

Differences in Osteonal Micromorphology Between Tensile and Compressive Cortices of a Bending Skeletal System: Indications of Potential Strain-Specific Differences in Bone Microstructure

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ABSTRACT *Background:* It has been hypothesized that bone has the capacity to accommodate regional differences in tension and compression strain mode and/or magnitude by altering its osteonal microstructure. We examined a simple cantilevered bone to determine whether regional differences in particular strain-related features are reflected in the microstructural organization of compact bone.

Methods & Results: The artiodactyl (e.g., sheep and deer) calcaneus has a predominant loading condition which is typified by prevailing compressive and tensile strains on opposite cortices, and variations in strain magnitudes across each of these cortices. Microscopic examination showed osteon density and cortical porosity differences between tension (caudal) and compression (cranial) cortices, averaging 11.4% more osteons in the compression cortex ($P < 0.01$) and 80.2% greater porosity in the tension cortex ($P < 0.01$). There is 43.5% more interstitial bone in the compression cortex ($P < 0.01$). Osteons in the compression cortex also have smaller areas in contrast to the larger area per osteon in the tension cortex. Although no definite transcortical gradient in osteonal density or cortical porosity is found, fractional area of interstitial bone is largest and osteon population density is lowest in the endocortical regions of both tension and compression cortices. The endocortical regions also have greater porosity than their corresponding middle and pericortical regions ($P < 0.01$).

Conclusions: These osteonal microstructure and cortical porosity differences may be adaptations related to regional differences in strain mode and/or strain magnitude. This may be related to the disparity in mechanical properties of compact bone in tension vs. compression. These differences may reflect a capacity of bone to process local and regional strain-related information. © 1994 Wiley-Liss, Inc.*

Key words: Bone remodeling, Cortical bone, Skeletal adaptation, Back-scattered electron microscopy, Rocky Mountain mule deer (*Odocoileus hemionus hemionus*)

The adaptation of cortical bone to its mechanical environment includes alteration in both its internal structure (remodeling) and its external shape (modeling) (Currey, 1984b; Frost, 1990a,b; Martin, 1991; Martin and Burr, 1989). Mechanical strain, or deformation, also plays an important role in adaptive responses that occur in bone when loading conditions are perturbed (Brown et al., 1990; Lanyon, 1987, 1991, 1992a,b; Martin and Burr, 1989). Mechanical strain is also thought to be an important factor in defining the thresholds for bone remodeling activity in normal bone. Martin and Burr (1989) describe bone strain as a complex interaction of several features including strain magnitude and strain mode (tension, compression, or shear). Recent evidence suggests that the structural/maternal objective of normal bone development is strongly influenced

by a bone's complete strain history, with other extrinsic factors having lesser importance (Burger et al., 1991; Carter, 1987; Carter et al., 1987; Frost, 1985, 1991; Hall and Herring, 1990; Lanyon, 1984, 1992a,b; Wong et al., 1992).

In vivo studies have shown that strain modes, strain magnitudes, and other aspects of strain histories differ between regions of the same bone (Biewener and Bertram, 1991; Biewener et al., 1986; Gross et al., 1991;

Received September 13, 1993; accepted March 11, 1994.

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Lanyon et al., 1979). Bones habitually subjected to bending stresses show regional differences in structural/material organization that appear to be related to either tension or compression loading (Albright, 1987; Boyde and Riggs, 1990; Carando et al., 1989, 1991; Carter et al., 1981; Cowin, 1984; Currey, 1984a; Lanyon, 1980; Lanyon and Baggott, 1976; Portigliatti-Barbos et al., 1983; Riggs et al., 1993a, b; Skedros and Bloebaum, 1991). The idea that bone can adjust its structural/material organization to regional heterogeneities in strain milieu has been used to explain the regional differences that occur in the fraction of primary bone that has been remodeled with secondary osteons, bone remodeling rates, and growth rates between different regions in limb bones (Amprino and Marotti, 1964; Anderson and Danylchuk, 1978; Bouvier, 1985; Burr, 1992; Enlow, 1966; Harris et al., 1968).

Variations in the population density (number/area), size and shape, and collagen fiber orientation of osteons, strongly influence the mechanical properties of bone (Ascenzi, 1988; Frost, 1986; Martin and Burr, 1989; Moyle et al., 1978; Pidaparti and Burr, 1992; Simkin and Robin, 1974). If regional differences in cellular activities (osteoclastic and/or osteoblastic) exist due to regional disparities in strain mode (tension vs. compression) or strain magnitude, they could be manifested as differences in microstructural organization. We hypothesize that in compact bone habitually loaded in bending, osteon microstructure will differ between the tension and compression cortices. We test this hypothesis by examining various static osteonal parameters in a natural "tension/compression skeletal system."

