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Patterns of humeral asymmetry among Late Pleistocene humans

L'asymétrie de la diaphyse humérale dans les populations humaines au Pléistocène récent

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ABSTRACT

Human humeral diaphyseal asymmetry in midshaft and mid-distal rigidity is assessed through the Late Pleistocene in samples of late archaic (Neandertal) and early modern humans. It is considered with respect to directionality (handedness), levels of asymmetry, body size and sexual differences. The overall Late Pleistocene sample indicates a right-handed preference in frequencies (right: 74.8%, left: 15.0%, ambiguous: 10.3%), which are similar to those of recent human samples. Average levels of humeral asymmetry are elevated relative to Holocene samples through all but the small Middle Paleolithic modern human and eastern Eurasian late Upper Paleolithic samples. Humeral asymmetry is especially high among the males relative to the females, and the possibility of a division of labor between uni-manual tasks (mostly male) and bi-manual tasks (mostly female) is considered. At the same time, there is a general pattern of increased asymmetry with larger body size, but it remains unclear to what extent it reflects body size versus sexual effects on bilateral humeral loading. There do not appear to have been substantial changes in humeral asymmetry through time, indicating a continuity of similar manual behavioral patterns through the Late Pleistocene, despite considerable changes in technology through the Late Pleistocene.

RÉSUMÉ

Mots clés :
Humérus
Néandertaliens
Hommes modernes
Propriétés géométriques de section
Diaphyse

L'asymétrie de la rigidité de la partie centrale et mi-distale de la diaphyse humérale est estimée sur un échantillon d'humains archaïques et modernes datés du Pléistocène supérieur. Les résultats sont discutés en termes de dominance, de degré d'asymétrie, de dimensions corporelles et de différences sexuelles. L'échantillonnage dans son ensemble présente une claire dominance de « droitiers », avec des fréquences similaires à celles des échantillons actuels (dominance à droite : 74,8 %, à gauche : 15,0 %, résultat ambigu : 10,3 %). Par rapport aux échantillons comparatifs holocènes, le degré d'asymétrie est élevé

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pour la plupart des groupes, à l'exception de deux petits sous-échantillons, les hommes anatomiquement modernes du Paléolithique moyen et les sujets d'Asie datés de la fin du Paléolithique supérieur. Ce degré d'asymétrie est particulièrement élevé chez les hommes comparativement aux femmes, et l'existence d'une division du travail pour les tâches unimanuelles (plutôt masculines) et les tâches bimanuelles (plutôt féminines) est discutée. Toutefois, une corrélation positive entre asymétrie et taille est observée. Il est ainsi difficile de distinguer l'influence de la division sexuelle du travail de celle de l'allométrie sur nos résultats. L'étude ne montre pas de variation diachronique significative, malgré des évolutions technologiques importantes, et semble ainsi indiquer la persistance de comportements similaires au cours du Pléistocène récent.

1. Introduction

In the past couple of decades, there has been considerable interest in human humeral diaphyseal asymmetry from bone biology and anthropological perspectives (cf. Auerbach and Ruff, 2006). Earlier studies (e.g., Jones et al., 1977; Ruff and Jones, 1981; Trinkaus et al., 1994) were primarily concerned with using humeral asymmetry to document potential degrees of diaphyseal plasticity, given that each individual serves as its own (bilateral) control (see also Ireland et al., 2013; Sakaue, 1997; Shaw and Stock, 2009; Warden et al., 2009). Involved in these analyses was the documentation of an extant human pattern of upper limb unilateral (primarily right-side) dominance through the genus *Homo* (e.g., Shaw, 2011; Stock et al., 2013; Trinkaus et al., 1994; Weaver et al., 2001), which complemented inferences from lithic technology, labial striations, and cerebral asymmetry (Bermúdez de Castro et al., 1988; Frayer et al., 2012; Holloway, 1981; Poza-Rey et al., 2015; Toth, 1985; Uomini, 2011; Volpato et al., 2012; Willman, in press). These considerations have been joined by assessments of humeral asymmetry as related to athletic activities (Ireland et al., 2013; Shaw and Stock, 2009; Trinkaus et al., 1994; Warden et al., 2009) and changes in subsistence activities and weaponry (e.g., Bridges, 1991; Churchill et al., 2000; Cowgill, 2008; Fresia et al., 1990; Knüsel, 2000; Ogilvie and Hilton, 2011; Rhodes and Knüsel, 2005; Sparacello et al., 2011, 2015; Weiss, 2009), as well as comparisons of past human samples to recent industrialized ones (e.g., Sakaue, 1997; Stock et al., 2013; Trinkaus et al., 1994). In addition, humeral asymmetry has been employed to identify and assess the effects of upper limb abnormalities, as related to bone plasticity, functional impairment and compensatory hypertrophy (e.g., Churchill and Formicola, 1997; Cowgill et al., 2015; Trinkaus, 1983, 2015; Trinkaus et al., 1994). Many of these analyses have also considered degrees of sexual dimorphism in humeral diaphyseal asymmetry. However, only some of them (e.g., Bridges, 1991; Churchill et al., 2000; Ogilvie and Hilton, 2011; Sládek et al., 2016; Weiss, 2009) have done so explicitly with respect to sexual division of labor. From these analyses, an appreciation has emerged for the potential extent of humeral diaphyseal asymmetry (under normal and pathological conditions), the patterns of handedness in *Homo*, and the difficulties of associating levels and patterns of asymmetry with specific activities.

