of the mandible inferior to the second molar and several millimeters above the inferior border. One strain gage was bonded on the facial (buccal) surface, while the other was bonded on the lingual surface. The alignment of the rosettes was determined from radiographs taken following the bonding procedure.

The two strain gages were miniature 120-ohm; stacked rosettes (SA-06–030WY-120, Micro-Measurements, Raleigh, NC). They were bonded to the cortical bone with a cyanoacrylate adhesive. The details of this procedure have been previously described (Hylander 1984, 1986; Hylander and Johnson, 1989). Strain gages were attached with the animal heavily sedated with acepromazine and ketamine (Connolly and Quimby, 1978). A local anesthetic (lidocaine HCl) containing epinephrine (1:1000,000) infiltrated the surgical site prior to strain gage bonding for hemostasis and additional anesthesia. A unique aspect of this procedure was the lingual placement of one strain gage. Surgical protocol for this placement required an incision along the lower border of the mandible. A small part of the anterior portion of the digastric muscle was displaced medially to allow access to the lingual side of the inferior border of the mandible. The strain gage site was prepared inferior to the attachment of the mylohyoid muscle on the mandible (mylohyoid line). The site for the other strain gage was easily prepared using the same surgical approach but with dissection on the facial aspect of the mandible without a need for an additional surgical incision. Lead wires were routed out through the surgical incision, which was closed with suture.

Each of the three strain-gauge elements in both rosettes formed one arm of a Wheatstone bridge. For each element, bridge excitation was 1 V. Conditioning and amplification of the voltage output was accomplished through the use of the Vishay 2100 System (Vishay Instruments, Raleigh, NC). Voltage output was recorded at 15 inches/sec with a 14-channel FM tape recorder (Bell and Howell CPR4020A, Datatape Division, Pasadena, CA). A record of whether the subject chewed on the right or left side was also made on the voice track of the tape recorder. Additional details of the recording procedure are described elsewhere (Hylander et al., 1991; Hylander and Johnson, 1997).

The monkey was placed in a primate restraining chair prior to recovery from sedation. The chair permitted normal head, neck, and jaw movements during mastication. After a 5-hour period, the animal was fully alert and was fed popcorn kernels, a hard food item for which the animal had a preference. Here we report on the results of 39 right side (working strain) chews and 46 left side (balancing strain) chews.

The zero level of strain was determined as the monkey sat at rest with no clenching or masticatory movements. Then the animal was fed for a period of time until she refused to eat additional food. At the end of the recording session, the monkey was sedated, strain gages were removed, surgical incisions were sutured, antibiotics were administered, and the animal was returned to her cage. Recovery and healing were uneventful and proceeded as normal.

Analysis of the bone strain recording was accomplished by first examining the signals by outputting the data on a six-channel chart recorder (Brush 260, Gould Inc., Cleveland, OH). Several complete chewing sequences were selected for analysis, including right- and left-sided chewing sequences. Through the use of a 16-channel analog-to-digital converter (Model NB-MIO-16H-9, 12-bit resolution, National Instruments Corporation, Austin, TX), the raw strains of the selected chewing cycles on FM tape were digitized at a rate of 500 Hz. with a channel separation time of 0.123 msec. The digitized values were stored on a computer hard disk for further processing and analysis with LabView 2 graphical programming system (National Instruments Corporation). The digitized raw strain values were filtered at 40 Hz. through the use of a digital low-pass Butterworth filter. Peak shear strain (γ_{max}) was used as the defining factor for peak strain as it was the absolute value of the difference between the maximum and minimum principal strains (ξ_p and ξ_q). At γ_{max} for each cycle, ξ_p, ξ_q, and the angle (α_r) of ξ_p relative to the direction of E_3 were calculated. From these data, maximum and minimum normal stress values (σ_p and (σ_q), and the angle of the maximum normal stress (Φ_σ) relative to the direction of E_3 were calculated according to the procedures discussed in the preceding section (Fig.2).

RESULTS

Elastic properties of macaque mandibular bone

No significant differences in density were found between cortical bone samples from the lingual aspect of the macaque mandible compared to the samples from the buccal aspect (Table 1). Mandibular bone on the buccal aspect averaged 2.003 g/cm^3 compared to 2.056 g/cm^3 on the lingual aspect.

Elastic moduli differed significantly (Table 2) between directions and between the two sites on the mandible. The cortical bone in the longitudinal direction (3 direction) was the most stiff, averaging 21.0 GPa on the buccal aspect of the mandible and 23.9 GPa on the lingual aspect. In the inferosuperior direction (2 direction), values of elastic moduli of cortical bone averaged about 75% of that in the longitudinal direction. Values in the direction normal to the bone (1 direction) were about 40% of that in the longitudinal direction. In all directions, cortical bone was slightly stiffer on the lingual aspect of the mandible than on the buccal aspect.

Shear moduli differed significantly (Table 3) between planes and between the two sites on the mandible. Cortical bone was most resistant to deformation by shear forces in the plane formed by the inferosuperior and longitudinal (2 and 3) directions. On average, this modulus was greater on the lingual side (8.2 GPa) than on the buccal side (7.0 GPa). On both sides, the bone was more resistant to shear in the plane made up of the normal and longitudinal (1 and 3) directions than in the plane made up of the normal and inferosuperior (1 and 2) directions. This difference was small, and shear moduli for these later two planes were considerably less than in the 2 and 3 plane. Shear moduli in the 1 and 3 plane were about 60% that in the 2 and 3 plane; and in the 1 and 2 plane, about half than in the 2 and 3 plane. In all planes, cortical bone was slightly more resistant to shear on the lingual aspect of the mandible than on the buccal aspect.

Significant differences were found between directions and between sites in Poisson's ratio (Table 4). At both sites, v_{31} had the largest average values, followed by v_{32}. v_{12} had the smallest average ratios on both sides. The remaining values were intermediate and fairly similar to each other. The relative rankings of the Poisson's ratios were approximately as expected given the relationships between the elastic moduli in the different directions. Poisson's ratios were higher in every direction at the buccal mandibular site than at the lingual site. The calculations of Poisson's ratios by ultrasonic measurements are the most derived of all the technical elastic constants and thus have more error, as was evident from the relatively high standard deviations. Fewer conclusions can be drawn from these ratios than from elastic and shear moduli. However, several of these values were needed for stress estimates. Values here were similar to those we have found at some sites in human bone, particularly at the symphysis (Dechow et al., 1992). For subsequent calculations, we used values of 0.184 for v_{23} and 0.214 for v_{32}.