MATERIALS AND METHODS

The artiodactyl (e.g., sheep, deer, and goats) calcaneus was the model selected for study since it has been documented by Lanyon (1973, 1974) to be a simply loaded natural (in vivo) tension/compression system, receiving simple bending confined to the sagittal plane. Ten large skeletally mature male Rocky Mountain Mule Deer calcanei (*Odocoileus hemionus hemionus*) were each oriented and sectioned transversely at 50 and 70% of length, with the 70% section being closest to the joint (Skedros and Bloebaum, 1991; Skedros et al., 1994) (Fig. 1 in companion paper). The sections were embedded in polymethyl methacrylate using conventional methods (Emmanuel et al., 1987). The distal surface of each embedded section was ground, polished, and prepared for imaging in the backscattered electron (BSE) mode of a JEOL scanning electron microscope (SEM). The methods of Bloebaum and Skedros and co-workers (Bloebaum et al., 1990; Skedros et al., 1993a,b) were used for BSE imaging; however, no attempt has been made to calibrate graylevels between imaging sessions. Images were developed on Polaroid 52 film.

In all sections the compression cortex was defined as being cranial to the medullary canal, and the tension cortex was defined as being caudal to the medullary canal. At the macroscopic level the boundary between cancellous and cortical bone was easily delineated; however, under the microscope at 50 \times magnification, a thin, porous transition zone between cortical and cancellous tissue types was seen. This zone consisted of

progressively enlarging porous spaces which grade into the porosity of the trabecular bone. Regions wherein the width of the bone between the porous spaces was less than the diameter of the porous spaces were considered to be characteristic of the porous transition zone, and thus were avoided in analysis. This insured that only cortical bone was analyzed.

Compression and tension cortices were each divided into three 1.6 by 2.3 mm regions: pericortical, middle, and endocortical. The middle region was located midway between the pericortical and the endocortical regions. The pericortical region was located immediately beneath the circumferential lamellae of the periosteal surface, without overlapping the middle region. The endocortical region was located near the endosteal margin of the cortex, without overlapping the middle region.

In each region one 50 \times image representing the entire 1.6 \times 2.3 mm area was captured in the SEM/BSE mode and saved for analysis. Additionally, within each region two 0.8 \times 1.1 mm areas were imaged at 100 \times magnification; one 100 \times image was located in the upper right quadrant and the other was located in the lower left quadrant of the 1.6 \times 2.3 mm region. In the few cases where the entire 50 \times region was not entirely comprised of cortical bone, the 100 \times images were taken as close as possible to these quadrants without including areas with large porous spaces. Without exception, 100 \times images did not overlap, did not fall outside the perimeter of the region defined by the 50 \times image, and did not contain cancellous bone or porous bone in the transitional zone.

Since the mechanical properties of primary bone differ from those of remodeled bone (Currey, 1984b), it was important to distinguish the primary osteons of primary bone from secondary osteons of remodeled bone. Secondary osteons are formed through a resorption and replacement process (Carter and Hayes, 1976; Smith, 1960) and thus their outer margin will intersect lamellae of surrounding bone. Since intersecting lamellae are not seen in primary bone, secondary bone can be readily distinguished from primary bone in most instances (Currey, 1959; Enlow, 1963, 1966; Saha and Hayes, 1977; Smith, 1960). Since the bone was highly remodeled, the small amount of bone that confidently could be considered primary (<5% of all bone cumulative areas sampled) was not considered separately, but was included as part of the interstitium.

In the 100 \times images the following were counted: secondary osteons with only one central canal and secondary osteon fragments with only one central canal. Although most osteons typically have only one central canal, in some cases there are two or more. This can be a result of branching of individual osteons (Cohen and Harris, 1958). In instances where two adjacent canals appeared to be nearly fused, having a constriction between them (for example, a dumbbell shape with a canal in each end), the structure was counted as two osteons. This occurred infrequently (< 0.5% of total osteons counted). However, if the boundaries circumscribing two closely associated central canals did not have a constriction between the canals, they were counted as one osteon (< 0.5% of total osteons counted). An osteon was counted if: (1) more than 80% of its area was distinguishable from contiguous osteons; (2) the

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borders of the osteon were distinguishable; (3) all or part of its central canal was present within the boundaries of an image (Barth et al., 1992; Corondan and Haworth, 1986). Because all of the above criteria for osteon selection require some observer judgment, all counting and osteonal differentiation were done by one trained investigator (M.W.M.), and were reviewed by a second trained investigator (J.G.S.).

