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Quantifying Dominance: An analysis of humeral bilateral asymmetry and implications for behavioral reconstruction

Cassandra M. Turcotte
University of Pennsylvania

Quantifying Dominance: An analysis of humeral bilateral asymmetry and implications for behavioral reconstruction

Abstract
A commonly cited characteristic of the human species, the concept of handedness represents a persistently enigmatic notion in modern society. Although important because the genesis of both handedness and language can be attributed to cerebral hemispheric lateralization in our evolutionary past, this feature remains ill defined and consequently defies analysis. Emerging CT technology, however, enables the application of morphometric techniques to human long bones, facilitating the quantification of bone's internal mechanical properties as a possible way to improve the assay of bilateral asymmetry in the humerus. This capacity was applied to the population of Hasanlu, a Bronze Age site in which archaeologists posited a sexual division of labor among inhabitants as the result of artistic and botanical evidence. This division would have had males engaging in lateralized activities such as engaging in battle with spears or farming occupations while the females dedicated their time to the rigorous bimanual task of wheat processing. Because of this, internal mechanical properties within the humeri of males and females were postulated to exhibit differences in the distribution of mechanical loading. Indeed, analysis found a significant degree of lateralization only in the midshaft of the male humerus, supporting the idea that the inhabitants of Hasanlu did engage in division of labor based on sex.

Disciplines
Anthropology

Quantifying Dominance:

An analysis of humeral bilateral asymmetry and implications for behavioral reconstruction

Cassandra M. Turcotte

Mentor: Dr. Janet Monge

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This capacity was applied to the population of Hasanlu, a Bronze Age site in which archaeologists posited a sexual division of labor among inhabitants as the result of artistic and botanical evidence. This division would have had males engaging in lateralized activities such as engaging in battle with spears or farming occupations while the females dedicated their time to the rigorous bimanual task of wheat processing. Because of this, internal mechanical properties within the humeri of males and females were postulated to exhibit differences in the distribution of mechanical loading. Indeed, analysis found a significant degree of lateralization only in the midshaft of the male humerus, supporting the idea that the inhabitants of Hasanlu did engage in division of labor based on sex.

Introduction:

One of society's great pastimes involves the delineation of what it means to be human. To this end, we traditionally understand traits such as higher mental faculties, bipedality, tool use and language to represent archetypal attributes of the human lineage. Another feature might also fall under this umbrella of human traits in the form of hand dominance, colloquially called handedness.

Handedness refers to the preferential use of one arm during bimanual movement for high-frequency actions requiring finer motor control (Uomini, 2009). As a result, this dominant limb displays a level of strength and dexterity exceeding its partner (Steele, 2000). Previously ascribed only to humans, handedness has now been reported in several primates (Cashmore et al., 2008; Braccini et al., 2010). In chimpanzees this behavior extends to an assortment of tasks in which the subject exhibits left or right side preferences, such as in nut-cracking or termite fishing (McGrew and Marchant, 2002; Cashmore et al., 2008; Braccini et al., 2010). Nevertheless, wild chimpanzee hand preference fails to present itself consistently on a population level or across a variety of tasks, distinctions that typologically divide human and non-human handedness. Recent studies, however, have challenged the anthropocentricity of these claims and call for a reevaluation of primatological data (Humle and Matsuzawa, 2008; Hopkins 2009; Hopkins et al., 2011).

Marchant and McGrew's (1997) classificatory system divides hand dominance into four discrete categories based on how many individuals in the population exhibit lateralized behavior as well as the number of tasks for which the side bias is apparent. Under this classification, *Homo sapiens* represents the sole extant organism to demonstrate true handedness, defined as a population-level hand bias across a variety of actions (Marchant and McGrew, 1997; Uomini, 2009b). Indeed, researchers have observed every documented population of modern *Homo sapiens* thus far to exhibit definitive hand preference, with an average of 90% of individuals in each population functioning as right-handed (Marchant and McGrew, 2007; Cashmore et al., 2008; Uomini 2009; Uomini 2009b). The precise function of human right-handedness remains unclear but a finer understanding of its evolutionary history is critical to the exploration of related but harder to study problems such as the evolution of language and brain asymmetry (Pobiner, 1999; Lazenby, 2002; Corballis et al., 2004; Cashmore et al., 2008; Uomini, 2009b).

In the past, assessments of handedness evolution have been based primarily on lithic remains. Such studies put forth 1.9-1.4 myr as the age of handedness on the basis of strike position on flakes (Toth 1985; Uomini, 2009b). Subsequent analysis on the part of Pobiner (1999) called Toth's (1985) premise and results into question using experimental techniques that found that Toth's right-hand strike position varied within individual and across sessions. This discovery cast serious doubt on Toth's methodology but effort continues to the present in order to refine and reinvent the discernment of lateralized behavior from lithic evidence so as to increase validity (Uomini, 2009b). Insufficiencies in this approach, however, call for a different tactic altogether to accurately assess handedness.