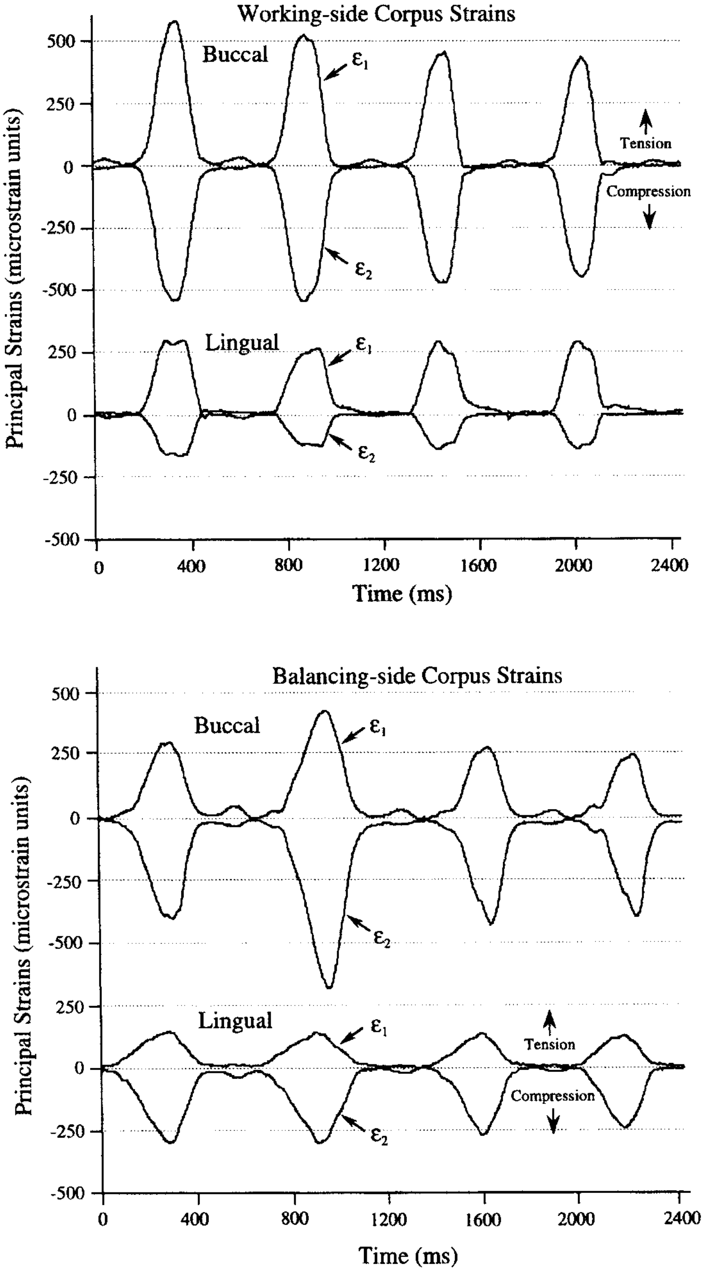


Fig. 2. Working-side (above) and balancing-side (below) plots of bone strain vs. time during mastication of popcorn kernels. Maximum and minimum principal strains are illustrated for strain gages positioned on both the buccal and lingual sides of the mandible. In this figure only, ξ_1 and ξ_2 are maximum (tensile) and minimum (compressive) principal strains following the convention used by Hylander (1979) and are the same as $\xi_p$and ξ_q, respectively, as used elsewhere in this paper.

Stress in macaque mandibles

The magnitude and orientations of the maximum and minimum principal strains during unilateral molar biting and during mastication have been described by Hylander (1979). Here they are presented to contrast them with the corresponding prin-

TABLE 1. Density[1]

Buccal mandible		Lingual mandible	
Mean	SD	Mean	SD
2.003	0.116	2.056	0.128

[1] Means are not significantly different. All values are in grams/cm^3.

TABLE 2. Elastic modulus[1]

	Buccal mandible		Lingual mandible	
	Mean	SD	Mean	SD
E_1	9.0	1.8	9.3	1.6
E_2	15.9	4.0	17.6	3.1
E_3	21.0	3.2	23.9	3.2

[1] Analysis of variance indicated significant differences among bone directions ($F = 102.6$, $P < 0.001$) and between buccal and lingual aspects of the mandible ($F = 4.7$, $P < 0.035$); interactive effects were not significant. E_1 is the elastic modulus in the 1 or mediolateral direction (normal) to the surface of the bone; E_2 is the elastic modulus in the 2 or inferosuperior direction along the bone surface; and E_3 is the elastic modulus in the 3 or longitudinal direction along the bone surface. All values are in gigapascals (GPa).

TABLE 3. Shear modulus[1]

	Buccal mandible		Lingual mandible	
	X	SD	X	SD
G_{12}	3.8	1.1	4.3	0.9
G_{13}	4.4	1.1	5.1	1.1
G_{23}	7.0	1.7	8.2	1.0

[1] Analysis of variance indicated significant differences among bone directions ($F = 51.2$, $P < 0.001$) and between buccal and lingual aspects of the mandible ($F = 6.5$, $P < 0.03$); interactive effects were not significant. G values are shear moduli in planes indicated by their subscripts. Directions indicated by subscripts are given in the notes concerning elastic moduli following Table 2. All values are in GPa.

TABLE 4. Poisson's ratio[1]

	Buccal mandible		Lingual mandible	
	X	SD	X	SD
v_{12}	0.075	0.071	0.055	0.069
v_{13}	0.206	0.090	0.135	0.085
v_{21}	0.131	0.114	0.107	0.158
v_{23}	0.184	0.079	0.130	0.079
v_{31}	0.450	0.183	0.325	0.231
v_{32}	0.214	0.095	0.173	0.106

[1] Analysis of variance indicated significant differences between bone directions ($F = 15.8$, $P < 0.001$), and between buccal and lingual aspects of the mandible ($F = 7.2$, $P < 0.01$; interactive effects were not significant. Directions indicated by subscripts are given in the notes concerning elastic moduli following Table 2. The first subscript denotes the direction of the normal strain, while the second subscript denotes the direction of the Poisson's strain. Note that Poisson's ratio is dimensionless, i.e., it does not have a unit of measurement.

cipal stresses (Tables 5–8 and Figs. 3 and 4). Overall, the principal stresses were oriented more closely to the orthotropic axes of the cortical bone than the principal strains. Likewise, compressive stresses tended to be larger in absolute magnitude relative to tensile stresses than compressive strains relative to tensile strains. The one exception was during transducer biting on the working side, where the relative values of compressive and tensile stresses compared to compressive and tensile strains tended to be similar.

On the working side during unilateral biting (Table 5), mean tensile (maximum principal) strains tended to be slightly higher in absolute magnitude than mean compressive (minimum principal) strains. This was also true for stresses, although tensile stresses were slightly larger than compressive stresses compared to strains, with the exceptions of Macaque 1, Experiment 1 and Macaque 6, Experiment 7. In these experiments, compressive stresses were absolutely larger than tensile stresses, and the ratio σ_q/σ_p was equal to or larger than ξ_q/ξ_p.

On the balancing side during unilateral biting, mean compressive and tensile strains were similar; the values were within 10% of each other in four out of six cases. However, compressive stresses were larger than tensile stresses for all six means with σ_q/σ_p ranging from 1.04 to 1.81.

On the working side during mastication (Table 7), compressive stresses were larger than tensile stresses for five out of eight means. In all five of these cases, σ_q/σ_p (range: 1.10–2.86) was larger than ξ_q/ξ_p (range: 0.96–1.76). In the other three cases, ξ_q/ξ_p was larger than σ_q/σ_p, but on average by a smaller amount of difference, e.g., 0.88 vs. 0.86, 0.65 vs. 0.47, and 1.02 vs. 0.87.

On the balancing side during mastication (Table 8), mean compressive strains and stresses were uniformly larger than mean tensile strains and stresses. Likewise, σ_q/σ_p (range: 1.37–11.97) was always larger than ξ_q/ξ_p (range: 1.03–11.09).