The fractional area of secondary bone (defined as the percent of cumulative cross-sectional bone areas occupied by secondary osteons), interstitial bone, and porous spaces (central canals and resorption spaces) were determined using a point counting technique (Parfitt, 1983; Russ, 1986). Eight millimeter grids used for point counting were prepared on transparent film and were randomly superimposed over each $50 \times$ BSE/SEM photomicrograph. There were between 117 and 123 points for each $50 \times$ image. Each point of the grid was classified as either secondary bone or interstitial bone. The area of secondary bone included the area occupied by their central canals. By definition, interstitial bone area did not include any central canals. The area occupied by porous (unmineralized tissue) spaces, invariably seen as central canals and resorption spaces, was calculated separately using a 4.5 mm grid superimposed over the $100 \times$ images, and only the points overlying central canals or resorption spaces were counted. There were an average of 452 ± 4 points in each $100 \times$ image. The fractional area of the secondary bone was defined as follows: total area of secondary bone (S) divided by total area of secondary bone plus interstitial bone (I), $[S/(S+I)]$. Correction for porosity was made by subtracting the porosity of central canals from the fractional area of secondary bone. Thus the influence of potentially larger canals in the tension cortex could be eliminated. Statistical analyses were conducted on the fractional area of secondary bone corrected for porosity. No correction was made for the unmineralized spaces represented by lacunae or canaliculi. Cracks, as seen in Figure 1, are unavoidable artifacts of fixation. The cracks were found to contribute less than 2% the total area of the image. The grid size used for fractional area of secondary bone measurements was too large to sample cracks (Russ, 1986). During porosity measurements, care was taken to exclude cracks from the data.

Osteon size, which is a feature that can be independent of the degree of remodeling, may be mechanically important. Area per osteon was estimated for each region by dividing the total area of secondary bone, including the central canals, by the number of osteons in the respective region. The mean area per osteon illustrates the regional differences in osteon size that are demonstrated by the observed data. Because these values were calculated, standard deviations could not be provided.

In summary the following data was obtained: (1) Number of osteons per bone area, (2) fractional area of secondary osteonal bone including central canals and resorption spaces, (3) fractional area of secondary osteonal bone excluding porous spaces, (4) combined area of primary and secondary interstitial bone, and (5) porosity including area of central canals and other porous spaces (i.e., all non-mineralized tissue and "void" spaces). For comparisons and statistical analyses, data was analyzed in several groupings. Comparison be-

tween tension and compression cortices were examined using a paired T-test. Comparisons between regions within each cortex were examined using an analysis of variance (ANOVA) design. An alpha level of < 0.01 was considered statistically significant.

RESULTS

Osteon Cross-Sectional Shape and Relative Mineralization Differences

Figure 1 shows representative BSE images from all regions of the compression and tension cortices in the 50% section of one animal. The relatively smaller, more uniformly circular-shaped osteons of the compression cortex contrast with the larger, more irregular-shaped osteons in the tension cortex. The graylevel differences within each image indicate relatively lower mineral content and younger tissue age, hence higher remodeling of bone in the tension cortex (Skedros et al., 1993a,b).

Osteon Population Density

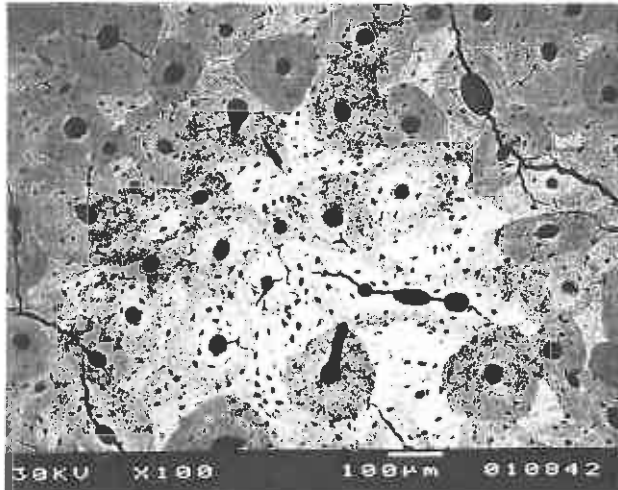
Analysis of combined data from all regions of the 50 and 70% sections shows significantly more osteons in the compression cortex than in the tension cortex ($P < 0.01$) (Fig. 2, Table 1). Transcortically, in the compression cortices of the 50 and 70% sections, the number of osteons does not differ significantly between the pericortical and middle regions ($P = 0.18$), but there are significantly fewer osteons in the endocortical region ($P < 0.01$). Similarly, in the tension cortices of the 50 and 70% sections, the number of osteons does not differ significantly between the pericortical and middle regions ($P = 0.14$), but there are significantly fewer osteons in the endocortical region ($P < 0.01$).

Osteonal population density data from the 50 and 70% sections were combined and compared between regions of the compression and tension cortices (Table 1). There were significantly more osteons in the pericortical region of the compression cortex ($48.7/\text{mm}^2$) than in the pericortical region of the tension cortex ($40.1/\text{mm}^2$) ($P < 0.01$). A similar difference is found between the middle region of the compression cortex ($45.0/\text{mm}^2$) and the middle region of the tension cortex ($36.9/\text{mm}^2$) ($P < 0.01$). However, in the endocortical regions of both compression ($20.6/\text{mm}^2$) and tensions ($25.7/\text{mm}^2$) cortices osteon density is not significantly different ($P = 0.05$).

