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“The Functional Morphology of Subchondral and Trabecular Bone in the Hominid Hindfoot”

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Introduction

Much study and debate has been devoted to examining the differences in primate foot and ankle morphology, especially of the hominoids, as they relate to locomotor function (reviewed by Harcourt-Smith and Aiello 2004). Studies of the external morphology of the foot and ankle bones, particularly the talus, has yielded surprisingly few characteristics that are able to distinguish among the hominoid species despite very different habitual postures and locomotor modes. Indeed, morphometric studies of some important fossil talus bones reveal unique mosaics of ape-like and human-like external features that complicate locomotor reconstruction of these extinct hominins.

Perhaps more informative than external bone morphology, which may be limited by numerous genetic as well as functional constraints, is the analysis of epigenetically sensitive traits that are modified by an individual’s activity pattern (Ward 2002). The internal structure of bone, both cortical and trabecular (cancellous), has been shown to be one such epigenetically sensitive trait (e.g., Biewener et al. 1996; McKay et al. 2011; Polk et al. 2008; Pontzer et al. 2006). Whereas external morphologies may be limited in morphological plasticity, the internal morphology of mammalian bone is highly dynamic, constantly remodeling its inner architecture to changing biomechanical environments (Mazurier et al. 2006). The goal of this study was to investigate whether the internal morphology of the ankle bones hold a diagnostic locomotor signal that may help to further characterize the mosaicism found among fossil hominid tali.

The increasing accessibility and application of non-destructive micro-computed tomography (μCT) to anthropological studies has allowed for the analysis of internal bony morphology. Recent studies have compared trabecular structure among primates with the hypothesis that habitual locomotor differences (broadly defined at the species level) are reflected in trabecular architecture (Fajardo and Müller 2001; MacLatchy and Müller 2002; Maga et al. 2006; Ryan and Ketcham 2002; Ryan and Ketcham 2005; Ryan and van Rietbergen 2005; Saparin et al. 2009; Scherf and Hublin 2010; Scherf et al. 2009). The relative apparent mineral density (estimated from radiodensity values of CT scans) and the relative thickness of the subchondral bone of joints has also been hypothesized to reflect patterns of habitual applied load (Ahluwalia 2000; Carlson and Patel 2006; Murray et al. 2001; Müller-Gerbl et al. 1989; Nowak et al. 2010; Patel and Carlson 2006; Patel and Carlson 2007; Polk et al. 2008).

The goals of this study were to characterize and quantify the variation of these bone properties in the hominoid distal tibia and talus to address the hypothesis that the morphology of these tissues are indicative of habitual stresses within the bone. If so, then it is first predicted that the subchondral bone and trabecular bone properties would exhibit coordinated or complimentary morphologies within an articular surface. Furthermore, since the load distribution within a joint is applied equally and oppositely to both articular surfaces, it is predicted that the distribution of bone properties in the talus would mirror that of the distal tibia. Finally, it is predicted that differences in the distribution of bone properties would be consistent with expectations based on differences in observed locomotor kinematics among species.

Methods

The taxa used in this study were modern human (*Homo sapiens sapiens*, n=18), gorilla (*Gorilla gorilla gorilla*, n=15), chimpanzee (*Pan troglodytes troglodytes*, n=20), orangutan (*Pongo pygmaeus*, n=13), and baboon (*Papio hamadryas sp.*, n=17).

Adult females of each hominoid species were selected for study in an effort to minimize the potential effects of body size on both locomotor behavior and bone morphology. Baboons were included in the study as a non-hominoid outgroup and also as a representative of terrestrial digitigrade quadrupedalism.

Each bone was scanned individually using a commercial μCT system (eXplore Locus SP, GE Healthcare Pre-Clinical Imaging, London, ON, Canada). Specimens were scanned at a resolution setting of 45 μm, which has been found to be small enough to produce morphometric results similar to histologic methods (Müller et al. 1996).

The subchondral bone plate was isolated from each image volume, then segmented into a 3x3 grid of nine anatomically-aligned regions. Thus each region was defined with dimensions of 1/3 of the maximum mediolateral length and 1/3 of the maximum anteroposterior length. The distribution of voxel radiodensity (Sc.Radiodensity) and subchondral bone thickness (Sc.Th) within each of the nine regions of the articular surfaces was quantified. The trabecular bone volume of each specimen was isolated, then segmented into nine roughly cubic regions directly corresponding to the overlying subchondral bone regions. Standard metrics describing the structure and orientation of the trabecular bone within each region was quantified, Tb.BV/TV, Tb.Th, Tb.N, Tb.DA, as well as the shape and orientation of trabeculae.

Results and Discussion

Overall, the results showed some differences in internal bone morphology among species in support of the hypothesis that subchondral bone and trabecular bone properties reflect habitual compressive load, but often not in the direction predicted by behavioral and postural observations.