The direction of changes (greater or lesser) in the ratio of mean compressive and tensile strains (ξ_q/ξ_p) compared to stresses (σ_q/σ_p) related to the orientation of the strains relative to the axes of orthotropy or symmetry (E_2 and E_3) of the bone (see Discussion). This can be more easily visualized when considering changes in the orientation of the maximum principal stresses (Φ_σ) compared to corresponding strains (Φ_ξ) (Figs. 3 and 4). The principal stresses always became oriented more closely to the axes of orthotropy or symmetry. The direction of change in the ratio σ_q/σ_p compared to ξ_q/ξ_p generally related to whether the shift in orientation of the maximum principal stress

TABLE 5. Mean strain and stress during transducer biting on the working side[1]

Animal and experiment number	ϵ_p	ϵ_q	σ_p	σ_q	ϵ_q/ϵ_p	σ_q/σ_p	Φ_ϵ	Φ_σ	$\Delta\Phi$
Macaque 1, experiment 1	491	−448	7.24	−5.97	0.91	0.82	40.8	35.3	5.5
Macaque 1, experiment 2	476	−443	6.49	−6.68	0.93	1.03	59.1	69.9	10.8
Macaque 2, experiment 3	534	−458	8.19	−5.89	0.86	0.72	37.3	28.4	8.9
Macaque 2, experiment 5	343	−263	5.07	−3.40	0.77	0.67	48.1	50.2	2.1
Macaque 3, experiment 6	364	−240	5.41	−3.03	0.66	0.56	54.7	62.3	7.6
Macaque 3, experiment 7	453	−505	6.16	−7.25	1.12	1.12	43.7	42.8	0.9

[1] ϵ_p and ϵ_q are the maximum and minimum principal strains; σ_p and σ_q are the maximum and minimum principal stresses; Φ_ϵ and Φ_σ are the angles of the maximum principal strain and stress expressed relative to the orientation of E_3 in a counterclockwise direction, and $\Delta\Phi$ is the difference between the angles of the maximum principal strain and stress. All strains are in microstrain ($\mu\epsilon$). All stresses are in megapascals (MPa). All angles are in degrees.

TABLE 6. Mean strain and stress during transducer biting on the balancing side[1]

Animal and experiment number	ϵ_p	ϵ_q	σ_p	σ_q	ϵ_q/ϵ_p	σ_q/σ_p	Φ_ϵ	Φ_σ	$\Delta\Phi$
Macaque 1, experiment 1	184	−194	2.47	−2.86	1.05	1.16	50.6	57.2	6.6
Macaque 1, experiment 2	327	−318	4.39	−5.19	0.97	1.18	67.9	78.2	10.3
Macaque 2, experiment 3	707	−894	8.84	−16.00	1.26	1.81	73.5	82.1	8.6
Macaque 2, experiment 5	247	−238	3.37	−3.49	0.96	1.04	54.1	63.0	8.9
Macaque 3, experiment 6	160	−146	2.18	−2.26	0.91	1.04	63.3	74.3	11.0
Macaque 3, experiment 7	225	−263	2.91	−3.99	1.17	1.37	50.9	58.4	7.5

[1] Key to symbols is given under Table 5. All strains are in microstrain ($\mu\epsilon$). All stresses are in megapascals (MPa). All angles are in degrees.

TABLE 7. Mean strain and stress during mastication on the working side[1]

Animal and experiment number	ϵ_p	ϵ_q	σ_p	σ_q	ϵ_q/ϵ_p	σ_q/σ_p	Φ_ϵ	Φ_σ	$\Delta\Phi$
Macaque 1, experiment 2	232	−223	3.13	−3.44	0.96	1.10	60.6	71.7	11.1
Macaque 2, experiment 3	212	−303	2.48	−5.09	1.43	2.05	59.3	71.3	12.0
Macaque 2, experiment 4	194	−341	2.02	−5.78	1.76	2.86	55.5	67.4	11.9
Macaque 2, experiment 5	362	−319	5.14	−4.40	0.88	0.86	49.7	54.4	4.7
Macaque 3, experiment 6	235	−153	3.72	−1.76	0.65	0.47	41.6	35.0	6.6
Macaque 3, experiment 7	240	−318	2.95	−4.95	1.33	1.68	50.2	57.7	7.5
Macaque 4, experiment 8	116	−118	1.82	−1.58	1.02	0.87	28.2	17.0	11.2
Macaque 4, experiment 9	316	−423	4.12	−6.22	1.34	1.51	39.0	33.9	5.1

[1] Key to symbols is given under Table 5. All strains are in microstrain ($\mu\epsilon$). All stresses are in megapascals (MPa). All angles are in degrees.

compared to strain was toward the orientation of E_2 or E_3.

The difference in orientation or angle ($\Delta\Phi$) of the maximum principal stress (Φ_σ) compared to the angle of the maximum principal strain (Φ_ξ) was low for all means. $\Delta\Phi$ ranges from a minimum value of 0.5° to a high value of 12.0°.

Strain gage experiment

Our new experiment suggested that during mastication, the magnitude of bone strain and stress was larger on the buccal than on the lingual side of the mandibular corpus. Also, as expected from previous studies (Hylander, 1979), working side bone strain was on average larger than balancing side strain. These relationships held true for both average strains and peak strains (Table 9). Similar relationships were also found for stress (Table 10).

Ratios of compressive strain relative to tensile strain (ξ_q/ξ_p) compared to the similar stress ratio (σ_q/σ_p) showed that on the buccal aspect of the working side, compressive stress and strain were similar in magnitude to tensile stress and strain, respectively. On the lingual aspect of the working side, tensile strain was twice that of compressive strain. This relationship was more exaggerated for stress; tensile stress was more than three times compressive stress. On the buccal and lingual aspects of the balancing side, compressive strain and stress were abso-

TABLE 8. Mean strain and stress during mastication on the balancing side[1]

Animal and experiment number	ϵ_p	ϵ_q	σ_p	σ_q	ϵ_q/ϵ_p	σ_q/σ_p	Φ_ϵ	Φ_σ	$\Delta\Phi$
Macaque 1, experiment 2	121	−124	1.62	−2.22	1.03	1.37	86.3	88.3	2.0
Macaque 2, experiment 3	226	−353	2.67	−6.81	1.56	2.55	89.1	89.6	0.5
Macaque 2, experiment 4	96	−130	1.15	−2.13	1.35	1.85	57.5	69.1	11.6
Macaque 2, experiment 5	233	−322	2.78	−5.55	1.38	2.00	64.2	75.9	11.7
Macaque 3, experiment 6	96	−120	1.22	−2.21	1.25	1.81	81.1	86.0	4.9
Macaque 3, experiment 7	161	−223	1.91	−3.72	1.39	1.94	59.2	71.1	11.9
Macaque 4, experiment 8	11	−122	−0.21	−2.56	11.09	11.97	74.9	83.9	9.0
Macaque 4, experiment 9	105	−279	0.86	−5.59	2.66	6.49	79.2	85.4	6.2

[1] Key to symbols is given under Table 5. All strains are in microstrain ($\mu\epsilon$). All stresses are in megapascals (MPa). All angles are in degrees.

lutely larger than comparable tensile strain and stress. Likewise, σ_q/σ_p was more than 50% greater than ξ_q/ξ_p on both buccal and lingual sides.

The orientation of the maximum principal strains varied by buccal or lingual aspect of the mandible and functional location (Table 10 and Fig. 5). On the buccal aspect of the working side, the maximum principal strain angled upward and backward at 35.3° clockwise to the orientation of E_3. This was in contrast to the lingual aspect of the working side where the maximum principal strain angled upward and forward. On the lingual aspect, the maximum principal strain was oriented 58.2° off-axis from the maximum principal strain on the buccal aspect.

On the buccal aspect of the balancing side, the maximum principal strain angled upward and backward at 80.7° clockwise to the orientation of E_3. The maximum principal strain on the lingual aspect was also oriented upward and backward and differed in direction from the buccal aspect of the mandible by 11.5°.

