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The expression of asymmetry in hand bones from the medieval cemetery at Écija, Spain

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Abstract
The unique nature of 'handedness' in modern humans poses questions about the development of this trait in both extinct hominid species and archaeological populations. An examination of the expression of hand preference in skeletal material is required to answer such questions. The main focus of previous research on asymmetry and hand preference has been on the bones of the upper limb, rather than those of the hand. This study addresses this issue by exploring the expression of asymmetry in the metacarpals and phalanges in 65 adult skeletons from the Medieval Muslim cemetery in Écija, Spain. From comparisons of metric properties of the bones and muscle marker development, varying patterns of asymmetry distribution were found. Sex was found to have a highly significant effect on metric properties, but not on asymmetry scores or muscle development. Age was not found to be significant in any of the analyses. These results suggest that the expression of hand preference varies throughout the hand, and is influenced by the method with which it is assessed. The bones of the hand have an important contribution to make to handedness research, as long as care is paid to associated methodological issues.

Keywords: bilateral asymmetry, handedness, musculoskeletal stress markers

Introduction

Anatomical and functional differences between the left and right hands have long been of interest to researchers. This interest stems, in part, from the observation that in living modern human populations, up to 90% of individuals exhibit a strong preference for performing tasks with the right hand (Heçaen and de Ajuriaguerra 1964; McManus 1999). This strong, population-level hand preference is in contrast to that of non-human primate species. For example in chimpanzees, conflicting findings regarding the pattern of handedness distribution are found. An extensive meta-analysis of hand use in free-ranging chimpanzees (McGrew and Marchant 1997) found little evidence for lateralised behaviour, and concluded that population-level 'handedness', as displayed in modern humans, is not present in the great apes. Studies of captive chimpanzees, however, have identified a much stronger degree of lateralised hand use (Hopkins et al. 2002, 2005; Hopkins and Cantalupo 2005). In light of these conflicting results, it is not currently possible to draw any firm conclusions about hand preference in non-human primates.

The question now remains as to when 'handedness' in modern humans emerged and developed. Examination of skeletal material is potentially the most informative way of answering this question (Lazenby 2002). Traditionally, the approach to identifying hand preference in skeletal material has been through the assessment of upper limb bilateral asymmetry, particularly in the humerus (Stirland 1993, Steele 2000, Steele and Mays 1995, Blackburn and Knüsel 2006). The bones of the hand have been largely absent from studies of hand preference. One reason for this is the difficulty of studying hand bones, either in terms of the paucity of accurately sided material available for study (particularly for extinct hominid species), or the minute differences in asymmetry due to the small size of the bones (Robb 1998). Some studies have attempted to look at the relationship between asymmetry and hand preference in the second metacarpal of humans (Garn et al. 1976; Plato et al. 1980; Roy et al. 1994; Mays 2002) and chimpanzees (Sarringhaus et al. 2005). They found that hand bones could be informative regarding the nature of the skeletal expression of handedness. However, more work is required to gain a complete understanding of the relationship between function and structure across the whole hand.

The aim of this study is to investigate the potential for the bones of the hand to provide a more complete picture of bilateral asymmetry in the upper limb. It also aims to shed light on the relationship between the expression of handedness in archaeological populations and living samples. To this end, the current study examines a range of data on the metacarpals and phalanges from an archaeological sample of modern humans. Both metric and musculoskeletal stress marker (MSM) analyses were performed. This allowed a comparison of two popular techniques, rarely used in tandem, to assess upper limb asymmetry. It will also explore the utility of MSM to provide information on the expression of asymmetry in the hand, an approach which has previously been avoided.

Materials

The Medieval Islamic site at Écija is situated approximately 80km east of Seville in southern Spain. It was a key town in the Muslim caliphate of al-Andalus during the Medieval period in the Iberian peninsula and the site of a significant battle in AD 711 (Jiménez nd;

Table 1. Measurements taken on metacarpals and phalanges (adapted from Bräuer 1988).

Code	Metacarpal and phalanx measurements	Description of measurement
mc*L	Length	Distance from the middle point of the surface of the base to the topmost point of the head
mc*RU	Radio-ulnar midshaft diameter	Maximum distance from the radial to the ulnar side at the midshaft, perpendicular to the long axis of the bone
mc*DP	Dorso-palmar midshaft diameter	Maximum distance from the radial to the ulnar side at the midshaft, parallel to the long axis of the bone
mc*PB	Maximum proximal breadth	Maximum breadth of the proximal end of the bone, measured perpendicular to the long axis of the bone
mc*DB	Maximum distal breadth	Maximum breadth of the distal end of the bone, measured perpendicular to the long axis of the bone
pp*L	Length of proximal phalanx	Distance from the middle point of the surface of the base to the topmost point of the head
ip*L	Length of intermediate phalanx	Distance from the middle point of the surface of the base to the topmost point of the head
dp*L	Length of distal phalanx	Distance from the middle point of the surface of the base to the topmost point of the head

*denotes metacarpal or phalanx number, e.g. mc1L, pp2L

Ortega nd; Román nd). Excavation of the town's Plaza de España between 1997 and 2002, uncovered the extensive Muslim cemetery, which appears to have been in constant use from the first post-Visigothic settlement in the early 8th century, until the region began to return to Christian rule in the 11th century. In osteological terms, Écija is of interest due to the size of the collection, the preservation of the material and the clear cultural identity of the sample. Rules regarding burial in Islamic society state that all individuals are equal in death. Bodies of the deceased must be wrapped or dressed in simple cloth and placed in graves without coffins, on their right side, facing Mecca. The depositing of grave goods is not permitted (Insoll 1999). Despite some variation in the adherence to these rules, these practices leave a clear archaeological signature, confirming the Muslim status of the Écija cemetery.

A total of over 4500 skeletons were excavated from the Écija site. Although the general preservation of individuals across the site was very good, several skeletons exhibited crushing due to the number of grave layers deposited on the site. Therefore, not all individuals were suitable for study. A total of 65 adults were included in the study. These were selected primarily on the basis of good preservation of the hand bones, and if possible, the humerus. Skeletons exhibiting pathologies likely to impair the proper functioning of the upper limb were excluded from analysis. Age and sex was determined by the methods outlined by Brothwell (1981), Lovejoy et al. (1985), Buikstra and Ubelaker (1994), Schwartz (1995) and O'Connell (2004). Within each of the sex categories, individuals were defined as either 'young adult' (17-30 years), 'middle adult' (30-45 years) or 'old adult' (45+ years). Only five individuals were classed as 'old adult', with majority scored as either 'young adult' (n=35), or 'middle adult' (n=25). Of the 65 skeletons, 35 (53.8%) were male and 30 (46.2%) female.

Methods

For each individual, a series of measurements were taken on the metacarpals and phalanges, on both the left and right sides. For the most part, hand bones were bagged according to side immediately after excavation. However, for a number of individuals, all hand bones were bagged together. On these occasions, metacarpals were siding using the methods described in Matshes et al. (2005). Although the siding of phalanges is known to be problematic, siding of mixed phalanges was attempted using the method proposed in Case and Heilman (2006). While the exact accuracy of this method on the Écija sample can not be known, it was considered accurate enough to warrant inclusion of this data in the current study, and potential siding issues were considered during the interpretation of the results of the phalanx data analysis.

The measurements encompassed both the metric properties of the bones, as well as analysis of MSM development. For the metacarpals and phalanges the measurements, taken from Bräuer (1988), are outlined in Table 1.

Radiographic and computer tomographic (CT) scanning facilities were not available for this study, so metric data was favoured over geometric data. Studies by Stock and Shaw (2007) and Pearson et al. (2007) have found a clear correlation between externally-derived and cross-sectional diaphyseal properties, suggesting that standard metric measurements still have relevance to analyses of diaphyseal robusticity. Due to time constraints, it was not

Table 2. Measurement error (mm) in the Great Chesterford metacarpal sample.