A different technique comes in the form of skeletal asymmetry. Handedness, as a behavior defined as the consistent use of a 'dominant' limb over the other during bimanual activities, denotes an asymmetric increase in the mechanical load of the preferred limb. According to the principle of bone functional adaptation, bone modifies itself in response to mechanical stress in a circuitous interplay of osteocytic bone resorption and apposition by osteoblast action; this production of new bone reduces strain by increasing bone strength, leaving behind at death asymmetric skeletal elements indicative of bilateral mechanical loading (Steele, 2000; Chen et al., 2010; Ruff et al., 2006; Ruff, 2008).

Traditionally, these skeletal indicators of handedness have been assessed using non-quantitative rugosity indices that sort the robusticity of musculoskeletal markers into categories based on visual estimation (Hawkey and Merbs, 1995). The resultant data were insufficiently rigorous, non-replicable and did not readily permit cross-trial comparisons (Cashmore, 2009). Additionally, researchers have begun to implement geometric morphometrics and cross-sectional morphology to address asymmetries in long bone mechanical response. This technique applies the requirements for strength and rigidity exhibited by an engineering beam to the geometric structure of bone (Trinkaus et al., 1994; Ruff, 2008). This relationship between lateralized behavior and upper limb asymmetries enables the reconstruction of behavioral patterns in skeletal populations (Trinkaus et al., 1994; Steele, 2000; Lazenby, 2002; Shaw, 2011). Using geometric morphometrics, Trinkaus et al. (1994) have been able to show pronounced side dominance in the upper limbs of athletes such as tennis players, interpreted as a functional result of their athletic endeavors (cf. Shaw, 2011). Additionally, they've shown a similar though more marked right-hand sidedness in Neanderthal skeletons, an indication of increased bilateral loading consistent, perhaps, with life activities such as spear-throwing (Schmitt et al., 2003; Shaw, 2011).

Because of this demonstrated relationship between cross-sectional morphology and behavior pattern, the application of geometric morphometrics to archaeological human populations could elucidate behavior patterns previously resistant to quantification. In doing so, the validity of the technique is also assessed. We therefore seek to examine the upper limb bones of a well-studied archaeological population of *Homo sapiens* in order to make predictions about the population's bilateral behaviors. If geometric morphometric techniques accurately assess mechanical properties in bone and are sensitive to asymmetry in paired long bones, then we should detect the same right-hand bias in this archaeological population of modern humans that we do in extant modern humans and Neanderthal skeletons. Deviations from these exemplars may be interpreted as differences in behavior.

Materials and Methods:

Materials

The assemblage used in this study comes from the Iron Age sites of Hasanlu and Dinkha Tepe in modern-day Iran, stored at the University of Pennsylvania. The Hasanlu population represents the left and right humerus from 14 adult male and 9 adult female specimens, selected for element completeness and absence of internal/exterior damage. The Dinkha Tepe site added 4 adult specimens of unknown sex.

The Hasanlu specimens were primarily the victims of a violent skirmish; evidence from manner of death, weaponry and artistic renderings of battle suggest that the Hasanlu people were actively engaged in warlike activities. The most common weapon at the site was the socketed spear, but there were also maces, swords, daggers, axes, pikes, bows and shields. A battle scene portrayed on an ivory plaque recovered from the site shows a male Hasanlu warrior equipped with a spear in his right hand and a shield in the left. This led to a prediction that the specimens of Hasanlu and Dinkha Tepe engaged in these activities would exhibit a strong bilateral asymmetry, due to a predetermined behavior observed in other archaeological evidence.

Another important behavioral observation comes in the form of diet. The site of Hasanlu shows evidence of cultivated plants, of which there were primarily cereals such as wheat, barley and millet. In order to be consumed, these plants first need to be processed through the removal of the hull via parching or milling. As observed elsewhere, contemporaneous methods of milling wheat required an intense, repetitive bimanual motion to grind the grain (cf. Molleson, 1994).

Methods

Free from the functional limitations of locomotion, asymmetries of the bipedal human upper long bones (the ulna, radius and humerus) are more likely to display the skeletal changes indicative of habitual lateralized behavior (Trinkaus et al., 2004; Shaw, 2011). Consequently, the humerus was chosen as the subject of this study.

As part of the University of Pennsylvania's Open Research Scan Archive (ORSA), the Hasanlu and Dinkha Tepe humeri were already a part of an online CT scan archive. A total of six cross-sectional scans along 35-40% and 50-55% the distal humerus were taken non-invasively for each right and left humerus using a Siemens SOMATOM Sensation CT scanner from the Children's Hospital of Pennsylvania (CHOP). Each scan was imported into Image J (http://rsb.info.nih.gov/ij) and analyzed using Moment Macro, a program developed by Dr. Christopher Ruff of Johns Hopkins and used in, among other studies, Trinkaus et al. (1994) (http://www.hopkinsmedicine .org/FAE/mmacro.htm).