As described in the previous section, the principal stresses always became oriented more closely to the axes of orthotropy or symmetry compared to the corresponding principal strains (Fig. 5). The orientation of the stresses differed from that of the strains by values ranging from 5.2° to 11.6°.

DISCUSSION

The relevance of studies of the elastic properties of bone relates to both the basic biology of bone structure, function, growth, and adaptation, and to an adequate assessment of the biomechanics of functioning skeletal structures (Dechow et al., 1993). Processes of bone adaptation in response to altered function and bone growth have been widely studied. Yet many basic features of changes in cortical bone architecture resulting from growth and adaptation remain elusive. Perhaps most elusive is the relationship between bone ultrastructure and material properties, and the effect of modeling and remodeling on this relationship. Recent studies suggest correlations between specific bone microstructure and variations in strain mode (tensile or compressive) (Skedros et al., 1996, 1997), and functional adaptations in directional differences (anisotropies) in cortical bone (Kohles et al., 1996, 1997). Such differences may reflect uncorrelated anisotropies in the mineralized and collagenous components of cortical bone (Takano et al., 1996).

Studies of collagen orientation in the lamella of osteons suggest a "rotated plywood" model (Wagner and Weiner, 1992) for osteonal bone that alludes to deviations from orthotropy in cortical bone elastic properties (Turner et al., 1995). The implications of deviations from orthotropy for lamella in the walls of single osteons is not clear for larger structural regions of bones like the mandible, where the cortex is constructed of complex combinations of primary and secondary bone, including osteons of undescribed overall shape, and interstitial bone. Although empirical data of ultrasound velocities in different directions suggest that orthotropy is a reasonable simplification for mandibular cortical bone structure (Dechow et al., 1993), how well this assumption actually fits requires further experimentation.

The relevance of studies of the elastic properties of bone for an adequate assess-

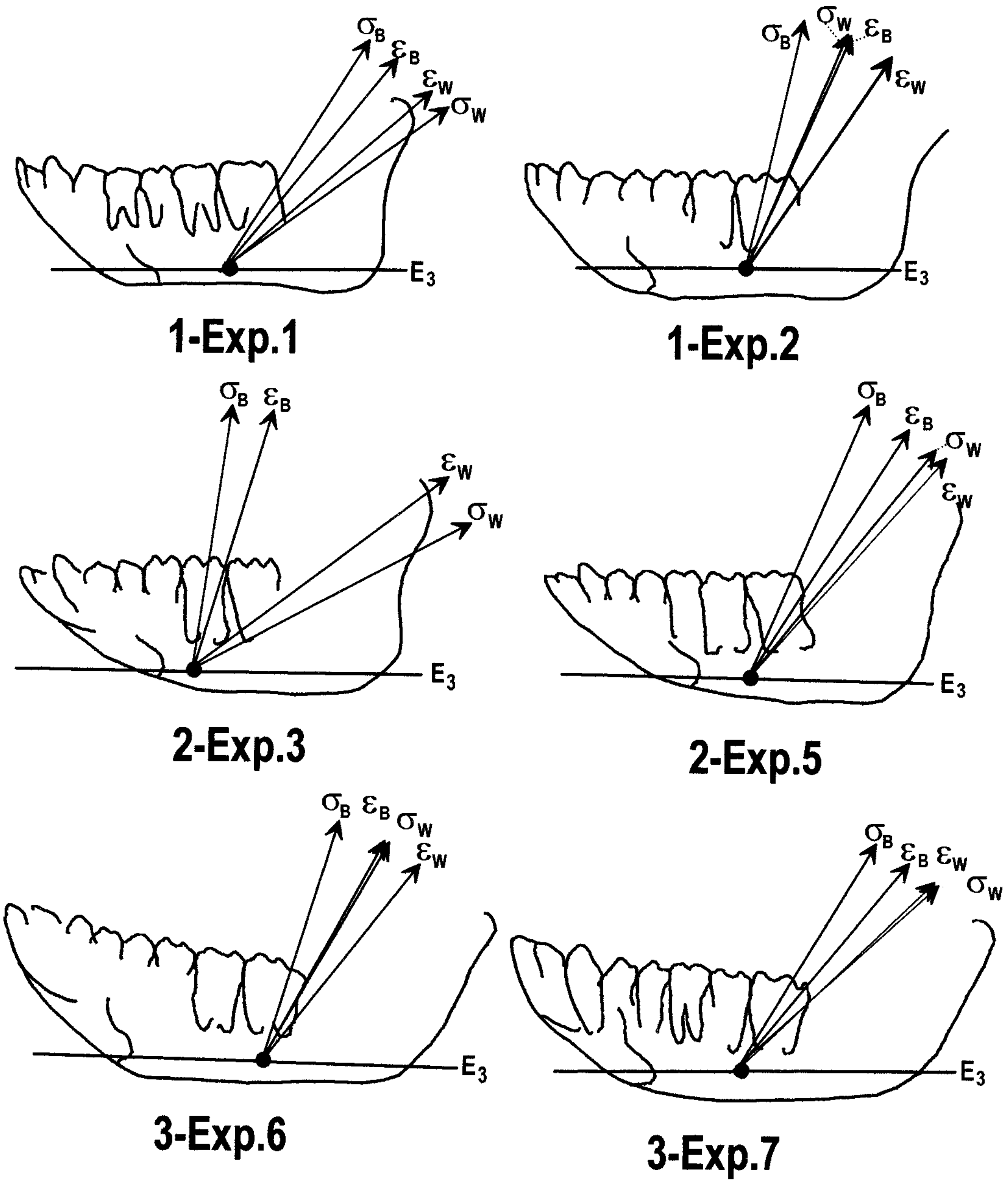
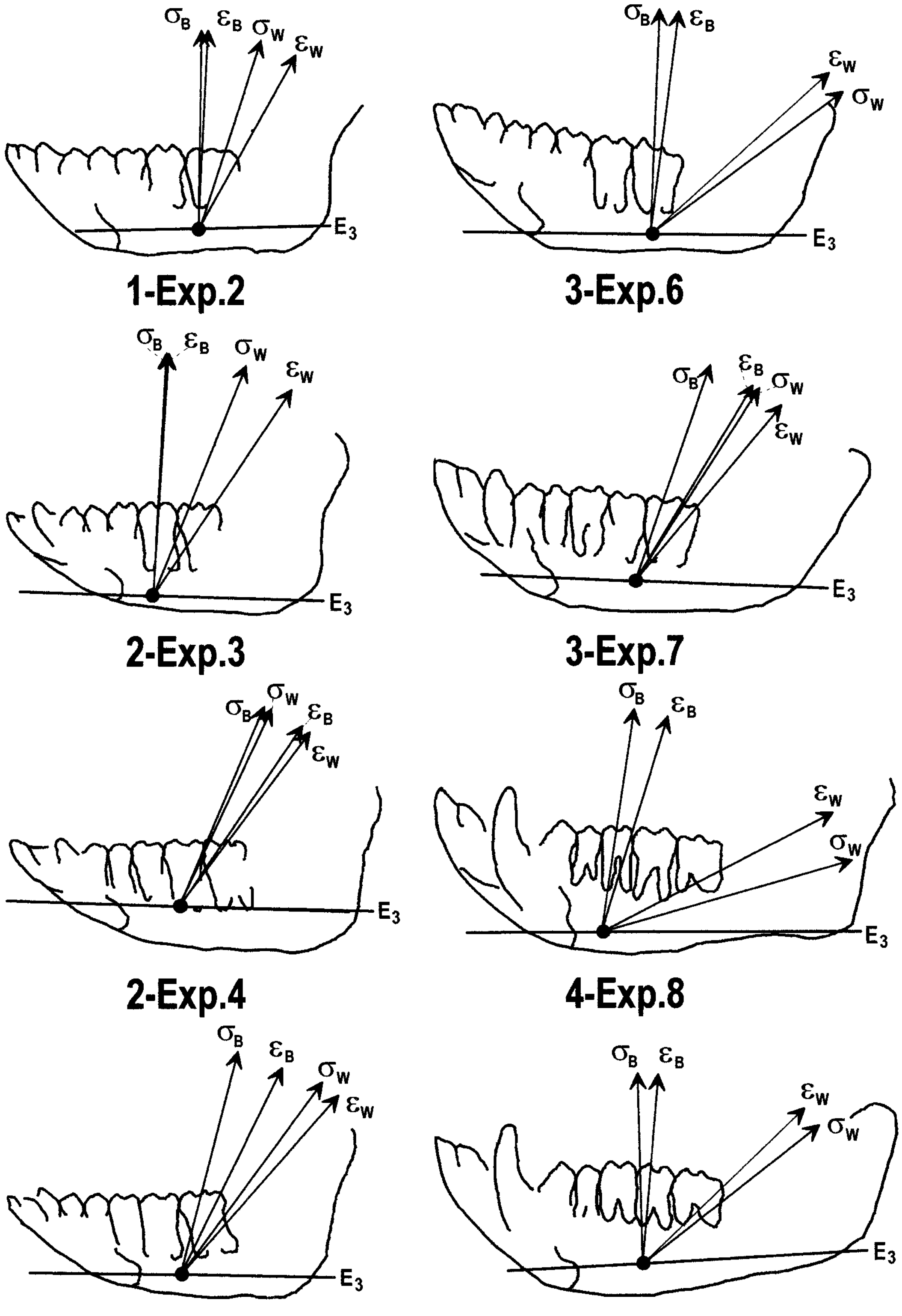