	Side	N	Average error	% error
mc1L	L	19	0.5	1.13
	R	17	0.3	0.77
mc2L	L	20	0.3	0.48
	R	21	0.5	0.69
mc3L	L	18	0.4	0.58
	R	23	0.3	0.41
mc4L	L	16	0.2	0.41
	R	20	0.5	0.86
mc5L	L	14	0.3	0.49
	R	19	0.3	0.53
mc1RU	L	18	0.3	2.64
	R	18	0.2	1.92
mc2RU	L	22	0.4	4.25
	R	21	0.3	4.12
mc3RU	L	20	0.1	1.58
	R	24	0.2	2.17
mc4RU	L	21	0.2	3.37
	R	21	0.2	3.45
mc5RU	L	17	0.5	6.25
	R	20	0.4	5.52
mc1DP	L	18	0.2	2.44
	R	18	0.2	2.22
mc2DP	L	22	0.2	2.76
	R	21	0.3	3.45
mc3DP	L	19	0.2	2.31
	R	24	0.2	2.28
mc4DP	L	21	0.3	4.27
	R	21	0.2	3.09
mc5DP	L	17	0.4	6.26
	R	20	0.5	6.86
mc1PB	L	19	0.4	2.70
	R	17	0.3	1.90
mc2PB	L	20	0.5	3.16
	R	21	0.7	4.22
mc3PB	L	17	0.6	4.26
	R	23	0.5	3.79
mc4PB	L	18	0.4	3.63
	R	20	0.3	2.71
mc5PB	L	12	1.0	8.33
	R	21	1.0	7.93
mc1DB	L	18	0.4	3.04
	R	18	0.5	3.18
mc2DB	L	19	0.7	4.97
	R	19	0.3	2.19
mc3DB	L	17	0.3	2.46
	R	22	0.5	3.29
mc4DB	L	19	0.3	2.35
	R	19	0.3	2.75
mc5DB	L	15	0.2	1.95
	R	18	0.2	1.31

possible to collect the duplicate data required to calculate measurement error for the Écija sample. However, measurement error was calculated for the metacarpal and phalanx material used in an earlier pilot study to assess the suitability of the methods. This pilot study was carried out on 26 skeletons from the Anglo-Saxon cemetery site of Great Chesterford, Essex (Evison 1994), curated at the University of Southampton. Measurement error was quantified as the absolute difference between two corresponding measurements, following Sarringhaus et al. (2005). Table 2 provides the results of this analysis for the Great Chesterford metacarpal material, represented as the average difference between corresponding measurements and this average difference as a percentage of the average measurement value. Table 3 provides the results of this analysis for the Great Chesterford phalanx material.

From Table 2, it can be seen that average measurement error for the metacarpals is low, with no variable showing an error greater than 1mm. These errors appear larger when considered as a percentage of the average measurement value. This is most likely due to the small size of the metacarpal measurements. This is evident when metacarpal length percentages, which represent the largest measurements, are compared with other metacarpal dimensions. While the majority of percentage errors are below 5%, six out of 50 (12%) are over 5%. These measurements are all for the fifth metacarpal, suggesting particular issues in taking measurements on this bone.

Again, this may be a reflection of the gracile nature of this bone relative to the other metacarpals. Observer experience may also contribute to the level of error, as this was limited in pilot study. Table 3 shows a low level of measurement error in the phalanx sample. With the majority of measurements having an average difference of less than 1mm. Twenty-six (93%) out of 28 measurements show a percentage error of less than 2%, and within acceptable limits (Auerbach and Ruff 2006). Small sample size is likely to be the cause of the greater than 2% measurement error found for left and right dp4L. Taken together, these results suggest that care must be exercised when taking hand bone measurements to ensure low measurement error.

Asymmetry in the Écija metacarpals and phalanges was assessed by calculating the percentage difference between corresponding left side and right side measurements using the equation by Trinkaus et al. (1994):

$$(\text{min value} - \text{max value})/\text{min value}) \times 100$$

This equation has been used in a number of studies (e.g. Churchill and Formicola 1997; Rhodes and Knüsel 2005; Sarringhaus et al. 2005; Lieverse et al. 2008), and benefits from maximising the perceived asymmetry between the sides, particularly in cases where the variation is small and stochastic in nature. This analysis was performed on a combined-sex, combined-age sample. To assess whether side dominances identified were statistically significant, Wilcoxon tests were performed on each pair of left and right measurements, and on the combined-age and combined-sex sample. To assess the effects of sex and age, an univariate General Linear Model (GLM) ANOVA was performed. A Mann-

Table 3. Measurement error (mm) in the Great Chesterford phalanx sample

	Side	N	Average error	%error
pp1L	L	19	0.4	1.52
	R	19	0.4	1.32
pp2L	L	16	0.5	1.38
	R	18	0.3	0.79
pp3L	L	16	0.4	1.00
	R	20	0.4	0.83
pp4L	L	17	0.6	1.41
	R	20	0.5	1.19
pp5L	L	16	0.4	1.34
	R	17	0.2	0.60
ip2L	L	11	0.4	1.79
	R	10	0.2	0.96
ip3L	L	13	0.3	0.92
	R	14	0.5	1.79
ip4L	L	10	0.3	1.21
	R	12	0.4	1.31
ip5L	L	10	0.2	0.92
	R	15	0.1	0.64
dp1L	L	9	0.3	1.40
	R	9	0.3	1.14
dp2L	L	5	0.3	1.55
	R	2	0.1	0.58
dp3L	L	6	0.3	1.34
		9	0.3	1.63
dp4L	L	2	1.2	6.67
	R	4	0.4	2.12
dp5L	L	5	0.3	1.85
	R	6	0.2	1.03

Whitney U test was carried out to assess the effects of sex on asymmetry scores.

Asymmetry was also assessed through the analysis of MSM development. Traditionally, the development of muscle attachments has been scored on an ordinal scale (i.e. Hawkey and Merbs 1995). In this system, features such as robusticity, stress lesions and ossification exostoses are graded on a scale of 0-4, with each number representing an increase in the expression of that feature. This system has a certain subjective element, as each researcher must establish the scale for each skeletal collection studied. While this method can be suitable for the long bones of the body (where the size of the muscle and therefore, the resulting muscle attachment site is relatively large), it is not suitable for the hand, where the muscle attachment sites are smaller and show less variation (Robb 1998). Instead, the current study uses an alternative method for assessing MSM proposed by al-Oumaoui et al. (2004). Rather than using a scalar method, MSMs are rated on a simple presence/absence basis. While an individual scoring system has to be set up for each sample, this method allows for muscle attachments of a smaller size to be studied and standardises MSM analysis for cross-study comparisons. Figure 1 illustrates the criteria used to determined presence and absence of MSM for the *opponens digiti minimi*.

Figure 1. Criteria used to assess the (a) absence (left), and (b) presence (right) of the *opponens digiti minimi* muscle attachment on the medial side of the fifth metacarpal. The areas of absence and presence are within the area of the circle marked on each picture.

A pilot study was conducted to test the applicability of the presence/absence methodology to the muscles of the hand. It was not possible to reliably identify and score a number of the muscle attachment sites on the metacarpals (where the majority of the muscles originate/attach). For this reason, muscles could not be selected based on their functional properties alone, (see Marzke et al. 1998). Instead, muscles were selected based on the ease at which they could be identified on dry bone. Table 4 outlines the muscles chosen for the current study. A McNemar test of association was performed to identify statistically significant differences between left and right MSM pairs. A chi-squared test (χ^2) was used to identify associations between sex, age and MSM score.

Results

Metric analysis

Figure 2 and Table 5 summarise the results of the asymmetry calculation for the metacarpals, plotted as percentage asymmetry values. These results indicate clear right-side dominance in the metacarpals, or that all of the measurements, are larger on the right side than the left. The magnitude of this right-side dominance, however, is variable, ranging from only 51% (mc3L) to 91.5% (mc5DP). In modern studies, the natural right to left side dominance has been estimated at around 90% (e.g. Heçaen and de Ajuriaguerra 1964; McManus 1999). In total, only 11 out of the 25 measurements exhibit an asymmetry value greater than 70%, suggesting that the expression of asymmetry across, and within, the metacarpals is more variable than might have been expected.

Table 4. Muscles of hand scored for development of musculoskeletal stress markers.