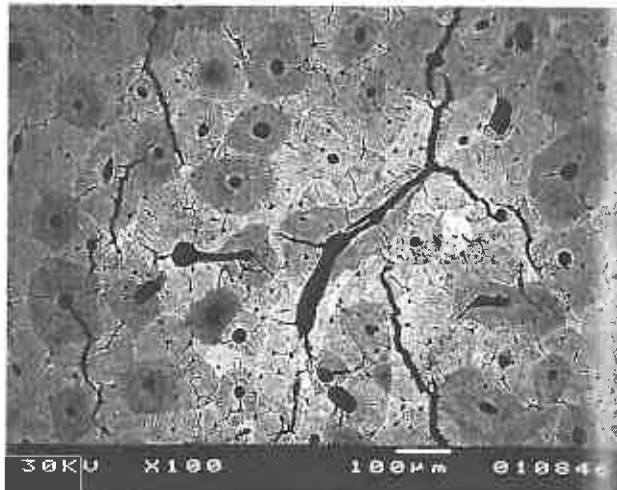
Fractional Area of Secondary Bone

The fractional area of secondary bone was combined for all regions of the 50 and 70% compression and tension cortices (Table 1). The fractional area of secondary bone is significantly lower in the compression cortices (64.8%) than in the tension cortices (75.5%) ($P < 0.01$). In the compression cortex, the fractional area of secondary bone is equivalent in the pericortical and middle regions ($P = 0.38$), but is significantly lower in the endocortical region ($P < 0.01$). Hence, the endocortical regions of the compression cortices contain a significantly larger fractional area of interstitial bone than found in either the pericortical or middle regions. Similarly, in the tension cortex there is no difference in fractional area of secondary bone between the pericortical and middle regions ($P = 0.27$), but the endocorti-