Fig. 3. Results of stress analysis applied to strain gauge experiments in which macaques bit unilaterally on a bite force transducer (strain data is from Table 3 and Fig. 8 in Hylander, 1979). All experiments are labeled as in Hylander (1979). For each experiment, the black dot indicates the position of the rosette strain gage. E_3 is the orientation of the longitudinal axis or 3 direction along which peak values of elastic moduli are found. The arrows indicate the direction of the maximum principal strain on the working side (ξ_w), the maximum principal stress on the working side (σ_w), the maximum principal strain on the balancing side (ξ_b), and the maximum principal stress on the balancing side (σ_b). Note that the arrows are not vectors; their lengths do not show the magnitude of stress or strain. For further discussion, see the text.

ment of the biomechanics of functioning skeletal structures was the primary focus of the current investigation. The mechanics of

Fig. 4. Results of stress analysis applied to strain gage experiments in which macaques masticated apples (strain data is from Table 8 and Fig. 13 in Hylander, 1979). For further explanation and a key to the symbols, see Figure 3 and the text.



1-Exp.2

3-Exp.6

2-Exp.3

3-Exp.7

2-Exp.4

4-Exp.8

2-Exp.5

4-Exp.9

Fig. 4.

TABLE 9. Bone strain on the facial and lingual sides of the macaque mandible during mastication of popcorn kernels[1]

Rosette location	Functional location	N	ϵ_p mean	ϵ_p SD	ϵ_p largest value	ϵ_q mean	ϵ_q SD	ϵ_q largest value
Buccal side	Working side	39	388	96	661	−410	81	−612
Buccal side	Balancing side	44	291	120	601	−414	174	−939
Lingual side	Working side	39	200	69	362	−100	38	−195
Lingual side	Balancing side	44	122	31	199	−250	76	−431

[1] ϵ_p and ϵ_q are the maximum and minimum principal strains. All strains are in microstrain ($\mu\epsilon$).

TABLE 10. Strain and stress in the macaque experiment[1]

Rosette location	Functional location	ϵ_p	ϵ_q	σ_p	σ_q	ϵ_q/ϵ_p	σ_q/σ_p	Φ_ϵ	Φ_σ	$\Delta\Phi$
Buccal side	Working side	388	−410	5.65	−5.63	1.06	1.00	35.3	26.7	8.6
Buccal side	Balancing side	291	−414	3.53	−7.78	1.42	2.20	80.7	84.8	5.2
Lingual side	Working side	200	−100	4.24	−1.26	0.50	0.30	157.1	168.7	11.6
Lingual side	Balancing side	122	−250	1.53	−5.37	2.05	3.52	69.2	79.1	9.9

[1] Key to symbols is given under Table 5. All strains are in microstrain ($\mu\epsilon$). All stresses are in megapascals (MPa). All angles are in degrees. The angles of the maximum principal strain and stress is expressed relative to the orientation of E_3 in a clockwise direction on the buccal aspect and in a counterclockwise direction on the lingual aspect—see Figure 5 to visualize this.

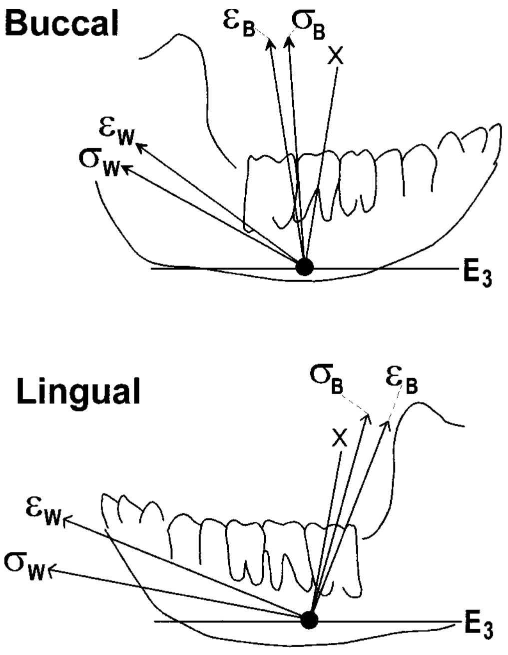


Fig. 5. Results of strain gauge experiment and stress analysis in which rosette strain gages were applied to the buccal and lingual surfaces of a macaque mandibular corpus. For further explanation and a key to the symbols, see Figure 3 and the text. The line marked “X” indicates the alignment of the A element of the rosette.

skeletal structures are dependent on the physical characteristics of the bone, including bone shape, size, structure, and orientation of trabecular bone, thickness of the cortical plate in various regions of the bone, and the details of applied loads on the structure. However, often overlooked are the material properties of the cortical bone itself. Despite the fact that directional differences in elastic properties can result in discordance between the primary directions of loading or stress in a structure (Carter, 1978; Cowin and Hart, 1990; Cowin et al., 1991; Ricos et al., 1996), and those inferred from strain gage studies (orientation of the maximum and minimum principal strains), elastic properties of bone are hardly ever considered in studies using bone strain as an indicator of skeletal loading patterns. The aim of this study was to assess the impact of anisotropies in cortical bone on the interpretation of bone strain in the functioning mandible.

Elastic properties of the macaque mandible

The first goal of this investigation was to document the elastic properties of the macaque mandibular corpus, specifically in those regions where strain gages were attached in previous studies and in the current investigation. We will review the new information on the elastic properties of the macaque mandible and compare these results with available information on elastic properties in other mammalian species.