Code	Muscle	Location of measurement	Action of muscle
FPL	Flexor pollicis longus	Palmar surface of base of distal pollical phalanx	Flexion of thumb
APT	Adductor pollicis (transverse)	Palmar surface of third metacarpal	Adduction and flexion of thumb
ODM	Opponens digiti minimi	Medial edge of fifth metacarpal	Rotation of mc5 into opposition with thumb, draw mc5 forward, assists in flexion of 5th carpometacarpal joint
FDP	Flexor digitorum profundus 2,3,4 and 5	Palmar surface of base of distal phalanges 2,3,4 and 5	Flexion of distal interphalangeal joints of 2-5. Assists in adduction of 2nd, 4th and 5th digits and flexion at wrist
FDS	Flexor digitorum superficialis 2,3,4 and 5	Both sides of the palmar surface of intermediate phalanges 2,3,4 and 5	Flexion of intermediate phalanges of digits 2-5, and wrist
PI2	Palmar interosseous 2	Palmar surface of second metacarpal	Adduction of digits towards centre of 3rd digit, at metacarpophalangeal joints.
PI3	Palmar interosseous 3	Palmar surface of third metacarpal	Assist in flexion of digits at these joints
PI4	Palmar interosseous 4	Palmar surface of fourth metacarpal	Assist in flexion of digits at these joints
DI1	Dorsal interosseous 1	Medial edge of mc1 and lateral edge of mc2	Abduction of 2nd, 3rd and 4th digits from the midline of the hand
DI2	Dorsal interosseous 2	Medial edge of mc2 and lateral edge of mc3	Abduction of 2nd, 3rd and 4th digits from the midline of the hand
DI3	Dorsal interosseous 3	Medial edge of mc3 and lateral edge of mc4	Abduction of 2nd, 3rd and 4th digits from the midline of the hand
DI4	Dorsal interosseous 4	Medial edge of mc4 and lateral edge of mc5	Abduction of 2nd, 3rd and 4th digits from the midline of the hand

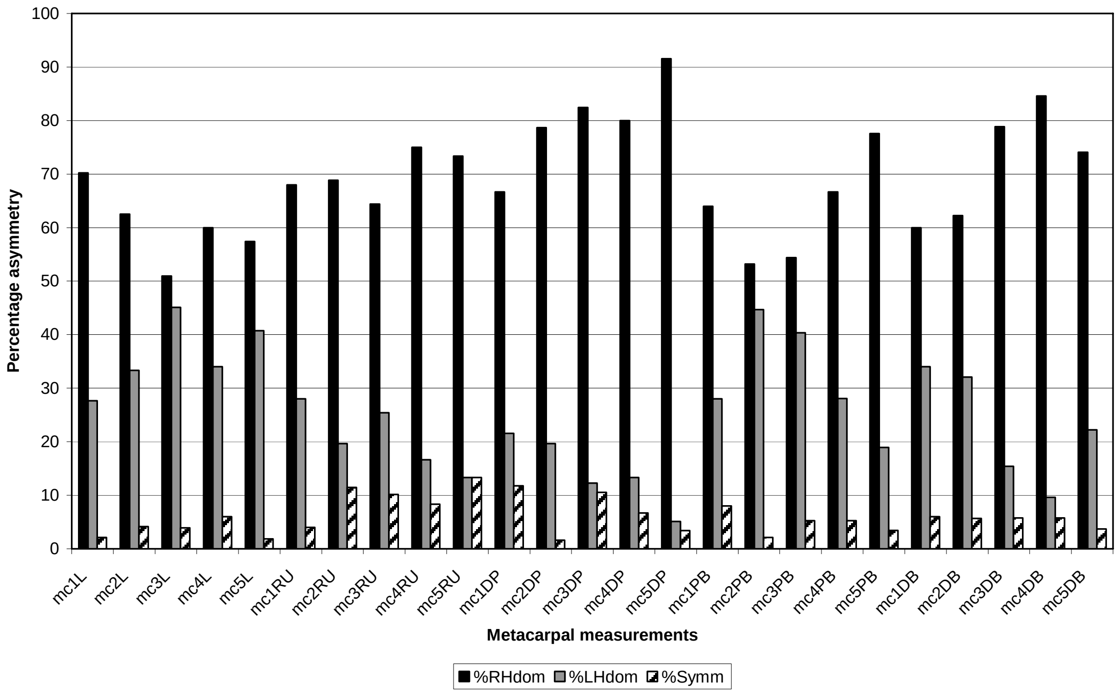

Figure 2. Percentage of right- and left-side dominant and symmetric individuals for all metacarpal measurements

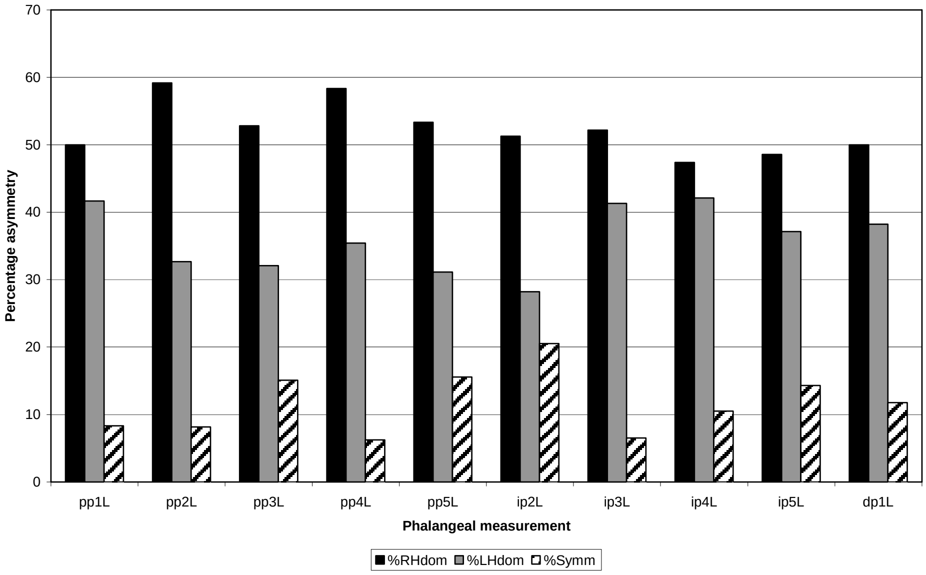

Figure 3. Percentage of right- and left-side dominant and symmetric individuals for all proximal and intermediate phalanx measurements. Due to small sample sizes, distal phalanges 2 to 5 were excluded from the analysis.

Looking at each of the metacarpal measurements in more detail identifies certain trends in the distribution of asymmetry. For metacarpal length, there is a decrease in asymmetry, moving medially across the metacarpal row (from mc1 to mc5), with a pronounced dip at mc3L, which is approaching symmetry. For the other metacarpal measurements, however, this pattern is reversed, with asymmetry increasing from mc1 to mc5.

While the level of asymmetry in the metacarpal measurements is generally low, there is variation between the measurements. The degree of asymmetry is greatest in the

dorso-palmar diameter measurements, with proximal breadth measurements showing the lowest levels of asymmetry. Generally, the metacarpal shaft, represented by mcRU and mcDP, appears to exhibit stronger right-side asymmetry than measurements of the head and base (mcDB and mcPB). This pattern supports the observation that, in the long bones, diaphyses tend to be more asymmetric than articular surfaces due to continued remodelling of the bone shaft after epiphyseal fusion (Ruff 2000).

When each metacarpal is studied individually, metacarpals 2 to 5 show a broadly similar pattern of asymmetry, with clear differences in asymmetry between the various measurements, but with the pattern remaining the same for each metacarpal. Metacarpal 1 is the exception, as asymmetry is almost constant across all measurements, with only a 10% difference between the largest and smallest right-side dominant values. Percentage asymmetry differences were also calculated for the phalanges, using the Trinkaus et al.'s (1994) equation (Table 6) Figure 3 plots these asymmetry values.

Table 5. Metacarpal asymmetry equation data.