In this context, the patterns of humeral asymmetry in Late Pleistocene humans have been variously described, with an emphasis on elevated levels of asymmetry among the Neandertals (Shaw et al., 2012; Trinkaus and Churchill, 1999; Trinkaus et al., 1994, 2014) (no other archaic *Homo* groups provide associated right-left humeral diaphyseal portions suitable for biomechanical analysis; KNM-WT 15000 retains only one humerus, and the Sima de los Huesos ones are unassociated). There have been variable assessments of the levels and patterns of change in humeral asymmetry through the Upper Paleolithic (Churchill and Formicola, 1997; Shackelford, 2007; Sládek et al., 2016; Trinkaus, 2015). Additionally, there have been inferences regarding the Late Pleistocene sexual division of labor, as inferred from humeral diaphyseal asymmetry (Churchill et al., 1996; Sládek et al., 2016), as well as humeral enthesopathies (Villotte and Knüsel, 2014; Villotte et al., 2010), with variable results. These various results could be due to sampling differences from an already small sample of Pleistocene fossils or caused by different pooling of individuals in geographical regions.

With these considerations and the results of previous studies in mind, we have reassessed the levels and patterns of adult humeral diaphyseal asymmetry among Late Pleistocene foragers. To the extent possible, we have maximized the available samples of paired humeri, considering the variation in asymmetry with respect to time period, broad geographical regions, body size and sex. The comparisons involve Middle Paleolithic late archaic and early modern humans from western Eurasia and especially Upper Paleolithic modern humans from Eurasia and North Africa. These analyses employ diaphyseal bone rigidity as a structural property reflecting functional adaptations most likely due to subsistence-induced activity patterns, and they should advance previous assessments in terms of increased sample sizes, a consistent methodology, and the incorporation of both body size and sex into the evaluations.

2. Materials and methods

The primary comparative data derive from four samples of paired right and left humeri of Late Pleistocene mature individuals and one late adolescent (Dolní Věstonice 14) (supplementary material, Tables S1–S5). The first two samples are of Marine Isotope Stage (MIS; Railsback et al., 2015) 5 to 3 Middle Paleolithic late archaic (Neandertals, $n = 8$) and early modern (MPMH, $n = 4$) humans from western Eurasia. The second two samples are of Upper Paleolithic *sensu lato* modern humans from Eurasia and North Africa; they are separated temporally at the last glacial maximum into Early (EUP; MIS 3a) and Late (LUP; MIS 2) Upper Paleolithic samples. The EUP ($n = 22$) sample derives predominantly from western Eurasia, with the addition of Nazlet Khater 2 and Tianyuan 1. The larger LUP sample ($n = 73$) is subdivided into samples from West Eurasia ($n = 26$), North Africa ($n = 37$), and East Eurasia ($n = 10$). Although there is evidence for varying degrees of population discontinuity through the Late Pleistocene, especially for the western Eurasian samples (Brewster et al., 2014; Fu et al., 2013, 2015; Posth et al., 2016; Trinkaus, 2007), the level of plasticity in humeral diaphyses is such that the variation is primarily influenced by the individuals' mechanical environments, and populational issues are not relevant to the analysis here.

The data (supplementary material, Tables S1 to S5) derive principally from personal research of the authors, with additional cross-sectional data from Churchill (1994), Crevecoeur (2008), Kimura and Takahashi (1992), Stock et al. (2005), and Vercellotti et al. (2008). A minority of the linear osteometrics (supplementary material, Table S1) come from published descriptions (Mallegni and Fabbri, 1995; Matiegka, 1938; McCown and Keith, 1939). Individuals with marked upper limb abnormalities are not included, but specimens with less pronounced lesions are considered (see SI Section II). Data from additional unpaired humeri are employed for the secondary assessment of humeral hypertrophy (supplementary material, Figs. S1 and S2) and cross-sectional geometry predictions (supplementary material, Tables S1 to S5).

The analysis of humeral diaphyseal asymmetry employs the cross-sectional geometry (CSG) at specified percentages (35% and 50%) of bone length, using the polar moment of area (J or Ip, in mm^4) as a measure of overall bending and torsional rigidity (Ruff, 2000). The method is based on the widely accepted notion that bone tissue optimizes to its mechanical environment so as to maintain physiological strains within the normal limits ("Wolff's Law", better referred to as "bone functional adaptation"; Pearson and Lieberman, 2004; Ruff et al., 2006). Bone tissue is deposited in the shaft's cross-section where mechanical loads require it to prevent strains in excess of the elastic limit, whereas below a certain strain threshold, the bone tissue is reabsorbed. By analyzing the cross-sections of the diaphysis, it is therefore possible to obtain variables that correlate with the bending moments (second moments of area: Ii) and overall torsional rigidity (polar moment of area: J or Ip) of the diaphysis. Bending moments are influenced by bone length and body mass of the individual; analyzing asymmetry is expected to factor out those influences, allowing for the study of a variable that is mainly determined by the differential use of the dominant arm.

The asymmetry data used here therefore consist of polar moments of area of the mid-distal (35%) and midshaft (50%) right and left humeri. The 35% sections provide a better estimate of minimum rigidity of the diaphysis; the 50% sections provide an overall assessment of midshaft rigidity and a larger sample (97 at 50% vs. 85 at 35%; 75 fossils provide right and left values for both diaphyseal positions; 10 provide only the 35% measures, and 22 furnish only the 50% ones). Amounts of asymmetry at the two diaphyseal levels are highly correlated across the Late Pleistocene samples for those individuals providing all four polar moments of areas ($r = 0.877$, $n = 75$), the slope is close to one (0.988; 95% CI: 0.86–1.11) and the intercept is insignificantly different from zero (1.68; 95% CI: −3.74–7.10).