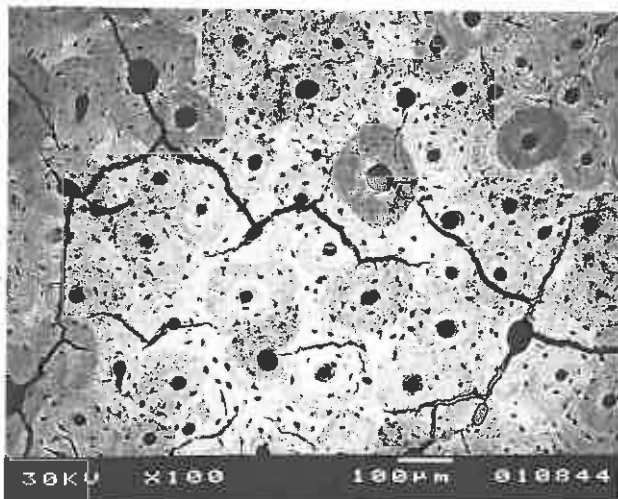
A. COMPRESSION PERICORTICAL



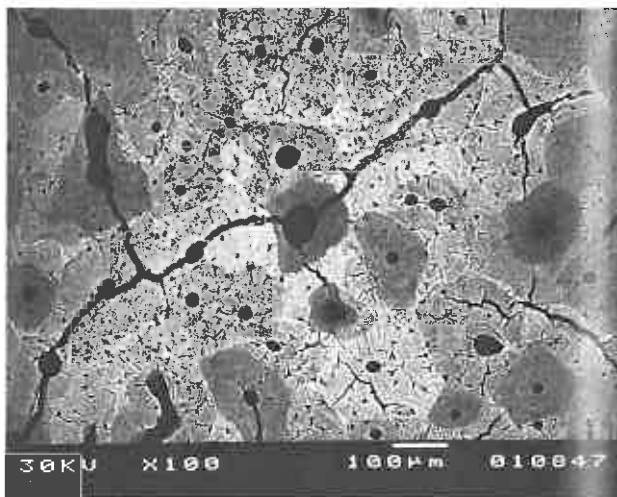
B. TENSION PERICORTICAL



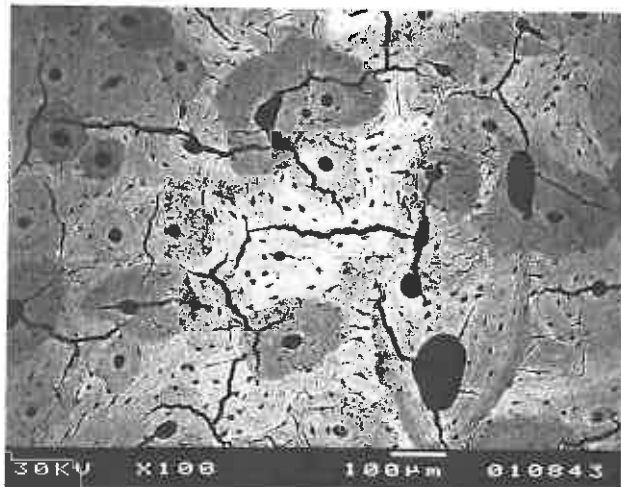
C. COMPRESSION MIDDLE



D. TENSION MIDDLE



E. COMPRESSION ENDOCORTICAL



F. TENSION ENDOCORTICAL

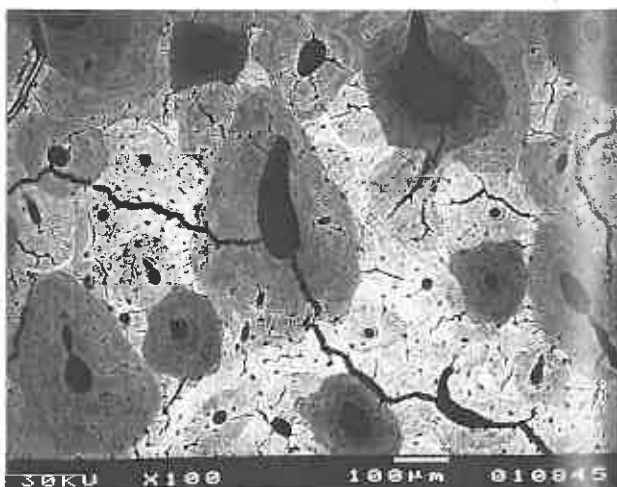


Fig. 1. Backscattered electron images showing representative fields of all regions analyzed from a 50% section of one calcaneus (each image 50×): (A) compression pericortical, (B) tension pericortical, (C) compression middle, (D) tension middle, (E) compression endocortical, and (F) tension endocortical. The cracks, which are unavoidable artifacts of fixation, were excluded from analysis.

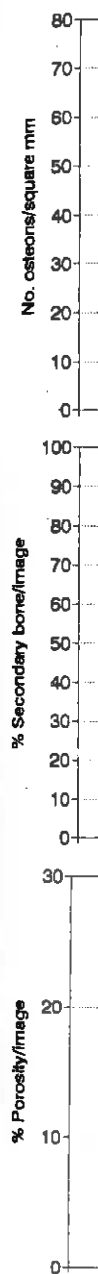


Fig. 2. T bone area/ image is 3.0 deviation. l tical region

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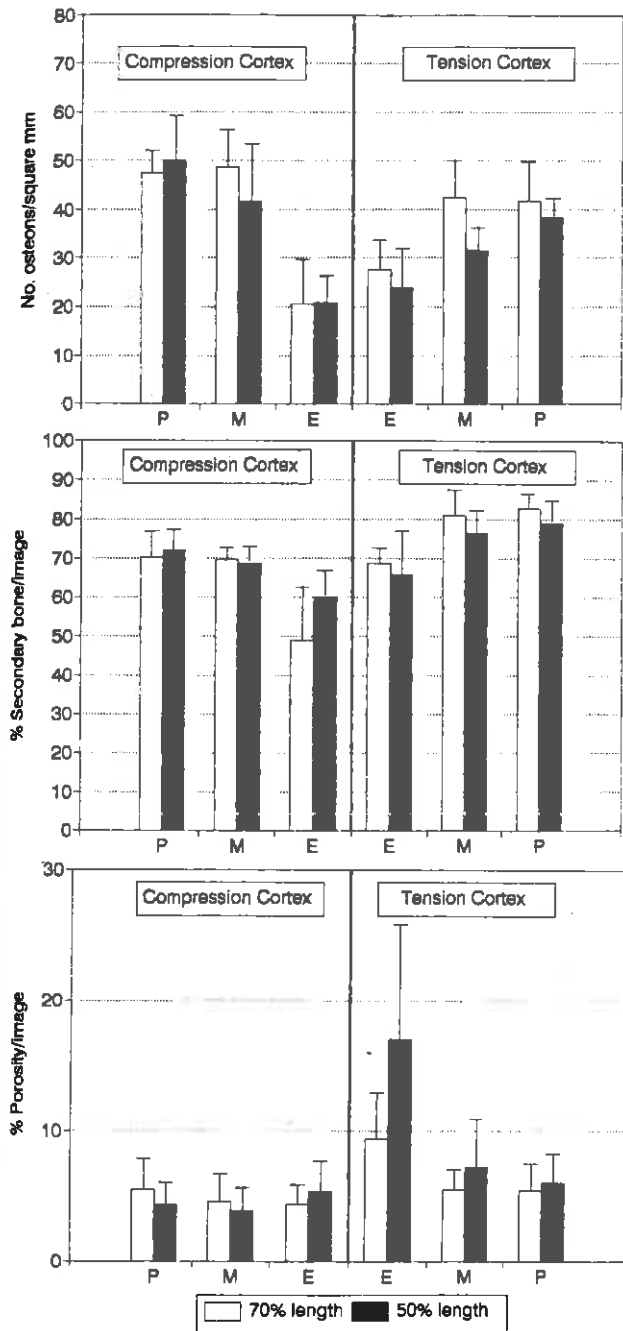


Fig. 2. **Top:** number of osteons/mm²; **Middle:** percent secondary bone area/50× image; **Bottom:** percent porosity/50× image. A 50× image is 3.6 mm². Bars represent means, lines represent one standard deviation. P = pericortical region, M = middle region, E = endocortical region.

cal region has significantly less secondary bone than either the pericortical or middle region ($P < 0.01$). In other words, the endocortical region of both tension and compression cortices has more interstitial bone compared to the other regions.