	N	% left-side dominant	% right-side dominant	% symmetrical
mc1L	47	27.7	70.2	2.1
mc2L	48	33.3	62.5	4.2
mc3L	51	45.1	51.0	3.9
mc4L	50	34.0	60.0	6.0
mc5L	54	40.7	57.4	1.9
mc1RU	50	28.0	68.0	4.0
mc2RU	61	19.7	68.9	11.5
mc3RU	59	25.4	64.4	10.2
mc4RU	60	16.7	75.0	8.3
mc5RU	60	13.3	73.3	13.3
mc1DP	51	21.6	66.7	11.8
mc2DP	61	19.7	78.7	1.6
mc3DP	57	12.3	82.5	10.5
mc4DP	60	13.3	80.0	6.7
mc5DP	59	5.1	91.5	3.4
mc1PB	50	28.0	64.0	8.0
mc2PB	47	44.7	53.2	2.1
mc3PB	57	40.4	54.4	5.3
mc4PB	57	28.1	66.7	5.3
mc5PB	58	19.0	77.6	3.4
mc1DB	50	34.0	60.0	6.0
mc2DB	53	32.1	62.3	5.7
mc3DB	52	15.4	78.8	5.8
mc4DB	52	9.6	84.6	5.8
mc5DB	54	22.2	74.1	3.7

What is immediately clear from Figure 3 is that, while there is a right-side dominance of all of the phalanges, the level of asymmetry is greatly reduced compared to that of the metacarpals. Right-side dominance ranges from 47.4% (ip4L) to 59.2% (pp2L), compared to the metacarpals, where only four variables (mc3L, mc5L, mc2PB, mc3PB) out of 25 had a right-side asymmetry value of less than 60%. This shows a very uniform distribution in asymmetry in the finger bones, with no clear pattern emerging. This may be a reflection of functional differences in the utilisation of the fingers compared to the metacarpals.

Table 6. Data from phalanx asymmetry equation

	N	% left-side dominant	% right-side dominant	% symmetrical
pp1L	48	41.7	50.0	8.3
pp2L	49	32.7	59.2	8.2
pp3L	53	32.1	52.8	15.1
pp4L	48	35.4	58.3	6.3
pp5L	45	31.1	53.3	15.6
ip2L	39	28.2	51.3	20.5
ip3L	46	41.3	52.2	6.5
ip4L	38	42.1	47.4	10.5
ip5L	35	37.1	48.6	14.3
dp1L	34	38.2	50.0	11.8
dp2L	5	40.0	60.0	0.0
dp3L	14	42.9	42.9	14.3
dp4L	10	60.0	30.0	10.0
dp5L	6	33.3	50.0	16.7

Wilcoxon tests (Table 7) performed on each pair of left and right measurements found that, for the majority of metacarpal measurements, the difference between the left and right sides was highly significant ($p<0.01$). The exceptions were mc3L ($p=0.49$), mc5L ($p=0.15$), mc2PB ($p=0.51$) and mc3PB ($p=0.36$). This supports the findings of the previous analysis, where these four measurements were the only ones exhibiting right-side dominance less than 60%. In keeping with the analysis in Figure 3, the Wilcoxon significance test for the phalanges (Table 8) identified only three significant left/right differences, pp2L ($p=0.05$), pp3L ($p=0.01$), and ip2L ($p=0.03$). Again, this is in line with the trends identified in the asymmetry analysis.

The GLM ANOVA (Table 9) shows that, for the metacarpals, sex was highly significant, with the only exceptions being right mc2L ($p=0.07$), and left and right mc5PB ($p=0.08$ and $p=0.82$, respectively). For age, the opposite was true, with only left mc5DB ($p=0.05$) showing significance. This was repeated in the phalanges (Table 10), with sex being strongly significant, with age less so. Perhaps due to small sample sizes for the distal phalanges, the effect of sex was limited in the distal phalanges, but if these are excluded (as per the previous analysis), then it only left ip4L ($p=0.06$), right ip5L ($p=0.15$) and left and right dp1L ($p=0.07$ and $p=0.21$, respectively) that do not have significant *p*-values.

The Mann-Whitney U test for the metacarpals (Table 11) found that, in contrast to the ANOVA on the metric properties, the influence of sex on metacarpal asymmetry was very limited, with significance only being found for mc2RU ($p = 0.03$), mc3RU ($p < 0.01$), mc3DP ($p = 0.05$) and mc4PB ($p = 0.02$). For phalanx asymmetry (Table 12), the effect was limited further, with only dp4L showing a significant sex effect ($p = 0.03$).

MSM analysis

The MSM development at four muscle insertion sites and eight origin sites (Table 4)

Table 7. Wilcoxon test results for the Écija metacarpal sample.

	Side	N	Mean	SD	Sig. (2-tailed)
mc1L	L	55	42.97	3.18	**p < 0.01**
	R	56	43.77	3.08	
mc2L	L	54	64.95	4.02	**p = 0.01**
	R	53	65.22	3.99	
mc3L	L	57	62.60	4.16	p = 0.49
	R	59	62.66	4.17	
mc4L	L	52	55.77	3.78	**p = 0.03**
	R	62	55.84	3.61	
mc5L	L	58	51.74	4.02	p = 0.15
	R	61	51.96	3.44	
mc1RU	L	57	11.55	1.12	**p < 0.01**
	R	58	12.00	1.05	
mc2RU	L	62	8.09	0.77	**p < 0.01**
	R	64	8.28	0.82	
mc3RU	L	62	8.27	0.72	**p < 0.01**
	R	62	8.42	0.73	
mc4RU	L	60	6.65	0.62	**p < 0.01**
	R	65	6.98	0.71	
mc5RU	L	61	7.56	0.77	**p < 0.01**
	R	64	8.02	0.95	
mc1DP	L	57	8.40	1.16	**p < 0.01**
	R	58	8.53	0.96	
mc2DP	L	62	8.72	0.87	**p < 0.01**
	R	64	9.00	0.85	
mc3DP	L	62	8.84	0.91	**p < 0.01**
	R	62	9.28	0.80	
mc4DP	L	60	7.32	0.82	**p < 0.01**
	R	65	7.63	0.85	
mc5DP	L	61	6.80	0.86	**p < 0.01**
	R	63	7.28	0.89	
mc1PB	L	56	14.85	1.59	**p = 0.02**
	R	58	15.10	1.43	
mc2PB	L	55	16.53	1.54	p = 0.51
	R	56	16.37	1.63	
mc3PB	L	61	13.50	1.19	p = 0.36
	R	60	13.57	1.08	
mc4PB	L	58	11.81	0.99	**p < 0.01**
	R	63	12.04	0.99	
mc5PB	L	60	11.18	1.14	**p < 0.01**
	R	63	11.74	1.09	
mc1DB	L	57	13.71	1.34	**p < 0.01**
	R	58	14.01	1.21	
mc2DB	L	58	13.42	1.12	**p < 0.01**
	R	58	13.64	1.19	
mc3DB	L	58	13.26	1.09	**p < 0.01**
	R	59	13.60	1.07	
mc4DB	L	55	11.39	0.89	**p < 0.01**
	R	61	11.74	0.91	
mc5DB	L	58	11.06	0.73	**p < 0.01**
	R	61	11.25	0.84	

Significant p values highlighted in bold.