The cross-sectional parameters were obtained, depending on the available technology, from CT scans of the humeri, subperiosteal molds plus biplanar radiography for cortical thicknesses, ellipse formulae employing external diameters and cortical thicknesses, and scaled photographs of fossilization breaks (O'Neill and Ruff, 2004). In addition, in order to include humeri now lost (Předmosti), ones with internal damage, or for which appropriate radiography is not available, one of two approaches was used: cross-sectional parameters were computed from the subperiosteal contour modeled as a solid section, and the CSG measures were computed based on recent human regressions (Sparacello and Pearson, 2010) or midshaft second moments of area were estimated from maximum and minimum subperiosteal diameters using a least squares multiple regression based on a pooled sample of Late Pleistocene humeri (supplementary material, Table S4a). The different techniques for obtaining cross-sectional parameters provide consistent results that are well within the variation produced by the variable preservation of the fossil remains, and can be therefore pooled (cf. Macintosh et al., 2013; O'Neill and Ruff, 2004; Sparacello and Pearson, 2010; Stock, 2002; supplementary material, Table S4a).

Asymmetry was computed as: (maximum−minimum)/minimum, expressed as a percentage (Trinkaus et al., 1994), and hence it represents an absolute (non-directional) asymmetry. Asymmetry was calculated from absolute values of J (i.e. not standardized by body size; Ruff, 2000), because any prior size standardization would be elided. However, in order to assess whether levels of asymmetry are related to variance in body size, the dominant arm polar moments of area were assessed against those of the non-dominant arm, in which a slope of one would indicate no change in asymmetry with size. In addition, since the polar moments of area reflect both body size and humeral hypertrophy, asymmetry values were assessed against estimated body masses for a subset of specimens; body mass was estimated in all cases from femoral head diameters following Ruff (2010).

It is possible to assess the sex of 103 of the individuals, and the majority of the sex determinations (74) were based on pelvic remains (supplementary material, Table S1). The degrees of humeral asymmetry are therefore considered across the samples with the sexes pooled and separated. The total sample yielded 56 males, 47 females, and 4 of uncertain sex. The EUP and West LUP samples have more males than females (14:7 and 16:10), the reverse applies to the East Eurasian sample (2:8), and the others are essentially equal in males versus females (3:2, 2:2 and 19:18). Yet, the female-male proportions of each individual sample and of the pooled total sample are not significantly different from 50:50 (binomial $P = 0.431$ for the total sample).

3. Results

3.1. Asymmetry directionality

In the pooled Late Pleistocene sample ($n = 107$), 96 individuals have polar moment of area asymmetries > 5% and hence are sufficiently asymmetrical to indicate side dominance (following Shaw, 2011). Of those 96 paired humeri, 80 (83.3%) have stronger right humeri (hence right-dominance), and 16 (16.7%) are left side dominant. Among the remaining individuals, seven have asymmetries < 5%, and four have contrasting asymmetry directions > 5% between the 35% and the 50% cross-sections.

3.2. Levels of asymmetry

The distributions of levels of humeral diaphyseal asymmetry (Fig. 1) for the six Late Pleistocene samples range from near zero (symmetry) to > 100% (dominant humerus with at least twice the rigidity of the non-dominant one). In the midshaft, three of the Eurasian samples have high average asymmetry (> 30%; supplementary material, Table S6) and show largely continuous distributions up to ≈ 80% with two high outliers (the La Quina 5 Neandertal and the West Eurasia LUP Arene Candide 2); the small MPMH sample has lower values. Variations in humeral asymmetry among the Neandertal, MPMH, EUP and West Eurasia LUP samples are not statistically significant after multiple comparison corrections (supplementary material, Table S6). In the North African sample, and especially the East Eurasian one, the levels of midshaft asymmetry are generally lower, but the former nonetheless extends up to ≈ 60%. The North African sample is significantly less lateralized than the West Eurasia LUP one ($P < 0.05$), while the East Eurasia sample is less asymmetric than both the Neandertals ($P < 0.05$) and the West Eurasia LUP sample ($P < 0.01$) (supplementary material, Table S6).

In the mid-distal comparison, the pattern is similar, with the higher values present in all but the MPMH and East Eurasia LUP samples (Fig. 1; supplementary material, Table S7). The North African mid-distal humeri have several values ≥ 60%, whereas similarly high values are absent from their midshafts. In this comparison, one Neandertal (Spy 2), three each of the EUP and West Eurasia LUP samples and one North Africa LUP individual (Afalou 27) have asymmetries ≈ 100%. In the mid-distal section, variation in humeral asymmetry among the time periods are non-significant (with multiple comparison correction), except for the East Eurasia sample, which is significantly less asymmetric than the EUP and West Eurasia LUP ones (supplementary material, Table S7).

Variations across the samples by sex are generally non-significant after multiple comparison correction, largely due to small sample sizes (Fig. 4; supplementary material, Tables S6 and S7). Indeed, the only significant comparison at $P < 0.05$ is between the two largest samples, the midshaft West Eurasia ($n = 14$) and North Africa ($n = 19$) LUP males, with the latter substantially less asymmetric on average.