Relationships among subchondral and trabecular bone variables

Overall, the hypothesis that there is a relationship between subchondral bone and trabecular bone strength is supported, although the properties are not as strongly coupled as predicted. Moderate to weak positive relationships were found between subchondral bone radiodensity and thickness and trabecular bone volume and thickness in all groups in both the distal tibia and talus. A weak negative relationship was also found between subchondral thickness and underlying trabecular number in some groups in the talus. However, the distribution of trabecular bone anisotropy in the distal tibia did not display a strong relationship with overlying subchondral bone properties. Subchondral bone radiodensity as quantified by Hounsfield units is correlated to subchondral thickness, thus maybe used as a proxy when radiodensity cannot be accurately measured, for instance in fossilized bone.

Overall Species means

A few species-level differences were found in internal bone morphology of both the distal tibia and the talus that may be used to distinguish among species. In general, these results separated the more terrestrial humans and baboons from the more arboreal great apes.

Humans were distinguished from the other groups in having overall absolutely thinner subchondral bone in both the distal tibia and the talus. Overall thinner subchondral bone may be an epigenetic response to humans loading their joints with low magnitude habitual loads relative to the apes and baboons, or it could be a genetic difference. Humans were also distinguished from other groups in having lower trabecular bone volume and more anisotropic, elongated trabeculae in both the distal tibia and the talus. This interspecific result has also been shown for the trabeculae in the hominoid proximal calcaneus (Maga et al. 2006) and the T8 thoracic vertebral body (Cotter et al. 2009). Thus it seems that humans systemically have less bone volume than other hominoids, even in regions where mechanical stress would be expected to be relatively greater in humans (i.e., proximal calcaneus). Additionally, as predicted, the degree of anisotropy was found to be greater in humans than the other groups suggesting that despite decreased bone volume, bone strength may derive from the alignment of trabeculae with habitual, predictable stresses. As a corollary, this suggests that the greater-volume, less-anisotropic arrangement of trabeculae in non-human hominoids may be better suited to withstand more habitually variable joint loads as would be encountered in daily activity.

Baboons overall displayed the greatest trabecular bone volume, and greatest trabecular thickness than the other species in both the distal tibia and talus. This suggests that perhaps the talocrural joint in baboons is habitually subjected to relatively greater duration, greater magnitude, or more variable stresses than the great apes. This is plausible because the baboons are documented to spend more time in active standing activities, thus loading their tibia more often, than apes (Hunt 1991; Hunt 2004). Furthermore, the joint loads that result from the relatively high-speed, longer sustained, terrestrial locomotion of baboons may involve greater strain rates than those generated from arboreal locomotion and thus may be relatively more osteogenic (Turner 1998).

Comparison of trabecular and subchondral bone morphology among species

Significant differences in subchondral and trabecular bone properties were found among regions of the distal tibia and talus in all groups.

Subchondral bone

The human distal tibia and talus did not show significant differences in subchondral radiodensity across the joint as predicted. Two interpretations of this result are: (1) that habitual stresses in the human ankle were consistent among individuals and were relatively homogenous across the distal tibia, or that (2) the subchondral bone radiodensity reflects habitual stresses that were variable among the sample individuals.

In the non-human groups, significant differences were found in subchondral bone radiodensity across the distal tibia and talus. Moreover they were much more consistent in pattern, supporting the hypothesis that subchondral bone radiodensity may be reflecting intraspecific similarities in joint stresses.

The regions that were significantly more radiodense in the African apes were found mostly medially in both the tibia and talus. This result is consistent with with the oblique posture of the ankle joint as facilitating an inverted foot for vertical climbing. During vertical climbing, it is intuitive that the greatest load would be borne on the medial aspect of the ankle joint. Thus, these results suggest that the subchondral bone radiodensity pattern in African apes may reflect bone strength related to the loads during habitual climbing activities.

Orangutans also showed regional differences, but unlike the African apes showed high radiodensity in the anterolateral regions of both the tibia and talus as well as the medial regions, suggesting that these differences may be related to the differences in habitual joint load between the semi-arboreal chimpanzee and gorilla and the fully-arboreal orangutan. The presence of an area of high subchondral radiodensity to the anterolateral as well as the anteromedial region of the joint agrees with that predicted from highly dorsiflexed postures.

Baboons had the greatest subchondral bone radiodensity and thickness in the posterocentral region in the tibia and the posterolateral region in the talus. Baboons also had less radiodense subchondral bone in the anteromedial region of the talus. In all other groups, the anteromedial region showed (often significantly) greater subchondral bone density and thickness, so the relatively decreased subchondral bone radiodensity there in baboons is distinctive. Baboons are distinguished from the apes by spending more time in a quadrupedal standing posture, moreover in a semi-digitigrade posture (Hunt 1991; Meldrum 1991; Schmitt and Larson 1995), which was predicted to place greater load on the posterior aspect of the joint. These results thus further support the hypothesis that subchondral bone morphology may be an indicator of habitual postural joint load. Medially to laterally, the subchondral bone properties were more evenly distributed in the baboon tibia, in agreement with the stereotype that the terrestrial baboon posture is largely held within the sagittal plane, with less abduction/adduction bias at the ankle than is found in the more arboreal great apes.