There are few comparable studies of the elastic properties of the mandible in any mammalian species with which to compare the data collected from the macaque mandible. Available studies include data from dogs (Ashman et al., 1985), and smaller samples from humans (Ashman and Van Buskirk, 1987; Carter, 1989; Arendts and Sigolotto, 1989, 1990; Rho, 1991). All these studies had small sample sizes, a low number of measured sites, or included functionally compromised individuals, such as bone from edentulous mandibles.

One problem with our investigation is that the elastic properties were measured on mandibles of a different macaque species (*Macaca mulatta*) than the species on which the strain gage studies were conducted (*Macaca fascicularis*). However, several studies from our laboratory have documented the elastic properties of primate and mammalian mandibles in more detail, including measurements from humans (Dechow et al., 1992, 1993; Schwartz-Dabney and Dechow, 1997), baboons (Dechow and Huynh, 1996), and pigs (Shinedling and Dechow, 1996). These studies showed similarities in the elastic properties of mandibular cortical bone between more distantly related taxa. Because of these similarities, the discrepancy between animal samples in the current study was not thought to be a significant problem. Especially, since rhesus and long-tailed macaques have great similarity in craniofacial structure with a minimal difference in size.

Humans, baboons, and macaques all show a similar amount of anisotropy in cortical bone from the mandibular corpus with bone being absolutely the most stiff along the long axis of the bone, less stiff in the inferosuperior direction, and least stiff in a direction normal to the surface of the bone. This pattern can also be found in the cortices of shafts of long bones, although the relative proportions of the elastic properties in the three perpendicular directions may differ.

Another common feature may be the increased stiffness of the bone on the lingual cortex compared to the buccal cortex. In human mandibles, there was a general trend in all measured regions, from the symphysis to the condylar neck, to have stiffer cortical bone on the lingual side of the mandible, and some of these differences were statistically significant (Dechow et al., 1992; Schwartz-Dabney and Dechow, 1997). However, relationships of stiffness and density versus location in human mandibular cortical bone were actually more complex with significant variations found anteroposteriorly and inferosuperiorly in the mandible, and in the muscular processes of the mandible.

Function and patterns of bone strain and stress in the macaque mandible

The second and primary goal of this study was to compare patterns of stress and strain in the macaque mandible using strain data from a previously published study (Hylander, 1979) and a new experiment. We asked: how different were the patterns of stress and strain, and do these differences result in any reinterpretation of our understanding of mandibular function in macaques.

Loading and expected patterns of stress.

When comparing patterns of stress and strain, we compared two important features: (1) the orientation of the maximum principal strain (Φ_ξ) and stress (Φ_σ), and (2) the ratio of the absolute values of the minimum and maximum principal strain (ξ_q/ξ_p) and the minimum and maximum principal stress (σ_q/σ_p). We suggested previously (Hylander, 1979; Dechow et al., 1993) that these factors were significant when analyzing strain patterns near the buccal surface of the lower border of the mandibular corpus because distinct patterns will result depending on whether the mandible was either parasagittal bent or twisted about its long axis. Because of the anisotropy in mandibular cortical bone, these relationships will hold true for stress but not for strain, although these expectations were originally presented for strain data (Hylander, 1979, Dechow et al., 1993). Strain data will show some deviation from calculated stresses given the anisotropic structure of mandibular cortical bone.

If the mandible is bent during biting or mastication and if the lower border of the corpus is compressed longitudinally, it is expected that at the lower border (1) Φ_ξ and Φ_σ will be perpendicular to the long axis of the mandible, while the orientation of the minimum principal or compressive strain and stress will be parallel to the lower border of the mandible, and (2) the absolute magnitude of ξ_q and σ_q will be larger than ξ_p and σ_p respectively, and ξ_q/ξ_p and σ_q/σ_p will be greater than 1.0. This pattern of bending with the lower border of the mandible in compression and the alveolar border in tension about their long axes is generally true on the balancing side of the mandible. However, on the working side, the pattern is more complex. Parasaggittal bending, little or no bending (Hylander, 1979), or even reverse patterns of parasagittal bending may be found. These variations presumably depend on the position of the bite point and the region of the corpus under study (Demes et al., 1984). Theoretically, regions of the mandible on the working side may undergo primarily torsion and/or direct shear with little bending, or have regions where the lower border of the corpus is experiencing tension and the alveolar border compression along their longitudinal axes (reverse parasagittal bending).

If the mandible is twisted about its long axis during biting or mastication, a characteristic pattern of stress and strain would result. Torsion results in eversion of the lower border of the mandible. Near the lower border of the buccal mandibular corpus beneath the premolars or molars, (1) Φ_ξ and Φ_σ would be oriented upward and backward at about 45° to the lower border on the buccal cortex, and (2) the absolute magnitude of ξ_q would be similar to ξ_p, and σ_q/σ_p would be about equal to 1.0. As when considering bending, this pattern may be more complex on the working side of the mandible depending on the mediolateral position of the bite point relative to the neutral axis of the mandible (Hylander, 1979).

Another consideration on the working side is the direct shear associated with molar occlusal forces. On the buccal cortex of the mandible, the result of direct shear would be a pattern similar to that for torsion. The combination of torsion and direct shear would be additive on the buccal cortex of the working side, resulting in greater stress and strain than would result from either torsion or direct shear alone. On the lingual cortex, the effect would be the opposite. Principal stresses along the lingual resulting from torsion would theoretically rotate 90° relative to their orientation on the buccal cortex, while stresses resulting from direct shear would have the same orientation on the buccal and lingual cortices. Thus, stresses resulting from torsion and direct shear would be subtractive on the lingual cortex of the mandible, resulting in lower lingual stress (Demes et al., 1984; Daegling and Hylander, 1998). For purposes of the work described in this paper, these predicted differences in stress pattern provided further tests of the interpretation of loading patterns from strain gage studies. In the mastication experiments reexamined from Hylander (1979), it was not possible to distinguish on the working side between torsion and direct shear. However, in our new experiment, one of the following patterns should reveal details about the loading regimen in the mandible during mastication:

1. Φ_ξ and Φ_σ will be oriented upward and backward at about 45° to the lower border on both the buccal and lingual cortex of the mandible. The absolute magnitude of ξ_q will be similar to ξ_p, and σ_q/σ_p will be about equal to 1.0. This pattern suggests direct shear as the primary pattern of loading.
2. Φ_ξ and Φ_σ will be perpendicular to the long axis of the mandible on both the buccal and lingual cortex. The absolute magnitude of ξ_q and σ_q will be larger than ξ_p and σ_p, respectively, and ξ_q/ξ_p and σ_q/σ_p will be much greater than 1.0. This pattern suggests parasagittal bending as the primary pattern of loading.
3. Φ_ξ and Φ_σ will be oriented upward and backward at about 45° to the lower border on the buccal cortex of the mandible, while Φ_ξ and Φ_σ will be oriented upward and forward at about 45° to the lower border on the lingual cortex of the man-

> dible. The absolute magnitude of ξ_q will be similar to ξ_p, and σ_q/σ_p will be about equal to 1.0. This pattern suggests torsion as the primary pattern of loading.

The most likely pattern was some combination of the above possibilities. For instance, superimposition of bending and torsion will result in deviations of stresses from 45° to the lower border of the mandible. σ_q will be more closely aligned with the lower border of the mandible. Likewise, the absolute magnitude of σ_q will be greater than σ_p. If direct shear and torsion were superimposed, we would expect reduced strains on the lingual cortex compared to the buccal cortex. As before, patterns can be inferred from both strain and stress data. The question was whether the interpretations based on strains compared to stresses differed significantly or if they were similar.