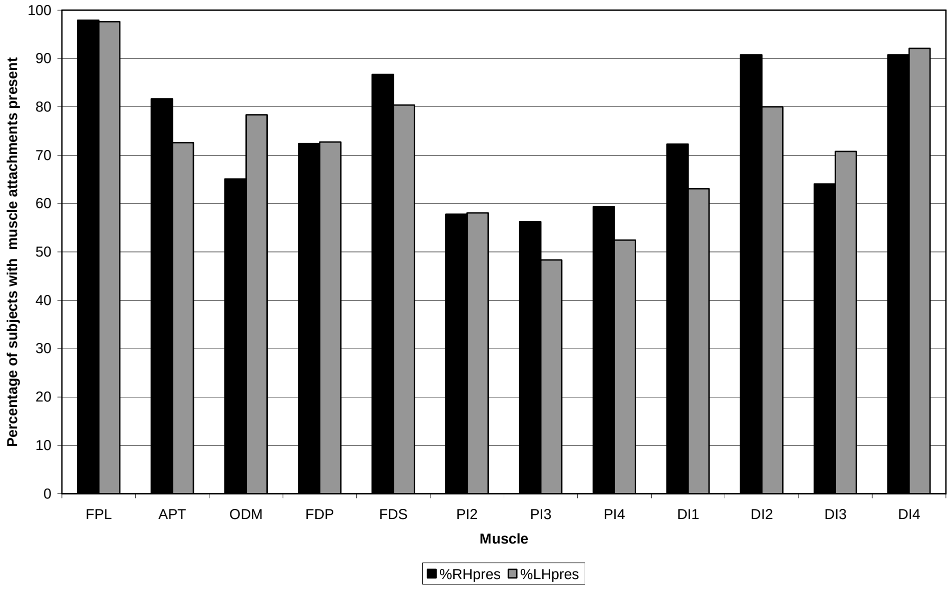

Figure 4. For all MSM, the percentage of individuals for which the muscle attachment was scored as 'present' for the right hand (black) and 'present' for the left hand (grey).

Table 8. Wilcoxon test results for the Écija phalanx sample.

	Side	N	Mean	SD	Sig. (2-tailed)
pp1L	L	53	28.53	2.30	p = 0.23
	R	53	28.64	2.31	
pp2L	L	53	38.48	2.55	**p = 0.05**
	R	54	38.38	2.56	
pp3L	L	57	42.52	2.94	**p = 0.01**
	R	59	42.81	2.77	
pp4L	L	52	40.25	2.63	*p = 0.07*
	R	58	40.10	2.84	
pp5L	L	52	31.51	2.09	*p = 0.08*
	R	52	31.89	1.96	
ip2L	L	45	22.77	1.83	**p = 0.03**
	R	49	23.00	1.76	
ip3L	L	50	27.59	2.67	p = 0.18
	R	53	27.80	2.58	
ip4L	L	41	26.27	1.93	p = 0.47
	R	48	26.19	1.80	
ip5L	L	41	18.54	1.64	p = 0.20
	R	51	18.38	1.60	
dp1L	L	42	21.52	1.76	p = 0.33
	R	46	21.84	1.82	
dp2L	L	11	17.01	1.19	p = 1.00
	R	14	16.49	1.15	
dp3L	L	18	18.09	1.30	p = 0.68
	R	26	18.22	1.34	
dp4L	L	17	17.63	1.52	p = 0.63
	R	16	17.61	1.17	
dp5L	L	10	16.42	1.90	p = 0.50
	R	17	16.14	1.60	

Significant p values highlighted in bold. P values approaching significance (i.e. between 0.055 and 0.1) highlighted in italics.

was scored as either 'present' or 'absent'. This scoring was repeated for MSM on both the left and the right hand. The percentage of individuals for which an attachment site was rated as 'present' was then plotted (Table 13, see appendix and Figure 4) in order to compare left and right hand MSM asymmetry.

Results shown in Figure 4 indicate that there is very little asymmetry in this sample in terms of MSM development.

Of the twelve MSM scored, seven showed a right-side dominance (i.e. scored as 'present' on the right side more frequently than on the left) and five showed a left-side dominance. The McNemar test of association (Table 14, see appendix) found that there were no statistically significant differences between left and right MSM pairs. The lack of asymmetry in the MSM is in contrast to the findings of the metric analysis, where all of the measurements showed clear right-side dominance.

Despite of the lack of asymmetry, a number of patterns can be identified in the right-side dominant muscles (FPL, APT, FDS, PI3, PI4, DI1, and DI2) compared to those that were left-side dominant (ODM, FDP, PI2, DI3 and DI4). While the flexors (FPL, FDP and FDS) and the mc5-centred muscles (ODM, PI4, dominance, muscles attached to the second metacarpal (DI1, DI2) and those attached to the third metacarpal (DI3, DI4) show the same pattern of dominance. While not conclusive, this suggests possible identifiable links between muscle function and the development of asymmetry.

It can be seen from Figure 4 that there are differences in the degree to which each muscle is rated as present. The *palmar interossei* (PI2, PI3, PI4) muscles in particular are recorded as 'present' less than 60% of the time. While this may be related to the function and expression of this muscle, it may also be a result of the difficulty with which these MSM sites were identified on dry bone. The FPL insertion site, by contrast, was identified as 'present' on approximately 98% DI4) do not show consistent patterns of side of occasions. While this muscle is readily identifiable on archaeological material, it is also a functionally prominent muscle in the function of the human hand (Susman 1988; Marzke 2000).

The χ^2 test (Table 15) revealed that sex was only significantly associated with left-FDS (p=0.04), right-DI1

Table 9. GLM ANOVA results for the effects of sex and age on metacarpal properties.

	Side	N	Mean	Sex		Age	
				F	Sig.	F	Sig.
mc1L	L	55	42.97	37.10	**p < 0.01**	0.17	p = 0.85
	R	56	43.77	10.86	**p < 0.01**	0.92	p = 0.41
mc2L	L	54	64.95	10.94	**p < 0.01**	0.37	p = 0.69
	R	53	65.22	3.45	*p = 0.07*	1.28	p = 0.29
mc3L	L	57	62.60	22.68	**p < 0.01**	0.60	p = 0.56
	R	59	62.66	18.42	**p < 0.01**	1.51	p = 0.23
mc4L	L	52	55.77	22.42	**p < 0.01**	0.77	p = 0.47
	R	62	55.84	20.85	**p < 0.01**	0.39	p = 0.68
mc5L	L	58	51.74	26.02	**p < 0.01**	0.71	p = 0.50
	R	61	51.96	25.43	**p < 0.01**	0.14	p = 0.87
mc1RU	L	57	11.55	10.42	**p < 0.01**	0.47	p = 0.63
	R	58	12.00	12.42	**p < 0.01**	1.56	p = 0.22
mc2RU	L	62	8.09	21.80	**p < 0.01**	0.25	p = 0.78
	R	64	8.28	11.47	**p < 0.01**	0.82	p = 0.45
mc3RU	L	62	8.27	11.16	**p < 0.01**	0.39	p = 0.68
	R	62	8.42	9.29	**p < 0.01**	0.85	p = 0.44
mc4RU	L	60	6.65	9.95	**p < 0.01**	0.70	p = 0.50
	R	65	6.98	6.64	**p = 0.01**	0.56	p = 0.58
mc5RU	L	61	7.56	9.38	**p < 0.01**	0.20	p = 0.82
	R	64	8.02	8.57	**p < 0.01**	1.24	p = 0.30
mc1DP	L	57	8.40	14.57	**p < 0.01**	0.02	p = 0.98
	R	58	8.53	12.97	**p < 0.01**	0.05	p = 0.95
mc2DP	L	62	8.72	7.65	**p < 0.01**	0.63	p = 0.53
	R	64	9.00	8.50	**p < 0.01**	0.22	p = 0.81
mc3DP	L	62	8.84	8.34	**p < 0.01**	0.15	p = 0.86
	R	62	9.28	6.82	**p = 0.01**	0.53	p = 0.59
mc4DP	L	60	7.32	11.26	**p < 0.01**	0.65	p = 0.52
	R	65	7.63	9.70	**p < 0.01**	0.30	p = 0.74
mc5DP	L	61	6.80	7.18	**p = 0.01**	0.05	p = 0.95
	R	63	7.28	4.99	**p = 0.03**	0.08	p = 0.92
mc1PB	L	56	14.85	15.47	**p < 0.01**	1.72	p = 0.19
	R	58	15.10	14.19	**p < 0.01**	2.09	p = 0.13
mc2PB	L	55	16.53	8.27	**p < 0.01**	1.50	p = 0.23
	R	56	16.37	5.32	**p < 0.01**	0.05	p = 0.95
mc3PB	L	61	13.50	16.23	**p < 0.01**	0.14	p = 0.87
	R	60	13.57	1.59	**p < 0.01**	0.42	p = 0.66
mc4PB	L	58	11.81	13.81	**p < 0.01**	0.10	p = 0.90
	R	63	12.04	6.78	**p = 0.01**	0.50	p = 0.61
mc5PB	L	60	11.18	3.28	*p = 0.08*	0.87	p = 0.42
	R	63	11.74	0.05	p = 0.82	0.92	p = 0.41
mc1DB	L	57	13.71	33.17	**p < 0.01**	0.66	p = 0.52
	R	58	14.01	21.03	**p < 0.01**	2.56	*p = 0.09*
mc2DB	L	58	13.42	21.40	**p < 0.01**	0.68	p = 0.51
	R	58	13.64	13.14	**p < 0.01**	0.79	p = 0.46
mc3DB	L	58	13.26	21.63	**p < 0.01**	0.31	p = 0.73
	R	59	13.60	15.43	**p < 0.01**	0.07	p = 0.93
mc4DB	L	55	11.39	11.69	**p < 0.01**	0.26	p = 0.77
	R	61	11.74	13.46	**p < 0.01**	1.14	p = 0.33
mc5DB	L	58	11.06	10.47	**p < 0.01**	3.09	**p = 0.05**
	R	61	11.25	16.01	**p < 0.01**	0.95	p = 0.39