Analysis of combined data from the 50 and 70% sections shows that the compression pericortical region

has a significantly smaller fraction of secondary bone (excluding pores) (71.0%) compared to the fraction of secondary bone in the tension pericortical region (80.7%) ($P < 0.01$). A similar difference is found between the middle region of the compression cortex (69.0%) and the middle region of the tension cortex (78.5%) ($P < 0.01$). A somewhat larger difference is found between the endocortical region of the compression cortex (54.5%) and endocortical region of the tension cortex (67.2%) ($P < 0.01$).

Porosity

Nearly all (> 99%) of the porous spaces are osteon central canals; resorption spaces are infrequently seen. Analysis of combined data for all regions in the 50 and 70% sections show that the compression cortex is significantly less porous (4.7% porosity) than the tension cortex (8.5% porosity) ($P < 0.01$) (Table 1). There are no significant differences ($P = 0.29$) in porosity in pericortical and middle regions of the compression cortices. In the compression cortex, endocortical regions are not significantly more porous than pericortical and middle regions ($P = 0.33$).

Analysis of combined porosity data from the 50 and 70% tension cortices demonstrates no significant differences between the middle and pericortical regions ($P = 0.4$), but the endocortical regions are significantly more porous than these other two regions ($P < 0.01$). There are no significant differences in the porosity of the pericortical regions of the compression (4.9%) and tension (5.7%) cortices ($P = 0.26$). However, the porosity of the middle region of the tension cortex (6.4% porosity) is significantly greater than the middle region of the compression cortex (4.2% porosity) ($P = 0.01$). The porosity of the endocortical region of the tension cortex (13.2% porosity) is also significantly greater than the porosity of the endocortical region (4.9% porosity) of the compression cortex ($P < 0.01$).

Area Per Osteon

Calculations show that osteons in the compression cortex are smaller (0.022 mm²/osteon) than osteons in the tension cortex (0.026 mm²/osteon). If cross-sectional shape is assumed to be circular, compression osteons would have a diameter of 165 μm compared to tension osteons which would have a diameter of 185 μm.

DISCUSSION

It has been suggested that a bone adapts its structural/material organization to achieve a uniform elastic modulus and/or safety factor to failure between discrete cortical regions throughout its entire volume (Cowin et al., 1985; Hart, 1988; Huiskes et al., 1987; Riggs et al., 1993a,b). Regional differences in cortical microstructure and ultrastructure have been observed, but often not quantified, in various bone types that are subject to the habitual presence of physiologic bending stresses (Amprino, 1943; Bacon and Griffiths, 1985; Biewener and Bertram, 1991; Biewener et al., 1986; Boyde and Riggs, 1990; Carando et al., 1989, 1991; Gross et al., 1991; Lanyon, 1974, 1984; Lanyon and Baggott, 1976; Lanyon et al., 1979; Lozupone, 1985; Minns et al., 1975; Portigliatti-Barbos et al., 1983; Reid and Boyde, 1987; Riggs et al., 1990, 1993a,b; Shah et al., 1990; Smith, 1960; Turner et al., 1975; Vincentelli,

TABLE 1. Cumulated data: 50 and 70% sections¹

Locations	Osteon density (no. of osteons/mm ²)	Fractional area of 2nd bone (%)	Porosity (%)
Compression cortex (all regions)	38.1 (15.1)	64.8 (10.6)	4.7 (2.0)
Tension cortex (all regions)	34.2 (9.6)	75.5 (8.8)	8.5 (5.9)
Compression pericortical region	48.7 (7.2)	71.0 (5.8)	4.9 (2.1)
Compression middle region	45.0 (10.4)	69.0 (3.2)	4.2 (1.9)
Compression endocortical region	20.6 (7.5)	54.5 (11.7)	4.9 (2.0)
Tension pericortical region	40.1 (6.5)	80.7 (4.9)	5.7 (2.1)
Tension middle region	36.9 (8.4)	78.5 (6.3)	6.4 (3.0)
Tension endocortical region	25.7 (7.4)	67.2 (8.0)	13.2 (7.6)

¹Figures indicate the means and (standard deviations).

1978). We hypothesized that strain-mode-specific mechanical adaptations, if present, would be seen as differences in cortical microstructure between tension and compression cortices. This was based on the fact that the mechanical properties of cortical bone are markedly different in tension and compression (Skedros et al., 1994).

