



Is 'hand preference' coded in the hominin skeleton? An in-vivo study of bilateral morphological variation

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ABSTRACT

The presumed link between bilateral asymmetry and lateralized habitual activity in extinct hominins is the basis upon which inferences of 'hand preference' often derive. While this presumption is reasonable, in-vivo comparisons of skeletal asymmetries and self-reported handedness are rare, and as a result the accuracy of these inferences is questionable. To assess this relationship in living humans, reported 'handedness' was compared against peripheral quantitative computed tomography (pQCT) derived bilateral measurements of humeral, ulnar, and tibial midshaft cortical area (CA) and torsional rigidity (J). Significant bilateral differences were found in the humerus for all groups, and in the ulna for the cricketer and field hockey sub-samples. Additionally, cricketers' non-dominant tibiae were more robust than their dominant tibiae. An assessment of 'Dominance Asymmetry' revealed that measures of CA and J were higher in the dominant humeri in ~90% of participants; in the ulna this was true in ~75% of cases, and in the tibia CA and J were higher in the dominant limb less than 50% of the time. Comparisons of (self) 'Reported' hand preference against 'Predicted' hand preference (based on the calculation of % Directional Asymmetry) revealed a low level of error for predictions based on both humeral (~4–5% error) and ulnar (6–11% error) asymmetry. Error was decreased with the exclusion of individuals displaying less than 2.5–5% asymmetry. Contrarily, predictions based on tibial analyses had a much higher level of 'error' (~45%). Overall, the results support currently accepted approaches for inferring 'hand preference' from measures of upper limb geometric asymmetry in the hominin skeleton.

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Introduction

'Handedness' refers to the preferential use of one hand for the majority of manipulative tasks. Accordingly, the dominant hand is generally associated with greater skill acquisition, strength and dexterity (Steele, 2000). While differences in the proportion of right and left hand dominant individuals exist across cultures (Marchant et al., 1995; Marchant and McGrew, 1998; Raymond and Pontier, 2004; Faurie et al., 2005), within living *Homo sapiens* right hand dominance is pronounced, and in certain groups defines more than 90% of all individuals (Raymond and Pontier, 2004). The role and importance of 'hand preference' (a more apt description than 'hand dominance' for skeletal populations (Marchant and McGrew, 1998)) in the daily activities of prehistoric hominins is as yet unresolved. The assessment of 'hand dominance' or 'handedness' is essential to a more nuanced understanding of hominin ontogeny and phylogeny as it relates to larger issues of behavioural

lateralization, language origins, and material culture (Pobiner, 1999; Lazenby, 2002; Corballis et al., 2004; Sarrinhaus et al., 2005; Llaurens et al., 2009). The assessment of hominin hand preference often involves the analysis of skeletal remains (cf. Auerbach and Ruff, 2006; Cashmore et al., 2008; Lazenby et al., 2008; Cashmore, 2009; Uomini, 2009; Braccini et al., 2010). The implicit assumption in these analyses is that throughout a lifetime skeletal morphology adapts to the preferential, bilateral biomechanical loading, and at the time of death the accrued asymmetric morphology is preserved and reflects the hand preference of that individual. Theoretically this position is well founded, as it derives from the concept of 'bone functional adaptation' (Ruff et al., 2006). Nevertheless, because the correspondence between self-reported handedness and skeletal asymmetry has never been rigorously tested in-vivo, the accuracy of this position remains questionable.

Previously thought to be a uniquely human trait, hand preference has now been documented in various primate species (cf. Byrne and Byrne, 1991; Fagot et al., 1991; Hopkins et al., 1993; Sugiyama et al., 1993; Westergaard and Suomi, 1996; Cashmore et al., 2008; Braccini et al., 2010). In chimpanzees, lateralized

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behaviour has been identified for tool-use intensive tasks including nut-cracking, termite fishing and fruit pounding, with individuals displaying either left- or right-hand preferences (Boesch, 1991; Sugiyama et al., 1993; McGrew and Marchant, 1996, 1997; McGrew et al., 1999). However, unlike living humans, there is little evidence to suggest a group-level bias for hand preference in wild chimpanzees (McGrew and Marchant, 1996, 1997; McGrew et al., 1999; Morbeck et al., 2002; Fletcher and Weghorst, 2005), although more recent studies have argued otherwise (Humle and Matsuzawa, 2008).

Primarily due to a paucity of fossil evidence, attributions of hand preference are rare for pre-australopithecines, australopithecines, habilines, and also for more recently described specimens (Brown et al., 2004; White et al., 2009; Berger et al., 2010; Haile-Selassie et al., 2010). Although relatively abundant, the co-mingled nature of the *Homo heidelbergensis* remains from the Sierra de Atapuerca, Spain (Carretero et al., 1997), make the assignment of associated right and left upper limb elements difficult. While few bilateral skeletal comparisons can be made from the remains of KNM WT-15000 (*Homo ergaster*), Walker and Leakey (1993) suggest a generalized right arm preference for this individual. More definite statements have been made for Late Pleistocene and Holocene *Homo*; comparisons of upper limb osteometrics and midshaft cross-sectional properties have provided conclusive evidence of right side dominance in Neandertals (cf. Trinkaus et al., 1994; Vandermeersch and Trinkaus, 1995; Steele and Uomini, 2005). The pronounced asymmetry associated with Neandertal upper limbs is thought to reflect intense and repetitive bilateral loading patterns rarely encountered by modern humans. Analyses of humeral diaphyseal rigidity for the skeletal remains of Upper Paleolithic *H. sapiens* from Asia, Europe and North Africa have also documented profound asymmetry suggestive of right-side hand preference (Shackelford, 2007).