Significant p values highlighted in bold. P values approaching significance (i.e. between 0.055 and 0.1) highlighted in italics.

Table 10. GLM ANOVA results for the effects of sex and age on phalanx properties.

	Side	N	Mean	Sex		Age	
				F	Sig.	F	Sig.
pp1L	L	53	28.53	9.57	**p < 0.01**	0.58	p = 0.56
	R	53	28.64	16.76	**p < 0.01**	0.20	p = 0.82
pp2L	L	53	38.48	27.94	**p < 0.01**	0.43	p = 0.66
	R	54	38.38	24.48	**p < 0.01**	0.20	p = 0.82
pp3L	L	57	42.52	32.47	**p < 0.01**	0.03	p = 0.97
	R	59	42.81	28.95	**p < 0.01**	0.21	p = 0.81
pp4L	L	52	40.25	26.24	**p < 0.01**	0.06	p = 0.94
	R	58	40.10	14.44	**p < 0.01**	0.26	p = 0.77
pp5L	L	52	31.51	19.86	**p < 0.01**	0.20	p = 0.82
	R	52	31.89	9.48	**p < 0.01**	1.93	p = 0.16
ip2L	L	45	22.77	18.23	**p < 0.01**	0.38	p = 0.69
	R	49	23.00	9.36	**p < 0.01**	0.80	p = 0.45
ip3L	L	50	27.59	8.84	**p < 0.01**	0.22	p = 0.81
	R	53	27.80	7.03	**p = 0.01**	0.13	p = 0.88
ip4L	L	41	26.27	3.89	*p = 0.06*	0.76	p = 0.47
	R	48	26.19	4.24	**p = 0.05**	0.43	p = 0.65
ip5L	L	41	18.54	9.03	**p < 0.01**	0.04	p = 0.96
	R	51	18.38	2.11	p = 0.15	0.54	p = 0.58
dp1L	L	42	21.52	3.62	*p = 0.07*	1.21	p = 0.31
	R	46	21.84	1.61	p = 0.21	0.13	p = 0.88
dp2L	L	11	17.01	0.82	p = 0.40	0.23	p = 0.80
	R	14	16.49	0.53	p = 0.48	0.39	p = 0.69
dp3L	L	18	18.09	1.45	p = 0.25	0.98	p = 0.40
		26	18.22	9.51	**p < 0.01**	0.74	p = 0.49
dp4L	L	17	17.63	7.05	**p = 0.02**	0.33	p = 0.73
	R	16	17.61	8.43	**p = 0.01**	0.05	p = 0.95
dp5L	L	10	16.42	2.94	p = 0.13	0.52	p = 0.50
	R	17	16.14	0.99	p = 0.34	1.03	p = 0.39

Table 11. Mann-Whitney U test for the effect of sex on metacarpal asymmetry.

	N	mean	sd	U	Sig. (2-tailed)
mc1L	47	1.37	1.13	213.0	p = 0.22
mc2L	48	0.93	0.91	250.0	p = 0.54
mc3L	51	1.11	0.81	318.5	p = 0.95
mc4L	50	1.25	0.98	265.5	p = 0.45
mc5L	54	1.24	1.02	340.5	p = 0.79
mc1R	50	4.33	3.47	229.5	p = 0.14
mc2R	61	5.52	4.50	306.5	**p = 0.03**
mc3R	59	3.98	3.15	263.0	**p < 0.01**
mc4R	60	6.29	4.40	436.5	p = 0.90
mc5R	60	6.85	6.01	340.0	p = 0.12
mc1D	51	3.94	3.62	233.0	*p = 0.10*
mc2D	61	4.91	3.35	413.0	p = 0.55
mc3D	59	5.73	4.42	313.0	**p = 0.05**
mc4D	60	5.07	3.54	431.0	p = 0.83
mc5D	59	8.23	5.84	418.0	p = 0.84
mc1P	50	4.22	3.11	249.0	p = 0.28
mc2P	47	4.32	3.54	257.5	p = 0.94
mc3P	57	3.18	2.44	358.0	p = 0.45
mc4P	57	4.45	3.19	247.5	**p = 0.02**
mc5P	58	6.47	5.19	311.5	*p = 0.10*
mc1D	50	2.78	2.03	297.5	p = 0.84
mc2D	53	3.23	2.51	279.0	p = 0.24
mc3D	52	4.01	2.49	321.5	p = 0.83
mc4D	52	4.06	2.61	299.5	p = 0.54
mc5D	54	3.64	2.42	296.5	p = 0.27

Table 12. Mann-Whitney U test for the effect of sex on phalanx asymmetry.

	N	mean	sd	U	Sig. (2-tailed)
pp1L	48	1.47	1.34	195.5	*p = 0.08*
pp2L	49	1.13	0.78	248.5	p = 0.34
pp3L	53	1.16	0.98	263.0	p = 0.19
pp4L	48	1.55	3.64	284.0	p = 0.97
pp5L	45	1.38	1.13	239.5	p = 0.87
ip2L	39	1.39	1.31	180.0	p = 0.81
ip3L	46	2.19	4.73	223.5	p = 0.43
ip4L	38	1.51	1.15	138.0	p = 0.31
ip5L	35	1.88	1.31	128.0	p = 0.42
dp1L	34	2.43	2.93	133.0	p = 0.91
dp2L	5	3.94	3.03	2.0	p = 0.80
dp3L	14	2.41	1.85	22.5	p = 1.00
dp4L	10	2.42	2.65	2.0	**p = 0.03**
dp5L	6	1.63	1.31	2.0	p = 0.53

Significant p values highlighted in bold

Table 13. Data from MSM presence/absence analysis.

MSM	Side	N	% present	% absent
FPL	L	42	97.6	2.4
	R	48	97.9	2.1
APT	L	62	72.6	27.4
	R	60	81.7	18.3
ODM	L	60	78.3	21.7
	R	63	65.1	34.9
FDP	L	23	72.7	27.3
	R	31	72.4	27.6
FDS	L	56	80.4	19.6
	R	60	86.7	13.3
PI2	L	62	58.1	41.9
	R	64	57.8	42.2
PI3	L	60	48.3	51.7
	R	64	56.3	43.7
PI4	L	61	52.5	47.5
	R	64	59.4	40.6
DI1	L	65	63.1	36.9
	R	65	72.3	27.7
DI2	L	65	80.0	20.0
	R	65	90.8	9.2
DI3	L	65	70.8	29.2
	R	64	64.1	35.9
DI4	L	63	92.1	7.9
	R	65	90.8	9.2

Key: FPL = flexor pollicis longus, APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDP = flexor digitorum profundus (2-5), FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous.

Table 14. McNemar test of association between left- and right-hand MSM.