Using Moment Macro, three measurements were computed per scan. The first was the polar second moment of area (J): [$I_{max} + I_{min}$], which represented the bending and torsional rigidity of the humerus at that location. Polar section moduli (Z) showed the bone's bending and torsional strength: [J^.73]. Lastly, percent cortical thickness (%CA): [CA/TA x 100] is a morphological character indicating the area of the cortical bone in a cross section, which, as Dr. Ruff (2008) asserts, shares a more tenuous relationship with mechanical loading.

For each individual humerus and measurement, the values for the six scans were averaged. A paired one-tail t-test was then performed for each category after removing one statistical outlier for the 35-40% subset.

Results:

In the total sample at 35-40% the distal humerus, as shown in Fig. 1, second moments of area; section moduli; and cortical bone thickness were all found to be significant at the .05 level. The same is true for the total sample at 50-55% the distal humerus, shown in Fig. 2.

Fig. 1: Results of paired t-test between the mechanical properties of the left and right humerus at 35-40% the distal humerus

	(n)	Left	Right	(p)
Polar second moments of area (J)	30	32.5917	46.4307	.0438*
Polar section modulus (Z)	31	12.6443	16.276	.0229*
Cortical area (CA)	31	8.82281	10.393	.0236*

Fig. 2: Results of paired t-test between the mechanical properties of the left and right humerus at 50-55% the distal humerus

	(n)	Left	Right	(p)
Polar second moments of area (J)	26	44.2868	82.7409	.0094*
Polar section modulus (Z)	27	15.1889	21.9851	.0145*
Cortical Area (CA)	28	11.2611	14.2291	.0112*

When the sample is divided by sex, the male sample at 35-40% the distal humerus is insignificant in all measures. This contrasts to the same male sample at 50-55% the distal humerus, in which each measure was found to be significant [Figs. 3 and 4].

Fig. 3: Results of paired t-test between the mechanical properties of the left and right humerus at 35-40% the distal humerus *in male specimens*

	(n)	Left	Right	(p)
Polar second moments of area (J)	14	34.1019	54.1019	.1094
Polar section modulus (Z)	15	14.1378	19.3174	.0541
Cortical Area (CA)	15	9.45095	11.5067	.0631

Fig 4: Results of paired t-test between the mechanical properties of the left and right humerus at 50-55% the distal humerus *in male specimens*

	(n)	Left	Right	(p)
Polar second moments of area (J)	14	65.1194	111.933	.0466*
Polar section modulus (Z)	14	19.4324	28.4324	.0428*
Cortical Area (CA)	14	12.5086	16.3896	.0267*

The female sample at 35-40% the distal humerus is insignificant in all measures. This holds true for the same female sample at 50-55% the distal humerus [Figs. 5 and 6].

Fig. 5: Results of paired t-test between the mechanical properties of the left and right humerus at 35-40% the distal humerus *in female specimens*

	(n)	Left	Right	(p)
Polar second moments of area (J)	9	17.0227	16.4952	.9186
Polar section modulus (Z)	9	7.36907	7.27084	.9466
Cortical Area (CA)	10	7.29138	7.18459	.8842

Fig. 6: Results of paired t-test between the mechanical properties of the left and right humerus at 50-55% the distal humerus *in female specimens*

	(n)	Left	Right	(p)
Polar second moments of area (J)	9	25.8135	24.895	.9072
Polar section modulus (Z)	9	10.1904	9.83716	.86
Cortical Area (CA)	9	8.63365	8.23916	.7767

Discussion and conclusion:

Based on cultural remains from the site of Hasanlu, archaeologists have posited a paradigm of sexual division of labor for this geographical region in this temporal range. Studies such as that of Dr. Molleson’s (1994) analysis of occupational markers for a nearby site of similar age supported this idea through the reconstruction of female daily life as devoted to the bimanual processing of food products like wheat and grain. Instead of occupational markers on the feet, spine and hands, this study looked to evaluate the lateralization of behavior in the upper arm of Hasanlu specimens using innovative morphometric techniques that quantify internal bone mechanics in order to discern this postulated sexual division of labor.

In the total population, the data showed a statistically significant difference in second moments of area, section moduli and the morphological feature of cortical bone thickness at both 35-40% and 50-55% the distal humerus. Therefore, there's evidence to suggest that, at the population level, handedness was indeed a feature.

When divided into categories by sex, only the male sample showed such statistical significance and then only in the 50-55% group. The female sample did not show a statistical difference at all. The fact that the male sample showed a significant difference only at 50-55% the distal humerus and not 35-40% the distal humerus may result from the interference of the deltoid tuberosity located at the midshaft of the human humerus, a muscle involved in the abduction of the arm from the body, instead of differences in internal mechanics or cortical bone thickness. This tentatively supports the archaeological reconstruction of males engaging in lateralized behaviors such as spear-throwing or normal farming duties while women pursued the equally rigorous but bilateral job of wheat grinding.

Thus the hypothesis of sexual division of labor at Hasanlu is supported through the mechanical and morphological data that demonstrate more bilateral female humeri than in lateralized males. Given the uncertain role of the deltoid tuberosity in the measure of the male sample, these results may be reevaluated through the lens of musculoskeletal markers in order to quantify the precise function of these characters on the mechanical properties of the bone.

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