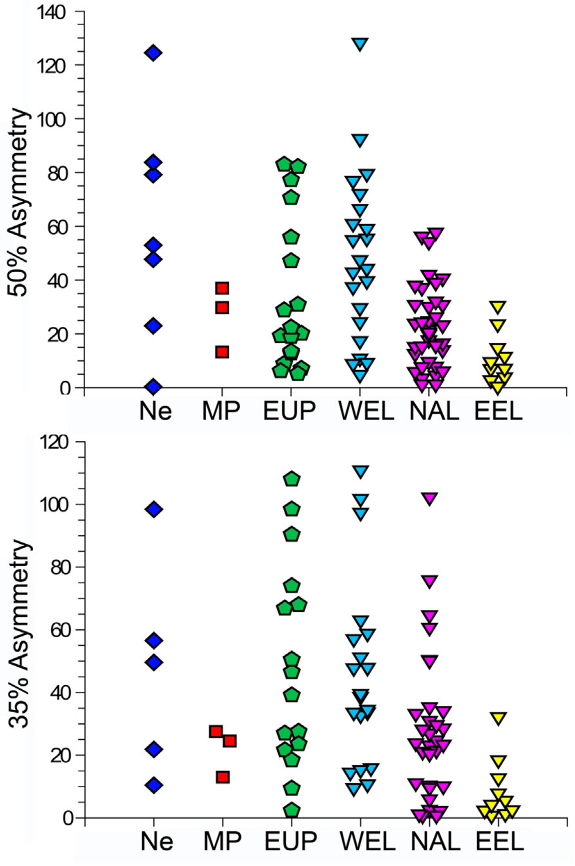

Fig. 1. Percent humeral diaphyseal polar moment of area asymmetry values for Late Pleistocene humans, for the mid-distal shaft (35%) and midshaft (50%). Sexes are pooled. Ne: Neandertals; MP: Middle Paleolithic modern humans; EUP: Early Upper Paleolithic humans; WEL: West Eurasia Late Upper Paleolithic humans; NAL: North Africa Late Upper Paleolithic humans; EEL: East Eurasia Late Upper Paleolithic humans.

Fig. 1. Valeurs du pourcentage d'asymétrie du second moment polaire d'aire de la section diaphysaire humérale à 35 % et 50 %. Les sexes sont regroupés. Ne : Néandertaliens ; MP : Hommes modernes du Paléolithique moyen ; EUP : Hommes modernes du Paléolithique supérieur ancien ; WEL : Hommes modernes du Paléolithique supérieur récent d'Eurasie de l'Ouest ; NAL : Hommes modernes du Paléolithique supérieur récent d'Afrique du Nord ; EEL : Hommes modernes du Paléolithique supérieur récent d'Eurasie de l'Est.

3.3. Asymmetry and size

In addition to variation with respect to time and space, plots of asymmetry that reflect humeral diaphyseal size (Fig. 2) and body size (Fig. 3) show an increase in asymmetry with larger dimensions across the Late Pleistocene samples. In the distribution of dominant versus non-dominant polar moments of area (Fig. 2), the mid-distal least squares slope of 1.37 (95% CI: 1.11–1.54) and the midshaft least squares slope of 1.26 (95% CI: 1.11–1.42) are both significantly > 1 (a slope of 1 indicating no change with size) (supplementary material, Table S8). In the comparison of asymmetry to estimated body mass (Fig. 3), the

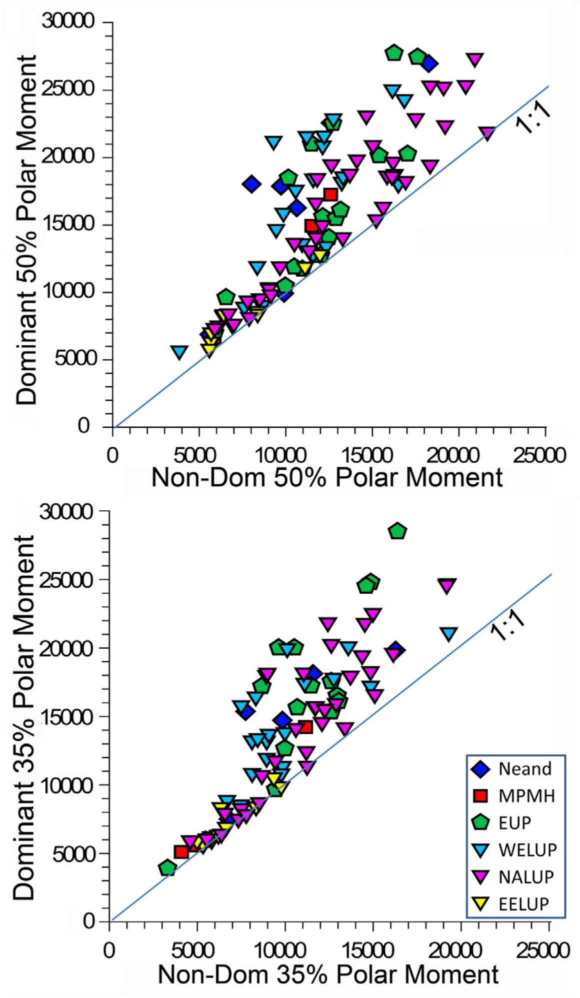

Fig. 2. Bivariate plots of dominant humeral polar moment of area versus the one from the non-dominant arm for Late Pleistocene humans, for the mid-distal shaft (35%) and midshaft (50%). Sexes are pooled. Neand: Neandertals; MPMH: Middle Paleolithic modern humans; EUP: Early Upper Paleolithic humans; WELUP: West Eurasia Late Upper Paleolithic humans; NALUP: North Africa Late Upper Paleolithic humans; EELUP: East Eurasia Late Upper Paleolithic humans. The 1:1 line represents symmetry.