MSM	N	Sig. (2-tailed)
FPL	35	p = 1.00
APT	57	p = 0.15
ODM	58	p = 0.18
FDP	19	p = 0.25
FDS	56	p = 0.29
PI2	61	p = 1.00
PI3	60	p = 0.15
PI4	60	p = 0.33
DI1	65	p = 0.24
DI2	65	*p = 0.07*
DI3	64	p = 0.45
DI4	63	p =1.00

N = number of comparisons performed. Due to the low number of instances where score changed between categories, binomial distribution was used instead of chi-squared statistic. See Table 4 for abbrieviations used.

Table 15. Chi-squared (χ^2) test of association between sex, age and hand MSM.

MSM	Side	Sex		Age	
		χ^2	Sig. (2-tailed)	χ^2	Sig. (2-tailed)
FPL	L	1.51	p = 0.41*	0.67	p = 1.00*
	R	1.31	p = 0.44*	0.90	p = 1.00*
APT	L	0.03	p = 1.00	0.02	p = 1.00
	R	0.57	p = 0.52	1.34	p = 0.31*
ODM	L	0.05	p = 1.00	3.44	p = 0.11
	R	4.22	*p = 0.06*	4.68	**p = 0.05**
FDP	L	0.03	p = 1.00*	2.78	p = 0.16*
	R	0.07	p = 1.00*	0.07	p = 1.00*
FDS	L	4.99	**p = 0.04***	2.00	p = 0.19
	R	0.93	p = 0.45*	0.14	p = 1.00*
PI2	L	1.93	p = 0.20	0.25	p = 0.79
	R	0.39	p = 0.62	0.05	p = 1.00
PI3	L	1.13	p = 0.31	0.01	p = 1.00
	R	2.81	p = 0.13	1.89	p = 0.19
PI4	L	0.36	p = 0.61	0.001	p = 1.00
	R	0.01	p = 1.00	0.01	p = 1.00
DI1	L	4.09	*p = 0.07*	0.73	p = 0.43
	R	4.22	**p = 0.05**	1.47	p = 0.26
DI2	L	3.48	p = 0.12	0.81	p = 0.53
	R	1.12	p = 0.40*	0.19	p = 0.69*
DI3	L	1.49	p = 0.28	1.16	p = 0.40
	R	0.01	p = 1.00	0.06	p = 1.00
DI4	L	6.37	**p = 0.02***	1.19	p = 0.38*
	R	3.68	*p = 0.09**	1.05	p = 0.39*

Significant p-values highlighted in bold and values approaching significance (between 0.055 and 0.1) highlighted in italics. Values marked with an asterisk (*) indicate those comparisons where the Fisher's Exact Test p-value was used due to low cell counts (in most instances, this test provides the same results as the standard χ^2).

(p=0.05) and left-DI4 (p=0.02). This clearly contrasts with the results of the metric analysis, where sex had a strong effect on metacarpal and phalanx measurements (but not on asymmetry values) and suggests that, in this sample at least, sex is not associated with MSM as strongly as previously thought. In keeping with the metric analysis, however, the χ^2 test showed that age is not associated with MSM development. The only exception to this was right-ODM (p=0.04).

Discussion

A clear right-side dominant asymmetry was found in the hand bones of the Écija sample, which was more pronounced in the metric properties of the bones than for the MSM. While this implies a right-hand preference in this sample, the magnitude of the asymmetry is much reduced from what might be expected in modern humans (Heçaen and de Ajuriaguerra 1964). These results are in keeping with those of Blackburn and Knüsel (2006), who found a discrepancy between asymmetry in skeletal measurements (humeral epicondylar breadth) and self-reported handedness in a living sample. Together, these results suggest that care must be taken in assuming a direct relationship between 'real-world' hand use and its representation in skeletal material.

The metric analysis suggested some potential functional patterns in metacarpal asymmetry. The metacarpal shaft measurements appear more asymmetric than the other metacarpal measurements. This suggests that the actions of the *palmar interossei* and *dorsal interossei* muscles vary between the left and right hands. The difference in the pattern of asymmetry between metacarpal 1 and the rest of the metacarpal row again suggests that the functional uniqueness of this bone has led to a potentially identifiable asymmetry signature. In contrast to the metric analysis of the metacarpals, the analysis of the phalanges shows a reduced level of asymmetry. This may be due to the organisation of the musculature of the hand, resulting in left/right differentiation between the role of the fingers compared to the metacarpals. This could, however, be a result of the problems inherent in the siding of phalanges (Case and Heilman 2006; Ricklan (1988 np). The reliability of the method varies across the phalanges, with the accuracy of siding the distal phalanges particularly poor. In practice, the method can be difficult to apply, particularly for phalanges of a smaller size. Therefore, it is unclear whether all the phalanges will be correctly sided, and in turn, whether the asymmetry profile of the phalanges in this sample is accurate.

Sex and age had contrasting effects on the metric properties of the metacarpals and phalanges. While sex was found to be statistically significant for most measurements, age was found to have very little effect. This strong association of sex is in contrast to the weak association found by Pomeroy and Zakrzewski (in press) on humeral diaphyseal shape in a sample from Écija. This suggests that, in this population, there may be more gendered divisions of tasks that strongly recruit the bones of the hand. Interestingly, neither the current study, nor that of Pomeroy and Zakrzewski found a significant effect of sex on asymmetry values, which indicates that sex is more strongly associated with the ways in which the upper limb is employed than with the asymmetry between left and right sides. The lack of a strong age association is perhaps surprising, but may reflect recognised problems with the accurate assessment of age in skeletal material (Molleson and Cox 1993). It may also reflect the rather arbitrary nature of the separating the adults in this study into 'young', 'middle' and 'old' categories.

In comparison to the relatively strong right-side asymmetry found in the metric analysis, the MSM analysis found a much more even distribution of right- and left-side dominance. In addition, the relative magnitude of asymmetry was much reduced. This may reflect a difference in the response of metric properties of bone and muscle attachment sites to the activity of the hand. It could also be due to a lack of sensitivity in either or both, the method used to assess MSM development, or the muscle attachment sites to accurately represent lateralised hand use. The identification of possible patterns in MSM asymmetry related to the second and third metacarpals suggest that there is potential for MSM of the hand to provide information regarding hand use and preference. Further investigation is required of the development of hand MSM to explore in more detail, the efficacy of the presence/absence approach for addressing questions of handedness, and also the choice of muscle attachment sites for study. Comparisons between the muscles of the hand and those of other regions of the upper limb (e.g. the humerus) would be informative.

Conclusions

This study has shown that the bones of the hand play an interesting and variable role in the expression of hand preference in skeletal material. The hand can, and arguably should, be included in discussions of handedness. Combining information from the hand with that from the rest of the upper limb will allow a more inclusive and revealing picture of bilateral asymmetry and its relationship to hand use in living populations. Comparisons of metric and MSM development in the hand has shown that the skeletal representation of hand use and preference is more fluid and more complex than had perhaps previously been thought and, therefore, care must be taken when assessing these traits. Selection of the appropriate methods of assessment and anatomical features for study is crucial. While methodological problems still surround analysis of the bones of the hand, further study will help to clarify these and ensure that the hand aids in a more comprehensive understanding of the unique functioning of the human upper limb.

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Literature cited

al-Oumaoui, I, Jiménez-Brobeil, S and du Souich, P. 2004. Markers of activity patterns in some populations of the Iberian Peninsula. *International Journal of Osteoarchaeology* 14: 343-359.

Auerbach, BM and Ruff, CB. 2006. Limb bone bilateral asymmetry: variability and commonality among modern humans. *Journal of Human Evolution* 50: 203-218.

Blackburn, A and Knüsel, CJ. 2006. Hand dominance and bilateral asymmetry of the epicondylar breadth of the humerus. *Current Anthropology* 47: 377-382.

Bräuer, G. 1988. Osteometrie. In Knussman, R (ed.), *Anthropologie: Handbuch der Vergleichenden Biologie des Menchen.* Stuttgart: Gustav Fisher. 212-213.

Brothwell, DR. 1981. *Digging Up Bones*. (3rd ed). New York: Cornell UniversityPress.

Buikstra, JE and Ubelaker, DH. 1994. *Standards for Data Collection from Human Skeletal Remains*. Arkansas Archaeological Survey Research Series No. 44.