Transcortical Differences in Osteon Parameters

Lanyon (1973, 1974) showed that the magnitude of in vivo compressive strains measured on sheep calcanei were typically greater than the magnitude of tensile strains. Since strain mode differences coexist with strain magnitude differences, the relative influences that these strain features have on the structural/material organization of the cortical bone are seemingly inseparable. Experimental evidence suggests that strain magnitude, independent of strain mode, may be important in bone adaptation (Albright, 1987; Currey, 1984a; Frost, 1990a,b; Martin and Burr, 1989; Rubin and Lanyon, 1985). Since, in homogenous materials, strain magnitude varies directly with distance from the neutral axis of bending, we made comparisons between regions across each cortex. The lack of differences in osteon population density, percent of remodeled cortex, or fraction of interstitial bone between pericortical and middle regions of either tension or compression cortices, suggests that it is unlikely that there is a linear strain-magnitude-related microstructural adaptation between regions of these cortices. However, bone is anisotropic and often non-homogenous and thus linear strain magnitude differences across the cortex would not necessarily be expected. It is possible that differences in the structural/material organization within a cortex contribute to the non-uniform strain patterns across the cortex. An alternative theory suggesting that strain-magnitude-related microstructural adaptation occurs across the cortex of a bone has been proposed by Frost (1990b) and is discussed in a separate section of this paper.

Osteon Population Density, Size, and Reconstruction

Unquantified observations suggest that the greatest osteon population density often appears within the compression cortex of bones loaded habitually in bending (Bouvier and Hylander, 1981; Carter et al., 1981; Gies and Carter, 1982; Lanyon and Bourn, 1979; Lanyon et al., 1979; Portigliatti-Barbos et al., 1983). Results of the present quantitative study show that in

the cantilevered mule deer calcaneus, the compression cortex has 11.4% more osteons per mm² ($P < 0.01$), 43.5% more interstitial bone ($P < 0.01$), and 80.2% lower porosity ($P < 0.01$) than the tension cortex. Thus, in the compression cortex, osteons are smaller. Using human compact bone specimens, Evans and co-workers showed that specimens with greater tensile strength or fatigue life typically had fewer, larger, and, in some instances, more irregularly shaped osteons (Evans, 1958; Evans and Bang, 1966, 1967; Evans and Riola, 1970; Evans and Vincentelli, 1974). Significant negative correlations have been shown between percentage of secondary osteons and impact tensile strength (Saha and Hayes, 1977) and fatigue life (Carter and Hayes, 1976). However, these previous studies did not specifically compare bone regions that were habitually loaded in tension vs. compression strain modes. In a study of fracture mechanics of cortical bone from compression (medial) and tension (lateral) aspects of proximal canine diaphyses, Moyle et al. (1978) found that the work-to-failure for slow tensile cracking (allowing for maximum energy absorption) was significantly higher in bone specimens from the tension domain. The specimens that failed by slow crack propagation had a greater osteon population density in the immediate vicinity of the fracture site. However, the average osteon diameter and osteon population density did not significantly differ between compression and tension cortices. In contrast, Moyle and Bowden (1984) showed that the work required to fracture specimens of human femoral bone in three-point bending was related to osteon cross-sectional area. Martin and Burr (1989, pg. 196) considered the regional difference in resistance to tensile cracking to be a manifestation of regional adaptation to these strain mode differences. We suggest that mechanically relevant differences in bone microstructure, if present, would be more evident in the mule deer calcaneus since it is a simply loaded, unambiguous tension/compression system, in contrast to the more complex loading conditions in proximal canine and human femora. Although the results of the present study do not prove that bone adapts to habitual and prevailing regional differences in strain mode, the literature reviewed above supports the hypothesis that these microstructural differences represent mechanically relevant adaptation.

Some investigators have suggested that topographic differences in osteon microstructure are remnants of regional differences in growth rates and related corti-

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cal drift phenomena and hence are not manifestations of adaptations to local differences in loading conditions (de Ricqles et al., 1991; Enlow, 1962, 1963; Smith, 1960). For example, Enlow (1962, 1963) noted that during bone growth in diaphyseal/metaphyseal regions, individual trabeculae are progressively incorporated into the cortex which yields osteons and interstitial bone with a variety of irregular shapes, proportions, and sizes. However, micromorphologies attributable to growth or cortical drift would be expected to be minimal in older skeletally mature animals since remodeling, and hence potential adaptation, continues after growth and cortical drift have ceased. Larger osteons and increased central canal size (hence, increased porosity) have also been described in the cortical bone of patients with postmenopausal osteoporosis and are attributed to increased remodeling rates (Burr and Martin, 1989).