Fig. 2. Graphiques bivariés du second moment polaire d'aire de la section diaphysaire humérale à 35 % et 50 % pour le côté dominant en fonction du côté non dominant. Les sexes sont regroupés. Neand: Néandertaliens ; MPMH : Hommes modernes du Paléolithique moyen ; EUP : Hommes modernes du Paléolithique supérieur ancien ; WELUP : Hommes modernes du Paléolithique supérieur récent d'Eurasie de l'Ouest ; NALUP : Hommes modernes du Paléolithique supérieur récent d'Afrique du Nord ; EELUP : Hommes modernes du Paléolithique supérieur récent d'Eurasie de l'Est. La droite 1:1 représente la symétrie.

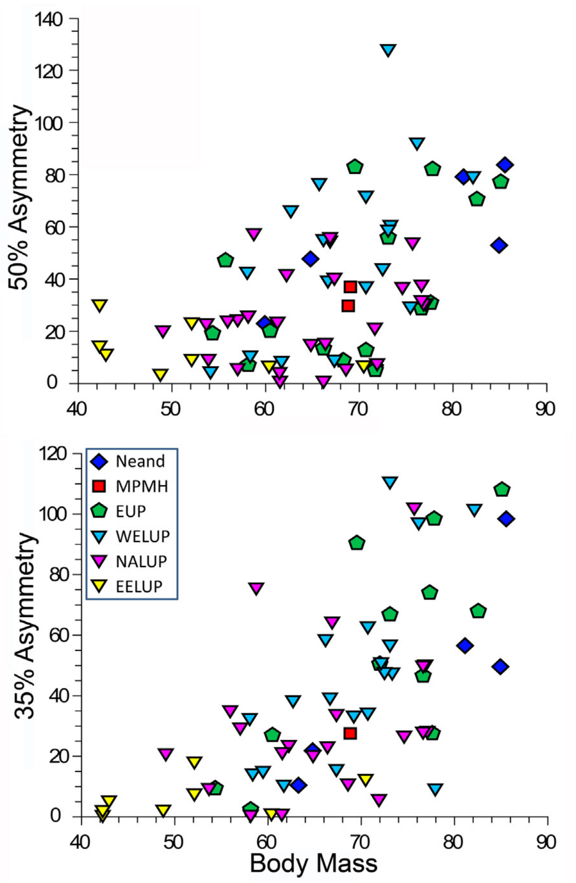

Fig. 3. Bivariate plots of percent humeral diaphyseal polar moment of area asymmetry values versus estimated body mass (in kg), for the mid-distal shaft (35%) and midshaft (50%). Sexes are pooled. Sample abbreviations as on Fig. 2.

Fig. 3. Graphiques bivariés du pourcentage d'asymétrie du second moment polaire d'aire de la section diaphysaire humérale à 35 % et 50 % en fonction de la masse corporelle (en kg). Les sexes sont regroupés. Voir la Fig. 2 pour les abréviations des échantillons.

mid-distal and midshaft least squares slopes of 1.90 and 1.36 (95% CIs: 1.34–2.45 and 0.83–1.90, respectively) are significantly >0 (a slope of 0 indicating no change with size) (supplementary material, Table S8). In a comparison of asymmetry to humeral length, the level of asymmetry increases slightly for the mid-distal level but not for the midshaft (supplementary material, Table S8).

Therefore, as humeral diaphyseal dimensions and body mass (but not especially humeral length) increased across these pooled samples, the level of asymmetry generally augmented. An increase in asymmetry with size, however, is absent or less pronounced in the individual regional samples, in part due to small sample sizes. Yet, these comparisons should be sufficient to open the question as to what extent body size, in addition to other factors (such as different upper limb loading patterns across regions and by sex), might be influencing levels of humeral asymmetry.

3.4. *Sexual differences in asymmetry*

The plot of humeral asymmetry by sample and sex (Fig. 4) provides lower average female levels of asymmetry for all except the small East Eurasia LUP sample. Across the pooled Late Pleistocene sample, the male and female samples are highly significantly different (Mann-Whitney U $P < 0.0001$ for 35% and 50%), although only the West Eurasia and North Africa LUP male-female 35% asymmetry values are significantly different after a multiple comparison correction (the EUP 35% comparison is close to the $P = 0.05$ level) (supplementary material, Tables S6 and S7).