Case, DT and Heilman, J. 2006. New siding techniques for the manual phalanges: A blind test. *International Journal of Osteoarchaeology* 16: 338-346.

Churchill, SE and Formicola, V. 1997. A case of marked bilateral asymmetry in the upper limbs of an Upper Palaeolithic male from Barma Grande (Liguria), Italy. *International Journal of Osteoarchaeology* 7:18-38.

Evison, V (ed.). 1994. *An Anglo-Saxon Cemetery at Great Chesterford, Essex*. Council for British Archaeology Research Report 91.

Garn, SM, Major, GH and Shaw, HA. 1976. Paradoxical bilateral asymmetry in bone size and bone mass in the hand. *American Journal of Physical Anthropology* 45: 209–210.

Hawkey, DE and Merbs, CF. 1995. Activity-induced musculoskeletal stress markers (MSM) and subsistence strategy changes among ancient Hudson Bay Eskimos. *International Journal of Osteoarchaeology* 5: 324-338.

Heçaen, H and de Ajuriaguerra, J. 1964. *Left-handedness: manual superiority and cerebral dominance.* New York: Grune and Stratton.

Hopkins, WD, Cantalupo, C, Wesley, MJ, Hostetter, AB and Pilcher, DL. 2002. Grip morphology and hand use in chimpanzees (*Pan troglodytes*): Evidence of a left hemisphere specialization in motor skill. *Journal of Experimental Psychology-General* 131**:** 412-423.

Hopkins, WD, Cantalupo, C, Freeman, H, Russell, J, Kachin, M and Nelson, E. 2005. Chimpanzees are right-handed when recording bouts of hand use. *Laterality* 10: 121-130.

Hopkins, WD and Cantalupo, C. 2005. Individual and setting differences in the hand preferences of chimpanzees (*Pan troglodytes*): A critical analysis and some alternative explanations. *Laterality* 10: 65-80.

Insoll, T. 1999. *The Archaeology of Islam*. Oxford: Blackwell Publishers Limited.

Jiménez, A. n.d. El sector noroeste. In Romo, A (ed.) *Intervención Arqueológica en la Plaza de España, Ecija. Memoria Final. Volumen 1: Memoria 1.* 183-193 (Unpublished site report on excavations in the Plaza de España, Écija).

Lazenby, RA. 2002. Skeletal biology, functional asymmetry and the origins of "handedness". *Journal of Theoretical Biology* 218: 129-138.

Lieverse, AR, Metcalf, MA, Bazaliiskii, VI and Weber, AW. 2008. Pronounced bilateral asymmetry of the complete upper extremity: A case from the early Neolithic Baikal, Siberia. *International Journal of Osteoarchaeology* 18: 219-239.

Lovejoy, CO, Meindl, RS, Mensforth, RP and Barton, TJ. 1985. Multifactorial determination of skeletal age at death: a method and blind tests of its accuracy. *American Journal of Physical Anthropology* 68: 1-14.

Marzke, MW. 2000. Precision grips, hand morphology, and tools. *American Journal of Physical Anthropology* 102: 91-110.

Marzke, MW, Toth, N, Schick, KD, Reece, SP, Steinberg, B, Hunt, K, Linscheid, RL and An, K-N. 1998. EMG study of hand muscle recruitment during hard hammer percussion manufacture of Oldowan tools. *American Journal of Physical Anthropology* 105: 315-332.

Matshes, E, Burbridge, B, Sher, B, Mohamed, A and Juurlink, BH. 2005. *Human Osteology and Skeletal Radiology: An Atlas and Guide.* Boca Raton, Florida: CRC Press.

Mays, SA. 2002. Asymmetry in metacarpal cortical bone in a collection of British post mediaeval human skeletons. *Journal of Archaeological Science* 29: 435-441.

McGrew, WC and Marchant, LF. 1997. On the other hand: current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. *Yearbook of Physical Anthropology* 40: 201-232.

McManus, IC. 1999. Handedness, cerebral lateralization, and the evolution of language. In: Corballis, MC and Lea, SEG (eds.) *The Descent of Mind: Psychological Perspectives on Hominid Evolution*. Oxford: Oxford University Press, pp194-217.

Molleson, TI and Cox, MJ. 1993. Spitalfields: The Middling Sort. *The Spitalfields Project, Volume 2.* CBA Research Report 86, Council for British Archaeology.

O'Connell, L. 2004. Guidance on recording age at death in adults. In Brickley, M and McKinley, JI (eds.) *Guidelines to the Standards for Recording Human Remains.* Institute of Field Archaeologists Paper No. 7, pp 18-20

Ortega, M. n.d. El sector noreste. In Romo, A (ed.) *Intervención Arqueológica en laPlaza de España, Ecija. Memoria Final. Volumen 1; Memoria 1.* 117-182.

(Unpublished site report on excavations in the Plaza de España, Écija).

Pearson, OM, Petersen, TR and Grine, FE. 2007. Prediction of long bone geometrical properties from external dimensions. *American Journal of Physical Anthropology* 132 (Supplement S44): 185.

Plato, CC, Wood, JL and Norris, AH. 1980. Bilateral asymmetry in bone measurements of the hand and lateral dominance. *American Journal of Physical Anthropology* 52: 27–31.

Pomeroy, EP and Zarzewski SR. in press. Sexual dimorphism in diaphyseal cross-sectional shape in the Medieval Muslim population of Écija, Spain and Anglo-Saxon Great Chesterford, UK. *International Journal of Osteoarchaeology*

Rhodes, JA and Knüsel, CJ. 2005. Activity-related change in medieval humeri: cross-sectional and architectural alterations. *American Journal of Physical Anthropology* 128: 536-546.

Ricklan, DE. 1988. *A Functional and Morphological Study of the Hand Bones of Early and Recent South African Hominids*. PhD Dissertation. University of the Witwatersrand, Johannesburg.

Robb, JE. 1998. The interpretation of skeletal muscle sites: A statistical approach. *International Journal of Osteoarchaeology* 8: 363-377.

Román, L. n.d. El sector suroestse. In Romo, A (ed.) *Intervención Arqueológica en la Plaza de España, Ecija. Memoria Final. Volumen 1: Memoria 1.* 195-233. (Unpublished site report on excavations in the Plaza de España, Écija).

Roy, TA, Ruff, CB and Plato, CC. 1994. Hand dominance and bilateral asymmetry in the structure of the second metacarpal. *American Journal of Physical Anthropology* 94: 203–211.

Ruff, CB. 2000. Biomechanical analyses of archaeological human skeletons. In Katzenberg, MA and Saunders, SR (eds) *Biological Anthropology of the Human Skeleton*. New York: Wiley-Liss. 71-102.

Sarringhaus, LA, Stock, JT, Marchant, LF and McGrew, WC. 2005. Bilateral asymmetry in the limb bones of the chimpanzee (*Pan troglodytes*). *American Journal of Physical Anthropology* 128: 840-845.

Schwartz, JH. 1995. *Skeleton Keys: An Introduction to Human Skeletal Morphology, Development and Analysis*. Oxford: Oxford University Press.

Steele, J. 2000. Skeletal indicators of handedness. In Cox, M and Mays, S (eds.) *Human Osteology in Archaeology and Forensic Science.* London: Greenwich Medical Media Ltd., pp 307-323.

Steele, J. and Mays, S. 1995. Handedness and directional asymmetry in the long bones of the human upper limb. *International Journal of Osteoarchaeology* 5: 39-49.

Stirland, AJ. 1993. Asymmetry and activity-related change in the male humerus. *International Journal of Osteoarchaeology* 3: 105-113.

Stock, JT and Shaw, CN. 2007. Which measures of diaphyseal robusticity are robust? A comparison of external methods of quantifying the strength of long bone diaphyses to cross-sectional geometric properties. *American Journal of Physical Anthropology* 134: 412-423.

Susman, RL. 1988. Hand of *Paranthropus robustus*. *Science* 240: 781–784.

Trinkaus, E, Churchill, SE and Ruff, CB. 1994. Postcranial robusticity in *Homo*: Humeral bilateral asymmetry and bone plasticity. *American Journal of Physical Anthropology* 93: 1–34.