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The impact of subsistence changes on humeral bilateral asymmetry in Terminal Pleistocene and Holocene Europe

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ABSTRACT

Analyses of upper limb bone bilateral asymmetry can shed light on manipulative behavior, sexual division of labor, and the effects of economic transitions on skeletal morphology. We compared the maximum (absolute) and directional asymmetry in humeral length, articular breadth, and cross-sectional diaphyseal geometry (CSG) in a large (n > 1200) European sample distributed among 11 archaeological periods from the Early Upper Paleolithic through the 20th century. Asymmetry in length and articular breadth is right-biased, but relatively small and fairly constant between temporal periods. Females show more asymmetry in length than males. This suggests a low impact of behavioral changes on asymmetry in length and breadth, but strong genetic control with probable sex linkage of asymmetry in length. Asymmetry in CSG properties is much more marked than in length and articular breadth, with sex-specific variation. In males, a major decline in asymmetry occurs between the Upper Paleolithic and Mesolithic. There is no further decline in asymmetry between the Mesolithic and Neolithic in males and only limited variation during the Holocene. In females, a major decline occurs between the Mesolithic and Neolithic, with resulting average directional asymmetry close to zero. Asymmetry among females continues to be very low in the subsequent Copper and Bronze Ages, but increases again in the Iron Age. Changes in female asymmetry result in an increase of sexual dimorphism during the early agricultural periods, followed by a decrease in the Iron Age. Sexual dimorphism again slightly declines after the Late Medieval. Our results indicate that changes in manipulative behavior were sex-specific with a probable higher impact of changes in hunting behavior on male asymmetry (e.g., shift from unimanual throwing to use of the bow-and-arrow) and food grain processing in females, specifically, use of two-handed saddle querns in the early agricultural periods and one-handed rotary querns in later agricultural periods.

1. Introduction

It is likely that human manipulative behavior changed significantly through the Terminal Pleistocene and Early Holocene in response to changes in foraging strategy (Binford, 1968, 1984; Flannery, 1969; Shott, 1993; Wright, 1994), the adoption of agriculture in the Early Holocene (Bender, 1978; Clark and Brandt, 1984; Wright, 1994; Larsen, 1995; Price, 2000; Milisauskas, 2002; Robb, 2013; Smith et al., 2015), and the intensification of agriculture during the Middle Neolithic and Copper Age (Sherratt, 1981, 1983; Milisauskas and Kruk, 2002; Greenfield, 2010). Other subsequent technological and social changes may also have affected behavioral use of the upper limb, including increasing urbanism (Schaub, 1982; Finkelstein, 1992; Issar and Zohar, 2004; Kristiansen and Larsson, 2005) and the beginning of metal ore mining and metallurgy (Craddock, 1995; Golden et al., 2001; Haaland, 2004; Johnston, 2008; Amzallag, 2009; Radivojević et al., 2010), as well as an increase in social complexity and occupational specialization (Clark and Parry, 1990; Cipolla, 1994; Johnson and Earle, 2000).

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One clue to human manipulative behavior in the past can be derived from assessments of handedness and upper limb bone bilateral asymmetry (e.g., Bridges, 1985, 1989, 1991; Constandse-Westermann and Newell, 1989; Fresia et al., 1990; Trinkaus et al., 1994; Churchill et al., 1996; Albert and Greene, 1999; Trinkaus and Churchill, 1999; Ledger et al., 2000; Stock and Pfeiffer, 2001, 2004; Weiss, 2003; Rhodes and Knüsel, 2005; Auerbach and Ruff, 2006; Marchi et al., 2006; Sládek et al., 2007; Kujanová et al., 2008; Stock et al., 2013; Macintosh et al., 2014; Sparacello et al., 2015). Bilateral skeletal asymmetry in the upper limb bones is significant among past and recent humans because the upper limb is directly influenced by the lateralized effect of manipulation and is free from the relatively symmetrical loading of the lower limbs associated with bipedal locomotion (Auerbach and Ruff, 2006). Bilateral asymmetry in the upper limb long bones has been found to be more pronounced in humeri than in ulnae and radii (Watson, 1974; Trinkaus et al., 1994; Bridges et al., 2000; Auerbach and Ruff, 2006). Upper limb bone lengths and articular breadths are less asymmetrical than diaphyseal breadths and measures of skeletal strength (i.e., cross-sectional geometric properties [CSG]; Ruff, 2008), possibly because they are less developmentally plastic (Jones et al., 1977; Ruff et al., 1994; Trinkaus et al., 1994; Sládek et al., 2007). In fact, it has been shown that CSG properties directly correspond with bilateral asymmetry in mechanical loading of the upper limbs, especially marked in athletes with different patterns of asymmetry in upper limb use (Jones et al., 1977; Roy et al., 1994; Ruff et al., 1994; Kontulainen et al., 2002; Shaw and Stock, 2009; Shaw, 2011). Moreover, studying bilateral skeletal asymmetry in CSG properties has other advantages for reconstructing manipulative behavior: comparing the right and left sides minimizes the effect of systemic non-mechanical factors such as diet, as well as variation in body size.