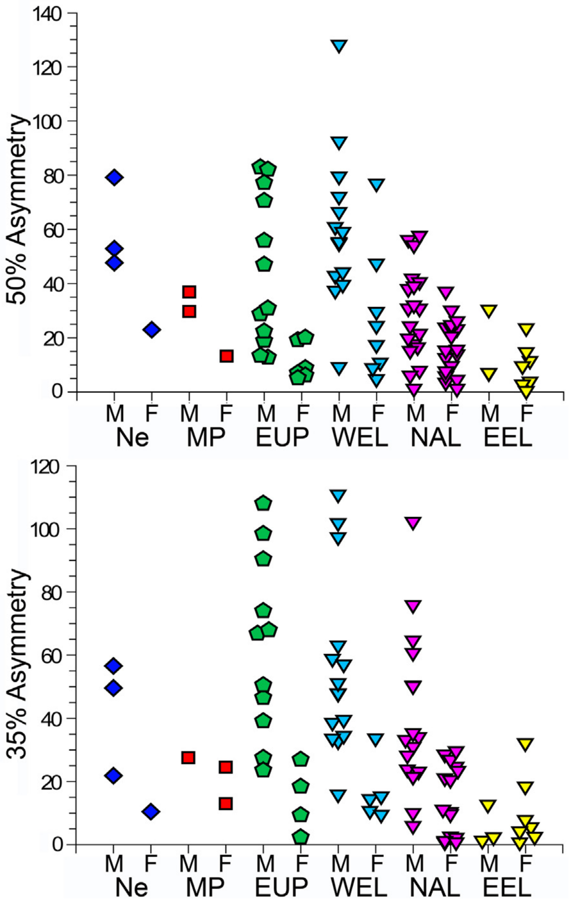

Fig. 4. Percent humeral diaphyseal polar moment of area asymmetry values, for the mid-distal shaft (35%) and midshaft (50%), by regional/temporal sample and by sex (M vs. F). Abbreviations as in Fig. 1.
Fig. 4. Valeurs du pourcentage d'asymétrie du second moment polaire d'aire de la section diaphysaire humérale à 35 % et 50 %, par région, période et sexe. Voir la Fig. 1 pour les abréviations concernant les échantillons.

When the samples are pooled and the sexes are plotted separately, as either dominant versus non-dominant polar moments of area (Fig. 5) or asymmetry values versus body mass (Fig. 6), the least squares slopes variably indicate increases in asymmetry with size (supplementary material, Table S8). In the dominant/non-dominant comparisons, only the female 35% section indicates a within-sex change in asymmetry with size, and the 95% CI (1.04–1.24) extends close to one. In the more appropriate asymmetry/body mass comparison, the females have little asymmetry change with size (35%: $P=0.059$; 50%; $P=0.644$), but the males (despite considerable scatter) show a significant increase in humeral asymmetry with larger body size at both diaphyseal locations (95% CIs: 35%: 0.70–2.95, $P=0.002$; 50%: 0.34–2.35; $P=0.010$).

4. Discussion

These comparisons across samples of Late Pleistocene human humeri largely conform to the patterns of humeral asymmetry previously documented (e.g., Shaw, 2011; Stock et al., 2013; Trinkaus et al., 1994; Weaver et al., 2001). Yet, they modify some of the former inferences and provide further insight into possible implications.

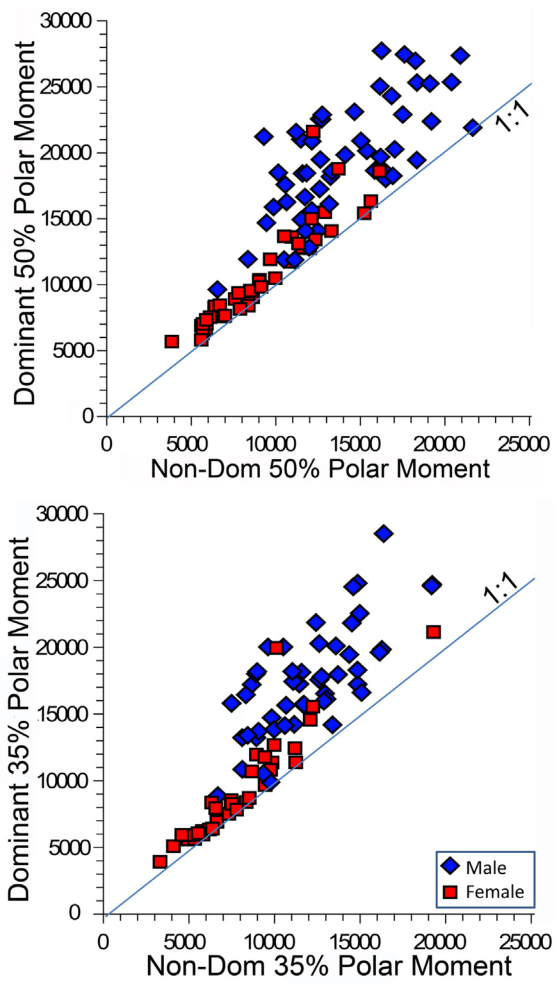

Fig. 5. Bivariate plots of dominant humeral polar moment of area versus the one from the non-dominant arm for males and females for the pooled Late Pleistocene human sample, for the mid-distal shaft (35%) and midshaft (50%). The 1:1 line represents symmetry.
Fig. 5. Graphiques bivariés du second moment polaire d'aire de la section diaphysaire humérale à 35 % et 50 % pour le côté dominant en fonction du côté non dominant d'individus masculins et féminins de l'ensemble de l'échantillon. La droite 1:1 représente la symétrie.

4.1. Handedness

The frequencies for right versus left versus ambiguous side dominance (74.8%, 15.0% and 10.3%, respectively) fall well within expected ranges across extant human samples (Cavanagh et al., 2016; Raymond and Pontier, 2004). As noted previously (see above), patterns of lateralization documented so far from multiple indicators through the genus *Homo* are indistinguishable from those of living humans.