Trabecular bone

The distribution of bone tissue quantity (BV/TV, Tb.Th and Tb.N) within the tibia and talus was much more consistent in the non-human species than in the humans. This result echoes that of the subchondral bone radiodensity variability in the tibia, and supports the conclusion that humans are relatively inconsistent in the regional distribution of bone tissue in the distal tibia.

In the great ape distal tibia, greater trabecular bone volume was located generally along the anterior and posterior regions and lesser volume was found in the mid-coronal regions. This somewhat agreed with predictions of increased bone strength anteriorly as an adaptation to a highly dorsiflexed posture during habitual locomotion. Peak magnitude loads occur in the joint while it is in a highly dorsiflexed posture during the propulsive phase of both terrestrial quadrupedalism and vertical climbing. But increased bone volume was also found posteriorly, which may also be related to posteriorly placed peak magnitude loads perhaps during terrestrial locomotion, or may be simply related to the shape of the bone.

By contrast, in baboons the trabecular bone volume resembled that of humans in that it was more evenly distributed into the mid-coronal regions of the tibia. If greater volume of trabecular bone serves to attenuate peak stresses, then this pattern implies that the center of the baboon distal tibia may experience the greatest impact loads during habitual locomotion.

A diagnostic locomotor signal was not found in the trabecular shape or primary orientation of trabeculae in the distal tibia that would be of help in interpreting locomotor behavior beyond features measureable in the external morphology. Trabecular shape indices quantified in the distal tibia do not distinguish among hominoid species with different locomotor behaviors. Humans, chimpanzees, and gorillas all show more plate-shaped trabeculae in the anterocentral and posterocentral regions which imply these regions withstood greater habitual loads in life. Both orangutans and baboons display more plate-shaped trabeculae in the central region, implying a different distribution of habitual load. The primary orientation of trabeculae in the distal tibia also was largely similar among species, although there were slight differences that agree with postural differences predicted by external morphology.

However, distinct differences among species in trabecular orientation in the talus may help in the interpretation of habitual locomotor behaviors from an isolated talar bone. Humans showed the greatest overall consistency in trabecular orientation throughout the talus, supporting the stereotype that humans are much less variable in the direction of habitual joint load within the ankle. Orangutans showed the greatest overall variance in trabecular orientation, supporting the stereotype that the joint loads in orangutan locomotion are more variable. The primary orientation of trabeculae in the talus differs among species in ways that were predicted from behavioral observations. Humans differed from the non-human groups in that the orientation of trabeculae in the posterolateral and anteromedial regions were directed toward the posterior calcaneal facet and talar head, respectively, while that of other groups tended to be normal to the trochlear surface.

Conclusion

Overall, the hypothesis that there is a relationship between subchondral bone and trabecular bone strength is supported, although the properties are not as strongly coupled as predicted. In both the distal tibia and talus, species could be distinguished from each other in overall differences in subchondral bone properties that may reflect habitual differences in postural or locomotor loads in the ankle joint. Humans had overall thinner subchondral bone, and baboons had overall more radiodense subchondral bone, than the great apes. Overall trabecular bone architecture in both the distal tibia and talus differs among species – humans have lower bone volume and greater anisotropy and baboons have greater bone volume and trabecular thickness, but fewer trabecular number and lower anisotropy than the other groups. Chimpanzees had greater trabecular number and lower trabecular thickness than all other groups.

Regional differences were found in the distribution of subchondral thickness and radiodensity and trabecular architecture, particularly bone volume and thickness, in each species that may be related to the regional distribution of habitual stress in the joint.

The hypothesis that the regional differences in subchondral bone properties are coincident within opposing surfaces of an articulation is supported. In all species, the regions found to be significantly different in the distal tibia largely matched the regions that were significantly different in the talus. However, the hypothesis that the regional differences in trabecular bone properties are coincident within two articulating bones is not supported. While some trabecular variables were found to be significantly different in the corresponding anterior regions of both articular surfaces, most often the regions that were significantly different within the tibia did not match the regions that were significantly different in the talus.

A diagnostic locomotor signal was not found in the trabecular shape or primary orientation of trabeculae in the distal tibia that would be of help in interpreting locomotor behavior beyond features measureable in the external morphology. However, distinct differences among species in trabecular orientation in the talus may help in the interpretation of habitual locomotor behaviors from an isolated talar bone. The primary orientation of trabeculae in the talus differs among species in ways that were predicted from behavioral observations. Humans differed from the non-human groups in that the orientation of trabeculae in the posterolateral and anteromedial regions were directed toward the posterior calcaneal facet and talar head, respectively, while that of other groups tended to be normal to the trochlear surface.