Bilateral asymmetry in the upper limb skeleton is shaped, at least in part, by handedness—that is, by the effect of the systematic preference of one hand for a particular task, where the dominant hand is associated with higher dexterity and skill acquisition (Perelle and Ehrman, 1994; Trinkaus et al., 1994; Steele, 2000; Raymond and Pontier, 2004; McManus, 2009; Shaw, 2011). Human handedness is strongly right-biased, with the proportion of left handers ranging from 1 to 11% based on certain behavioral measures such as different hand skill (Hardyck and Petrinovich, 1977) to 4–28% based on a more generalized motor skill test (Perelle and Ehrman, 1994: Table 1). It has also been shown that there is culturally mediated handedness variation influenced by factors such as gender differences (Perelle and Ehrman, 1994), education, and socio-economic status (Leiber and Axelrod, 1981; Annett and Kilshaw, 1983; Perelle and Ehrman, 1994; Raymond and Pontier, 2004), as well as the negative perception of left-handedness (Wile, 1934; Hardyck and Petrinovich, 1977).

However, handedness is not the only factor involved in the asymmetric use of the upper limb because maximum load is not always directly imposed on the dominant hand, i.e., the side with the greater degree of motor control. There are highly unilateral activities that directly subject the dominant hand to the highest mechanical loading, such as professional tennis playing (Jones et al., 1977; Kontulainen et al., 2002), and woodworking and warfare-related weapons training (Rhodes and Knüsel, 2005; Sparacello et al., 2011, 2015). However, there are also activities that employ both hands equally without respect to the dominant hand, such as grain grinding using a saddle quern (Sládek et al., unpublished results) and digging activities (Marshall, 1976; Lee, 1979; Ledger et al., 2000). Finally, there are activities involving reduced loading of the dominant hand because the dominant hand is used for better skill control compared to the non-dominant limb, which is used for stabilization (e.g., see the distribution of maximum muscle activity between the right and left hand during underhand spear thrusting in Shaw et al., 2012).

Based on the recent frequency of right-handedness and high frequency of right-handed individuals in the Upper Pleistocene (see review bilateral asymmetry among Neanderthals and Early Upper Paleolithic humans in Trinkaus et al., 1994; Churchill and Formicola, 1997), we can expect that right-biased bilateral hand asymmetry dominated Terminal Pleistocene and Holocene Europe. However, the degree of bilateral asymmetry need not have been constant or always different from zero, especially when the separate subsistence roles of males and females are considered. Changes in hunting strategy observed during the Terminal Pleistocene, e.g., from “short-distance” to “long-distance” killing, and including more exploitation of small game and other local resources (Flannery, 1969; Binford, 1984; Churchill, 1993; Churchill et al., 1996; Churchill and Rhodes, 2009), might be expected to result in a more significant change in upper limb use among males than among females, given that hunting was primarily a male activity (Bridges, 1985; Binford, 2001; Kelly, 2013; Sadvari et al., 2015). The

Table 1
Summary of the study sample by temporal period and sex.[a]

	Abbrv.	C^{14} BP[b]	logYearsBP[c]	Males[d]			Females[d]			Total[d]		
				Right	Left	Paired	Right	Left	Paired	Right	Left	Paired
Early Upper Paleolithic	EUP	33,400–26,400	4.52–4.42	8	10	8	5	8	5	13	18	13
Late Upper Paleolithic	LUP	21,900–11,350	4.34–4.06	12	12	10	5	6	5	17	18	15
Mesolithic	Meso	10,500–6050	4.02–3.77	24	25	20	14	18	11	38	43	31
Neolithic	Neol	7300–4600	3.86–3.66	77	77	61	54	54	47	131	131	108
Copper Age	CopA	4600–3950	3.66–3.60	42	47	31	30	28	22	72	75	53
Bronze Age	BA	4350–2950	3.64–3.47	102	98	79	82	87	71	184	185	150
Iron Age	IA	2250–1700	3.35–3.23	64	64	45	63	55	50	127	119	95
Roman	Roman	1900–950	3.28–3.22	39	38	32	40	37	32	79	75	64
Early Medieval	EMed	1300–950	3.13–2.98	142	133	111	95	90	73	237	223	184
Late Medieval	LMed	925–550	2.97–2.74	204	211	172	187	175	146	391	386	318
Recent	Recent	320–10	2.51–1.00	129	135	115	90	86	81	219	221	196
Total				843	850	684	665	644	543	1508	1494	1227

[a] The number of individuals indicates the maximum individuals preserved in each period. The number of individuals varies according to preservation of the respective parameter. The final number of individuals used in each analysis is provided in the results and summary tables. For details about sample sizes and sites and European regions by temporal periods included in the studied sample see Table S1.
[b] Range of the maximum and minimum calibrated C^{14} BP date for period.
[c] Range of the minimum and maximum natural logarithm of the C^{14} BP date.
[d] Maximum number for right humerus (Right), left humerus (Left), and individuals with both right and left sides preserved (Paired) by sex. The preservation is given as the number of total preserved individuals with humeral maximum length (HML).