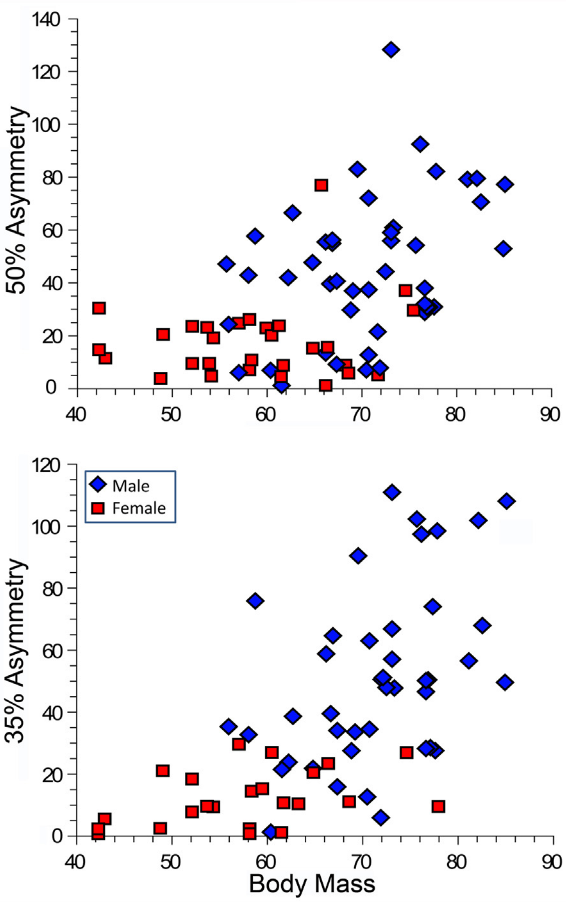

Fig. 6. Bivariate plots of percent humeral diaphyseal polar moment of area asymmetry values versus estimated body mass (in kg) for males and females for the pooled Late Pleistocene human sample, for the mid-distal shaft (35%) and midshaft (50%).

Fig. 6. Graphiques bivariés du pourcentage d'asymétrie du second moment polaire d'aire de la section diaphysaire humérale à 35 % et 50 % en fonction de la masse corporelle (en kg) d'individus masculins et féminins de l'ensemble de l'échantillon.

4.2. Levels of asymmetry

Our data, using a larger dataset of Middle and Upper Paleolithic fossil humans, further document that high levels of humeral asymmetry are common in the Late Pleistocene, as shown in previous studies (Churchill, 1994; Churchill et al., 1996, 2000; Holt et al., 2000; Shackelford, 2007; Trinkaus, 2015). Asymmetry is especially high among males (except for East Eurasian LUP humans) and generally reaches or surpasses 30% on average, with individual values ranging up to more than 100%. For comparison, recent human individual values generally range up to ≈20–40%, and most sample means are < 20% (including recent human foragers); agricultural samples generally show levels of asymmetry around 10%, as do industrial sedentary samples (Ogilvie and Hilton, 2011; Shaw and Stock, 2009; Sládek et al., 2016; Sparacello et al., 2011; Stock et al., 2013; Trinkaus et al., 1994; Weiss, 2009). Therefore, it is not only the Neandertals that developed marked humeral asymmetry, but individuals in samples spanning the substantial technological and adaptive changes through the Middle and Upper Paleolithic.

Modern athletes with unilateral arm loading frequently reach levels of humeral diaphyseal asymmetry similar to these Late Pleistocene humans (Haapasalo et al., 2000; Ireland et al., 2013; Shaw and Stock, 2009; Trinkaus et al., 1994; Warden et al., 2009), which has led to suggestions that frequent spear throwing (with or without a spear thrower) influenced the high level of asymmetry in Pleistocene humans (Churchill and Rhodes, 2009; Churchill et al., 2000). This activity is not only strenuous during hunting but requires continuous training during development for both strength and aim (Cattelain, 1997; Rhodes and Knüsel, 2005; Whittaker and Kamp, 2006). The high and intermittent loading rates correspond to the pattern that best stimulates osteogenic response (Burr et al., 1996, 2002; Robling et al., 2002). Patterns of humeral enthesopathies in at least the Upper Paleolithic (Villotte and Knüsel, 2014) further support the importance of throwing among these Late Pleistocene humans. However, other activities may have contributed to the differential hypertrophy of the humeri through the Late Pleistocene, since repetitive domestic activities such as scraping involve asymmetric recruiting of upper limb muscles (Shaw et al., 2012).

4.3. Asymmetry and size

Given the increases in humeral asymmetry with humeral diaphyseal and body dimensions, and the ranges of body sizes evident on Figs. 2 and 3, body size needs to be considered in interpretations of humeral asymmetry. In particular, could the low levels of asymmetry in the East Eurasia LUP sample be due to their generally small body dimensions (Baba and Endo, 1982; Shackelford and Demeter, 2012)? Could body size account for the moderately lower asymmetry level of much of the North Africa LUP sample compared to the western Eurasian ones, as well as of the MPMH sample (Shackelford, 2007; Trinkaus et al., 2014)? Furthermore, given the Late Pleistocene sexual dimorphism in body size (Fig. 6), it raises the question as to how much of the perceived sexual differences in humeral asymmetry are secondarily due to larger average body mass in males.

Yet, a significant correlation between body mass and asymmetry is found principally in the pooled male sample (supplementary material, Table S8), and it is present only in the mid-distal section of West Eurasian LUP males when the samples are separated by region/period and sex. Given variation in body size across the Late Pleistocene subsamples and between the sexes, it remains uncertain to what extent regional/temporal, as well as sexual, differences in upper limb differential loading reflect behavioral patterns *per se* versus a combination of a size effect and behavioral variation.