Differences between patterns of bone stress and strain and their significance. Comparison of bone stress and strain near the lower border of the mandibular corpus (Tables 5–9 and Figs. 3–5) led to several observations. (1) The anisotropy of the mandibular corpus resulted in consistent patterns of differences between the orientations of the principal stresses and strains. (2) The differences in the orientations of the principal stresses and strains in most cases were relatively small. (3) Changes in the ratio σ_q/σ_p compared to ξ_q/ξ_p were not always predictable but generally related to whether the shift in orientation of the maximum principal stress compared to strain was toward the orientation of E_2 or E_3. If the orientation shifted toward E_2, σ_q/σ_p was usually less than ξ_q/ξ_p. If the orientation shifted toward E_3, σ_q/σ_p was usually greater than ξ_q/ξ_p. There were several exceptions, mostly at values of σ_q/σ_p close to 1.0. (4) The differences between the ratios σ_q/σ_p and ξ_q/ξ_p were negligible in some cases and large in others varying, respectively, from no difference to a maximum difference of 2.66 versus 6.49.

Based on the loading models presented above, the consistent differences between the orientation of stress and strain slightly overemphasized the importance of torsion or direct shear. Inspection of each result in Tables 5–8 and 10 (also Figs. 3–5) showed that σ_p was always oriented closer to the orientation of E_2 (inferosuperior) or E_3 (longitudinal) than was ξ_p. If $\Phi_\xi < 45°$, than $\Phi_\sigma < \Phi_\xi$, placing the orientation of σ_p closer to that of E_3 than ξ_p was to E_3. If $\Phi_\xi < 45°$, then $\Phi_\sigma > \Phi_\xi$, placing the orientation of σ_p closer to that of E_2 than ξ_p was to E_2. Because our loading models suggested that orientation of the principal stresses close to 45° indicated torsion or direct shear, and in all cases the orientation of ξ_p was closer to 45° than was the orientation of σ_p, the result of mandibular anisotropy was to overemphasize the relative importance of torsion or direct shear compared to bending. However, the magnitude of overestimation was not large, as the angular differences varied between a minimum difference of less than a degree to a maximum difference of 12.0°.

Differences between the orientation and relative magnitudes of principal stresses and strains were consistent on the balancing side of the mandible. Hylander (1979) found that strain patterns on the balancing side of the mandible indicated that the corpus was primarily bent during both mastication and transducer biting. Orientations of principal strains were closer to 45° during transducer biting than mastication, indicating a relatively greater amount of torsion. Principal stresses (Tables 6 and 8) suggested similar conclusions, and resulted in a small de-emphasis in the importance of torsion during transducer biting, although more torsion was still indicated than that found during mastication. In all cases, σ_p was oriented closer to E_2 than ξ_p was to E_2. All values of σ_q/σ_p were greater than corresponding values for ξ_q/ξ_p and were larger than 1.0. In contrast to expectations, some values of ξ_q/ξ_p were less than 1.0. Comparison with σ_q/σ_p, showed that these low values for ξ_q/ξ_p were a consequence of mandibular anisotropy, and not relatively low compressive stress longitudinally or relatively high tensile stress inferosuperiorly.

Interpretations of the differences between principal stresses and strains and the determination of corresponding loading patterns was more problematic on the working side of the mandible (Tables 5 and 7). Overall, differences between the orientation and relative magnitudes of stresses and strains generally underemphasized variability in mechanically relevant variables. Orientations of σ_p were more variable than ξ_p. For transducer biting and mastication combined, Φ_ξ ranged from 28.2° to 60.6°, while the corresponding range of Φ_σ was 17.0° to 71.7°. This was because values of Φ_ξ below 45° had lower values for Φ_σ, while values of Φ_ξ above 45° had higher values for Φ_σ. Likewise, values of ξ_q/ξ_p ranged from 0.65 to 1.76, while values of σ_q/σ_p ranged from 0.47 to 2.86. Interpretation of these stresses and corresponding strains suggested either the presence of torsion or direct shear of the mandibular corpus, as originally suggested by Hylander (1979). However, the wide deviations of Φ_σ from 45° and values of σ_q/σ_p larger and smaller than 1.0 in some experiments suggested the superimposition of torsion or direct shear and other patterns of loading. The importance and range of these other superimposed loading patterns was less pronounced when considering strain values alone.

What other loading patterns might be superimposed on torsion or direct shear on the working side? Possibilities included some of those patterns suggested earlier in this paper (cf. Hylander, 1979). Data for macaque 1-experiment 2 during transducer biting (Table 5) and macaque 1-experiment 2, macaque 2-experiments 3–4, and macaque 3-experiment 7 during mastication (Table 7) indicated parasagittal bending with the lower border of the mandible in compression and the alveolar border in tension. In these experiments, $\sigma_q > 45°$and $\sigma_q/\sigma_p > 1.0$. Data from several other experiments, such as macaque 1-experiment 1, and macaque 2-experiment 3 during transducer biting (Table 5) and macaque 3-experiment 6 during mastication (Table 7), indicated reverse parasagittal bending with the lower border of the mandible in tension and the alveolar border in compression. In these experiments, $\sigma_q < 45°$ and $\sigma_q/\sigma_p < 1.0$. Data from some of the other experiments in Tables 5 and 7 did not readily fit any of the loading patterns described previously.

It was important to realize that loading patterns in the mandibular corpus below the bite point may be difficult to interpret because of stress concentrations and associated stress gradients associated with the force application at the bite point or region. Interpretation was made more difficult in this case because of lack of knowledge of the exact location of the bite point relative to the position of the strain gauge in each experiment. Furthermore, data considered in this study were mean data taken from Hylander (1979) and did not include results from individual trials; since stress gradients were expected over small regions of cortical bone inferior to the bite point, individual data may vary and lead to incorrect interpretations when averaged. In any case, further investigation is needed to investigate the complexity of patterns of strains and stresses in the working side mandibular corpus, inferior to the bite point.

Bone stress and strain on the lingual surface compared to the buccal surface of the mandible. Strains and associated stresses from both the buccal and lingual cortices of the mandible (as reported in Tables 9 and 10 and Fig. 5) suggested that (1) the mandible was primarily bent parasagittally on the balancing side during mastication, as described by Hylander (1979), and (2) the mandible experienced torsion on the working side coupled with other possible superimposed patterns of loading. On the balancing side, Φ_σ on both the buccal and lingual cortices was very much greater than 45°. A small deviation from 90° suggested a minor amount of torsion. σ_q/σ_p was also substantially greater than 1.0 on both buccal and lingual cortices, as expected when the inferior border of the mandible was in compression. Interestingly, stresses were relatively more similar in magnitude between buccal and lingual cortices than were strains. This was because the elastic modulus was stiffer on the lingual cortex.

The meaning of strains and stresses was again more problematic on the working side of the mandible. However, some interpretations could be suggested. The angle of principal stress differed by 142° between cortices such that the orientation of the principal strains and stresses was upward and posterior on the buccal cortex and upward and anterior on the lingual cortex. This pattern confirmed the suggestion (Hylander, 1979) that during the power stroke of mastication, the working side was primarily twisted about its long axis with the lower border everted and the alveolar border inverted.

These data did not suggest that direct shear was superimposed on torsion on the working side. The expectation of lower strains and stresses on the lingual compared to the buccal cortex on the working side was found. However, strains and stresses were equally dissimilar to each other between buccal and lingual cortices on the balancing side as on the working side. Bending should result in similar stress magnitudes on both cortices of the corpus of the mandible. Thus, this difference may be a result of experimental error, as considerable variations in strain magnitude may result depending on the quality of the bonding of the strain gage to bone. Additional experiments are needed to confirm these results.