Cortical Porosity

In both the compression and tension cortices of the mule deer calcaneus, the porosity was equivalent between pericortical and middle regions, but increased in the endocortical regions. This difference in porosity may accompany differences in remodeling, where the rate of remodelling and the degree of porosity is typically greater in the endocortical region than in the middle and pericortical regions of diaphyseal bone (Amprino and Godina, 1947; Atkinson and Woodhead, 1973; Bouvier and Hylander, 1981; Currey, 1984b; Frost, 1990a,b; Martin, 1991; Martin et al., 1980; Smith and Walmsley, 1959; Vasciaveo and Bartoli, 1961). Other factors may also contribute to the increased osteon size and porosity in the endocortical regions, including the greater degree of blood supply in the endosteal envelope (Vasciaveo and Bartoli, 1961), and the larger vessels in the endocortical regions (Singh et al., 1991). The insertion of the plantar ligament may also affect porosity in the tension cortex by requiring enhanced perfusion, by altering the quality or complexity of the local loading conditions (Lanyon et al., 1979), or by requiring more bone surface area to accommodate its insertion. We emphasize that interpretations of cortical porosity based solely on loading history should be considered provisional in the mule deer calcaneus.

Support for Strain-Magnitude-Dependent Adaptation: Frost's Tension/Compression System

Lanyon's (1973, 1974) *in vivo* strain measurements on the lateral cortex of sheep calcanei showed peak strain levels of approximately 160 microstrain in tension and 240 microstrain in compression. Frost (1988a,b, 1990a,b) suggests that differences in strain magnitudes between tension and compression cortices, in addition to surface curvature and strain mode, produce mechanically relevant differences in cortical structural/material organization in skeletal tension/compression systems. In his models, however, strain magnitude is considered to have a preeminent role in governing bone remodeling (Frost, 1990b). He predicts that the compression cortex will be thicker, more highly mineralized and less porous than the tension cortex, and will have osteons that are smaller and more

numerous than those in the tension cortex. The data in the present study are consistent with this hypothesis.

Frost (1990b) describes three remodeling intervals, each defined by different levels of strain magnitude, and each characterized by different remodeling activities: (1) remodeling is activated below a "minimum effective strain" (MES) and ultimately yields increased porosity, (2) remodeling is repressed by conditions of normal mechanical usage above an MES but below the excessive strains that cause microdamage, and (3) remodeling is again activated above excessive strain magnitudes and ultimately yields decreased porosity. The lower porosity, more interstitial bone and the smaller osteons found in the compression cortex, seems to be, according to Frost's analysis, largely a result of strain magnitudes above the MES. In contrast, the tension cortex may be stress shielded by the load-sharing tension members (i.e., plantar ligament and tendon of superficial digital flexor) which may cause the habitual strains in this cortex to be lower than the MES of a cortex loaded in tension. The tendency for these tension members to shift the neutral axis toward the tension cortex may further serve to reduce stress in this cortex.

The differences between the endocortical envelope and other regions of the mule deer calcaneus may also be related to the differences in strain-magnitude-related remodeling thresholds. In the mule deer calcaneus, strain magnitude progressively increases from the endosteum to the periosteum. It is possible that strains in the endocortical region are below the MES, and that maximal strains in the pericortical and middle regions are above this MES, but below the threshold required for microdamage-mediated remodeling (Frost, 1990b). Consequently, different remodeling activities would not necessarily be expected between pericortical and middle regions. This could explain why increased remodeling activity and remodeled bone was not seen at the pericortical margins of the limb bones examined by Currey (1984b). Therefore, the lack of osteon microstructure or porosity differences between pericortical and middle regions does not necessarily preclude the hypothesis that strain-magnitude-related influences are manifest in bone organization.

The coexistence of increased number of osteons and apparently decreased remodeling rate in the compression cortex cannot be explained entirely by Frost's theory. In the compression cortex, the increased number of osteons would indicate an antecedent history of prevailing strain magnitudes above the microdamage threshold, but the decreased remodeling rate in the sections examined would indicate a more recent history of prevailing strain magnitudes below the microdamage threshold. Therefore, the described differences in the cantilevered artiodactyl calcaneus may be related in part to differences in strain mode.

The microstructural differences described between the tension and compression cortices of the mule deer calcaneus may be adaptations that are related to the regional differences between prevailing strain modes and/or magnitudes. Although these differences are associated with differences in prevailing strain mode, equally tenable associations with strain magnitude differences cannot be rejected based on these data alone. If the microstructural differences described in the present work represent relevant mechanical adapta-

tion to the prevailing strain environment, it follows that these characteristics, particularly in the compression cortex, may have been optimized by integrative activity of local bone multicellular units for the normal physiologic strain environment engendered in this bone. However, generalizing these data solely in the context of mechanically based interpretations would be reckless since there are tenable nonadaptive explanations for some of the differences described in the present study. In order to further test the hypothesis that there may be regional differences in bone organization which reflect local and/or regional regulation of cellular responses to specific strain stimuli, additional studies examining this idea are warranted.

ACKNOWLEDGMENTS

This work was supported by the Department of Veterans Affairs Medical Research Funds, Salt Lake City, UT. We thank Mark T. Nielsen for his help in completing this manuscript. We are grateful for the technical assistance of Gwenevere Shaw, Cathy Sanderson, and Matthew Anderson.

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