4.4. Sexual differences in asymmetry

Given these considerations, the differences between male and female asymmetry values in most of the Late Pleistocene samples, and the differences in the male and female distributions and slopes when humeral asymmetry is compared to body mass, it is likely that some of the variation is due to differential bilateral loading of the humeri between female and male Late Pleistocene humans. In this context, it needs to be kept in mind that, although high levels of asymmetry result from markedly differential loading of the dominant arm, low levels of asymmetry can be the product of either general gracility or bilateral hypertrophy from bi-manual activities (Ogilvie and Hilton, 2011; Shaw and Stock, 2009). Because the Late Pleistocene pattern occurred in the context of no significant sexual differences in humeral diaphyseal hypertrophy once scaled to body mass and humeral length (SI Section V), it is likely that the average sexual differences were due as much to elevated bilateral loading in individuals with low asymmetry as to differentially increased loading of the dominant arm in those with high asymmetry.

Pleistocene female humeral asymmetry in diaphyseal rigidity has been considered previously to be high (Churchill, 1993), suggesting that Paleolithic females, like males, were habitually engaged in activities (such as throwing) that generated high bending stresses on the dominant limb (Holt et al., 2000). Sexual division of labor in the use of throwing weapons is nearly universal among modern hunter-gatherers (Murdock and Provost, 1973; Testart, 1986; Watanabe, 1968; Wood and Eagly, 2002). However, among the Agta of the Philippines, women regularly hunted (Estioko-Griffin and Griffin, 1981; Goodman et al., 1985), and among high-latitude hunter-gatherers, given the importance of large game acquisition, widows and their daughters could become habitual hunters (Briggs, 1970; Jenness, 1922; Landes, 1938). Nevertheless, the inference that a sexual division of labor might have been less marked in the Pleistocene has been questioned by the male bias of unilateral medial epicondyle enthesopathies suggesting throwing (Villotte and Knüsel, 2014; Villotte et al., 2010) and by sexual differences in humeral diaphyseal asymmetry in a small European LUP sample (Sládek et al., 2016).

Some of these sexual differences in humeral asymmetry may be secondary to sexual differences in body size. Yet, differences in average asymmetry between male and female tennis players (females: ≈40%, males: ≈75%; Haapasalo et al., 2000; Jones et al., 1977) suggest that other physiological factors might play a role in the development of extreme levels of structural adaptations between the sexes (see, for example, Stini, 1969; Stinson, 1985). However, the contrasts in the male-female distributions relative to body size appear to be substantial enough to suggest the presence of a sexual division of labor affecting the upper limb among most of these Late Pleistocene groups.

It is possible to hypothesize behavioral scenarios to account for these patterns, as with assessments of sex differences in humeral asymmetry in Holocene archeological samples (e.g., Marchi et al., 2006; Ogilvie and Hilton, 2011; Sládek et al., 2016; Sparacello and Marchi, 2008; Weiss, 2009), recognizing that, despite the average sex differences, there is considerable overlap in the sex-specific distributions. Females could have been differentially engaged in bi-manual processing activities, although currently identified Paleolithic grindstones appear to be uni-manual ones (Revedin et al., 2010). Males could have been more commonly involved in uni-manual processing, such as scraping (Shaw et al., 2012) or throwing weapons (Villotte and Knüsel, 2014; Villotte et al., 2010). Although it is tempting to explain patterns of asymmetry (and sexual dimorphism in this trait) throughout the Pleistocene to the use of throwing spears (not thrusting spears; Shaw et al., 2012), this inference would have to account for similarly high levels of asymmetry through the Late Pleistocene despite the evolution of hunting weapons from heavy wooden and lithic tipped spears (Middle Paleolithic) to lighter throwing spears (early Upper Paleolithic) to spear throwers and light spears (late Upper Paleolithic).

In this context, it needs to be emphasized that the sexual differences in humeral asymmetry, and hence behavioral implications for females versus males, apply throughout the Late Pleistocene, to both late archaic and early modern humans, to Middle, early Upper and late Upper Paleolithic humans. They are distinctly counter to arguments (e.g., Kuhn and Stiner, 2006) that a sexual division of labor was derived for Upper Paleolithic modern humans.

5. Conclusion

This reassessment of humeral diaphyseal asymmetry among Late Pleistocene humans, across Eurasia and North Africa, through the Middle and Upper Paleolithic, provides a consistent pattern among these samples of foragers. High levels of diaphyseal asymmetry are frequent among these humans, with only the East Eurasia LUP sample showing lower (“Holocene”) levels. Yet, given the association of humeral asymmetry with body size, especially among males, the regional (but not temporal) differences may be more related to body size variation than to regional behavioral contrasts. There is also a consistent sexual difference in humeral asymmetry across the pooled Late Pleistocene sample and within the larger body size regional/temporal samples. These sexual differences probably principally reflect a sexual division of labor related to uni-manual versus bi-manual forceful and/or repetitive activities, possibly compounded by sexual differences in body size.

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This contribution to the thematic issue: *Hominin biomechanics, virtual anatomy and inner structural morphology: From head to toe. A tribute to Laurent Puymerail*, is our modest tribute to Laurent Puymerail, who took the analysis of human fossil diaphyses to a much further step than we have been able to do. If only he were with us to continue this process! We thank R. Macchiarelli and C. Zanolli for the opportunity to contribute to this tribute.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.crpv.2016.09.001.

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