In general, the human upper limb is free from the functional constraints of locomotion. Upper limb bilateral asymmetry is therefore thought to reflect the differential use of the right and left arms for highly stress-inducing, and possibly repetitive activities, including habitual subsistence activities (see Rubin and McLeod, 1994; Frost, 1997; Qin et al., 1998; and Fritton et al., 2000, for more on loading magnitude and frequency and their influence on bone structure). Variation in upper limb bilateral asymmetry is most often determined through comparisons of cross-sectional properties of long bone diaphyses, which allow for an estimate of a bone's robusticity: the strength or rigidity of a structure relative to a mechanically relevant measure of body size (Ruff et al., 1993). The habitual performance of highly intensive lateralised behaviours has been shown to correspond with pronounced asymmetries in upper limb morphology (cf. Shaw and Stock, 2009a). Based on an understanding of this correspondence, variation in the level of bilateral asymmetry among skeletal populations has been used to reconstruct the activity patterns of late-Pleistocene and Holocene hominin populations (Trinkaus et al., 1994; Steele and Mays, 1995; Lieberman, 1997; Steele, 2000; Lazenby, 2002; Auerbach and Ruff, 2006).

There is a presumed link between asymmetric skeletal morphology and lateralised behaviour. However, the only in-vivo study to test this using self-reported handedness found epicondylar breadth to be larger in the dominant humerus in only 68% of individuals (Blackburn and Knüsel, 2006). Claiming to be 'left-handed' implies that the left upper limb is favoured during the performance of fine and gross motor tasks. Following from this, it could be hypothesized that the presumed greater biomechanical load (intensity and/or repetition) imposed upon that limb would result in increased bone size and rigidity, relative to the opposite limb. If this hypothesis is generally supported, current

interpretations of upper limb bilateral asymmetry remain robust, however, if not, inferences of hand preference derived from fossil and skeletal remains should be questioned.

This study takes the initial steps towards assessing the relationship between reported 'handedness' and variation in diaphyseal midshaft rigidity by comparing bilateral measurements of humeral, ulnar and tibial cross-sectional geometry from modern human athletes and controls. Two primary questions are asked: 1) Does reported 'handedness' correspond with in-vivo measures of bilateral asymmetry, and, if so, is this correspondence consistent among skeletal locations? 2) Does a relationship exist between known behaviour patterns and the magnitude of asymmetry in the upper and lower limbs?

Materials and methods

Eighty-one males aged 19–30 years contributed to this study. Subgroups included varsity-level field hockey players (15), distance runners (15), swimmers (15), cricketers (16), and non-athletic controls (20). All participants were recruited from the University of Cambridge and Anglia Ruskin University, Cambridge, UK. All were without a history of disease or medication known to affect bone metabolism, and had no history of upper and lower extremity fractures. The groups did not differ by age (mean of 22.0 (± 2.5): hockey players (21.5 ± 1.5), runners (23.2 ± 3.2), swimmers (21.9 ± 2.5), cricketers (22.0 ± 2.5), controls (21.6 ± 2.5)). Details of the athletic history of these individuals are available in Shaw and Stock (2009a, b).

The study protocol was approved by the University of Cambridge Human Biology Research Ethics Committee, and the Essex 2 Research Ethics Committee. All participants received a verbal and written description of the protocol prior to participation. Following this, each participant provided written informed consent. Athletic, lifestyle, and medical history was obtained through a questionnaire completed prior to all other measurements being taken. Among others, questions were posed to ascertain the duration and type of physical activities that were undertaken beginning in late childhood until the time of participation in the study a detailed description of this questionnaire is available in Shaw and Stock (2009b). 'Handedness' was primarily determined through the questionnaire, which required the participant to identify whether they were 'right' or 'left' handed. Participants were then prompted to describe any repetitive or strenuous habitual activities that they performed with their (self-identified) non-dominant hand, which included, among other examples, the playing of racquet sports and throwing. If, through the admission of the habitual performance of strenuous behaviours with the non-dominant hand, individuals were deemed 'ambidextrous' they were excluded from the analyses performed here.

Peripheral quantitative computed tomography (pQCT), a non-invasive technique, was used to capture two dimensional, cross-sectional images of bone and surrounding soft tissue. The pQCT measurement techniques used in this study have been previously described in Shaw and Stock (2009b). A single scan from each of the left and right arm, forearm, and lower leg of each participant resulted in a total of 486 cross-sectional pQCT images captured at 50% of limb segment length using an XCT 2000 (Stratec Medizintechnik GmbH, Pforzheim, Germany). Each scan provided a 2.5 mm thick slice (pixel size of .5 mm).

The images derived from pQCT scans allow for the identification of osseous tissue in cross-section. Raw cross-sectional pQCT images of the humerus, tibia, and ulna were imported into Image J (<http://rsb.info.nih.gov/ij/>) and analyzed using Moment Macro (http://www.hopkinsmedicine.org/FAE/mm_macro.htm). The contribution of diaphyseal geometry to bone strength or rigidity was measured

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