These results did not mean that direct shear, which is unavoidable and must be there and torsion were never superimposed in the suggested pattern on the working side. This pattern may only result in specific regions of the working side when the bite force was appropriately placed. As suggested above, more detailed study of loading patterns during individual bites with more specific information on exact regions of loading are needed to sort out complex strain patterns in the mandible inferior to the region of biting on the working side.

Arguments could be made for other superimposed loading patterns on the working side of the mandible. Here, the orientation (Φ_σ) of the maximum stress was closer to the mandibular long axis than the minimum stress on both buccal and lingual cortices. Likewise, the value of σ_q/σ_p on the lingual side was low. These data indicated that the lower border of the mandible was in tension as would be found in reverse parasagittal bending. Further, the differences in strain between buccal and lingual cortices, if confirmed by further experiments, might suggest wishboning or transverse bending of the mandible, which would increase compression on the buccal cortex and increase tension on the lingual cortex.

The effects of considering the anisotropies of the mandible in the analysis of this experiment were much the same as those described above in the reinterpretation of data from Hylander (1979). On the buccal aspect, the results from this experiment were parallel to those found in the previous investigation.

Empirical results and theoretical predictions of misalignment between strain and stress

Given the small number of studies of both local variations in skeletal material properties and in vivo strain gage studies, it was not surprising that there were few empirical estimates of bone stress. Carter (1978) described methods to calculate bone stresses from strains in bone if the material properties were known. He determined bone stresses in the anteromedial (bare area) of a human tibia during walking from an experiment by Lanyon and colleagues (1975). The differences between strain and stress in the tibial example were similar to those found here in the macaque mandible.

Cowin and Hart (1990) created a general model for determining errors of orientation in the principal stress axes in bone, if the bone was modeled as isotropic when it was actually orthotropic or anisotropic. These errors were equivalent to differences between the orientations of principal strains and stresses, because their orientations would coincide in an isotropic material. Cowin and Hart demonstrated that these differences could be as large as 45°. They also stated that while most errors were not that large, a typical error did represent a significant difference. However, their one example from the human femur had an error or difference of 8.69° between the two axes. It was not clear from Cowin and Hart's study what specific strain patterns would result in larger errors in orientation, or how these strain patterns might have interacted with the known range of material properties in cortical bone in producing errors. It was interesting that their example fell within the range of errors noted in our macaque studies. The question of what magnitude of error in orientation is significant is debatable. An error of 8° is huge in any precision instrument, but in measurements of biological systems, such errors may be small to moderate, and depend primarily on the nature of the measurement and its intended purpose. Cowin and Hart did not discuss possible shifts in the relative proportions of minimum and maximum principal strains and stresses.

Empirical studies of in vivo deformation in bone using strain gages are limited by the technology to relatively few sites. Loading regimes can be suggested that comply with the data collected at these sites. Finite element analysis (FEA) provides a useful method for extending the work of strain gage studies. FEA produces computer models, which after validation through experimental work, can be extended to study larger overall patterns of stress and strain distributions in skeletal elements. A recent study by Ricos and colleagues (1996) demonstrated that modeling bones using a global simplified constitutive characterization such as isotropy can lead to some marked differences in computed stress and strain distributions. However, the degree of difference in modeled turkey ulnas depended on the type of loading; results from torsional loading simulations were more influenced than axial loading simulations. Although several mandibular models have been created with FEA (Hart et al., 1992; Korioth et al., 1992), these have not addresses the question of the influence of changes in material properties on stress and strain patterns under different loading conditions. We would expect similar differences as those found in the turkey ulna by Ricos and colleagues (1996).

CONCLUSIONS

In mechanical studies of the skeleton, cortical bone strain can be measured and used as an approximation for bone stress in inferring in vivo loading patterns. If bone were isotropic, principal strains and stresses would coincide in orientation; also magnitudes of stress and strain would be proportional in different directions. However, cortical bone was anisotropic leading to differences between stress and strain.

In this study, we measured the elastic properties of a region of the lower border of the macaque mandible on its buccal and lingual cortices, and used these data along with the results of several in vivo strain gage experiments (Hylander, 1979 and the current investigation) to assess the magnitude and significance of differences between the principal stresses and strains. Specifically, we asked four questions:

1. What are the elastic properties of the mandibular corpus?

Our measurement of elastic properties indicated similar values to those found in human mandibles. Near its lower border, macaque mandibles were most stiff in a longitudinal direction, less stiff in an inferosuperior direction, and least stiff in a direction normal to the surface of the bone. The region measured on the lingual aspect of the mandible was found to be slightly stiffer than the region on the buccal aspect.

2. What are the magnitudes and directions of stress in the macaque mandible during function?

The largest values of calculated stresses near the lower border of the corpus of the macaque mandible during function ranged from a compressive stress of −16.00 GPa to a tensile stress of the 8.84 GPa. Since these values were derived from averaged strains, individual stresses would be greater in magnitude. The orientation of the principal stresses depended on specific activities. On the balancing side of the mandibles, maximum principal stresses were oriented nearly perpendicular to the lower border. On the working side of the mandibles, the orientation of the maximum principal stresses was more variable than on the balancing side, indicating a larger range of possible mechanisms of loading.

3. How well do directions and relative magnitudes of principal stresses and strains correspond?

Near the lower border of the mandible, differences between the orientation of stresses and strains were 12° or less. These differences were considerably smaller than the maximum theoretical differences of 45° (Cowin and Hart, 1990). Ratios between maximum and minimum stresses (σ_q/σ_p) were generally more extreme (further away from a ratio of 1.0) than ratios between maximum and minimum strains (ξ_q/ξ_p). Differences between σ_q/σ_p and ξ_q/ξ_p ranged from no difference to a maximum difference of 6.49 compared to 2.66.

4. Do differences between these axes result in any reinterpretation of our understanding of mandibular function in macaques?

While our results did not provide any major reinterpretations of our understanding of mandibular function in macaques, it was equally important to address the impact of studies of skeletal material properties on the interpretation of strain gage experiments in general. Our null hypothesis was that although there were significant differences by direction in the elastic properties of the mandibular corpus in macaques, as in the human mandible, the impact of these differences was small compared to the full range of theoretical differences, resulting in minor reinterpretations of studies of function of the mandible based on strain gage techniques. Did the results support this hypothesis? Unfortunately, the answer was equivocal. The significance of differences between the orientations and relative magnitudes of stresses and strains must be addressed on a case by case basis. The differences between stresses and strains on the balancing side of the mandible generally supported the view that the mandible was bent and twisted slightly both during mastication and transducer biting. The calculated stresses also served to de-emphasize slightly the relative importance of torsion. On the working side, the greater range of variability in the stress analysis compared to the strain analysis suggested that a more detailed examination of loadings and stress patterns in each individual experiment would be useful to interpret the results. Torsion was evident on the working side, but in a number of experiments, further information was needed to interpret other superimposed regional loading patterns, including but not limited to parasagittal, reverse parasagittal, and transverse bending in separate experiments.

ACKNOWLEDGMENTS

This investigation was supported by Merit Award DE04531 to WLH and research grant DE07761 to PCD from the National Institute of Dental Research, and BNS-8711842 to WLH from the National Science Foundation. We thank Dr. David Daegling for a critical reading of the manuscript.

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