Opponens Pollicis Mechanical Effectiveness in Neandertals and Early Modern Humans

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ABSTRACT

Researchers have repeatedly noted a flange of bone along the distodorsoradial margin of the Neandertal first metacarpal diaphysis, marking the insertion of the opponens pollicis muscle. It has been argued that this flange represents both greater muscle volume and greater leverage for the opponens pollicis. Here we assess the potential for increased mechanical effectiveness of the opponens pollicis in rotation and abduction in Neandertals as compared with Middle Paleolithic, Mid Upper Paleolithic, and recent modern humans. The radial displacement of the insertion for the opponens pollicis was assessed as a proxy for the moment arm for this muscle in rotation and abduction. Radial protrusion, both absolute and scaled to body size, was found to be greater in Neandertals and the Middle Paleolithic modern humans as compared with more recent humans, suggesting greater mechanical effectiveness of this muscle in Middle Paleolithic populations. This pattern may be the result of increased technological advancement after the Middle Paleolithic, resulting in a decreased need for muscular strength.

INTRODUCTION

Paleoanthropologists have noted several aspects of the Neandertal upper limb that likely signify the ability to produce larger joint torques compared to those of early and recent modern humans. These include increased scapular spine height, more medial orientation of the radial tuberosity, increased diaphyseal curvature of the radius, relative lengthening of the neck of the radius, increased palmar tuberosities of the scaphoid, trapezium and hamate, pollical phalangeal proportions, and opponens flanges on the external diaphyses of metacarpals 1 and 5 (Churchill and Rhodes 2006; Hambücken 1993; Musgrave 1971; Trinkaus 1983, 2006; Trinkaus and Churchill 1988; Villemeur 1994). These differences would theoretically increase joint leverage, allowing Neandertals to have generated larger joint torques for a given muscle volume. In particular, one of these features, the bony flange on the distodorsoradial margin of the metacarpal 1 diaphysis, has been argued to reflect both an hypertrophy of and a greater moment arm for the opponens pollicis muscle.

The presence of a prominent opponens flange on the Neandertal distodorsoradial metacarpal 1 diaphysis for the opponens pollicis (OP) muscle has been repeatedly noted since it was first highlighted by Sarasin (1932), in both mature individuals (Bonch-Osmolovskij 1941; Heim 1982a; Kimura 1976; Musgrave 1971; Trinkaus 1983; Vandermeersch 1991; Villemeur 1994; Vlček 1975, 1978) and young Neandertals (Heim 1982b; Vlček 1975). It has been used to infer an hypertrophy of the OP muscle (Bonch-Osmolovskij 1941; Heim 1982a; Trinkaus 1983; Vlček 1975), although the size and rugosity of the muscle insertion area on the radiopalmar edge of the flange can be relatively easily matched among early and recent modern humans (Kimura 1976). It was further suggested (Trinkaus 1983: 274) that it might have increased the moment arm of the muscle, an hypothesis that remains untested.

Given that the OP muscle is a central muscle for abduction and flexion at the first carpometacarpal (CMC1) joint, and hence for opposition of the human thumb (Close and Kidd 1969; Cooney at al. 1985; Forrest and Basmajian 1965; Long et al. 1970), the hypothesis of a greater moment arm for OP, and hence greater torque in the context of at least similar muscle size, is evaluated here. In this analysis, it is fully recognized that the moment arm of this muscle at the first metacarpal (MC1) reflects only a part of both its biomechanical effectiveness and its role in pollical movements. However, given the skeletal nature of the paleontological record and the central position of the OP moment arm at the MC1, an evaluation of this relative moment arm among the Neandertals and Late Pleistocene early modern humans should provide insight into a significant element of their evolving manipulative anatomy.

MATERIALS

The samples consist of the sufficiently complete later Pleistocene human first metacarpals for which a scaled photograph of the original in palmar view and/or a high-quality cast is available. The resultant Pleistocene sample includes the Amud 1, La Chapelle-aux-Saints 1, Feldhofer 1, La Ferrassie 1 and 2, Kebara 2, Kiik-Koba 1, Regourdou 1, Shani-

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Figure 1. Select fossil first metacarpals in palmar view. A, Tabun 1; B, La Ferrassie 2; C, Skhul 5; D, Qafzeh 9; E, Sunghir 1; F, Pataud 6. C, D and F are shown as mirror images to facilitate comparison.

dar 4, and Tabun 1 Neandertals (N=10), the Qafzeh 9 and Skhul 5 Middle Paleolithic modern humans (MPMH), and the Minatogawa 1 to 3, Pataud 4 and 6, Pavlov 31, and Sunghir 1 Mid Upper Paleolithic (MUP) modern humans (N=7). All of these fossil metacarpals are largely complete with only minor edge damage (Figure 1). To provide a comparative baseline, a recent human cadaver sample (N=50) was used.

The comparative sample contains associated hand remains, without documentation of sex or age-at-death. Given this, and the small fossil sample sizes for which only 14 have known sex (64%), sexes were pooled. For the majority of the fossils, only one side per individual is available, and sample sizes would not allow separate analysis for each side. To determine if pooling left and right MC1s would compromise the analysis, comparisons were made between right and left MC1s in the cadaver collection. No significant differences were found between right and left MC1s for any dimension measured (L, P=0.459; B_b, P=0.303; B_h, P=0.438; B_r, P=0.417; see Figure 3 below for abbreviations). All comparative specimens were prime age adults, with no observable abnormalities.

METHODS

For each MC1, a scaled photograph was taken in palmar view. Maximum length (L), breadth of the head (B_h), and breadth of the base (B_b) were measured on the photographs using Photoshop CS3 (Adobe Systems Inc.). In order to assess the effect of taking measurements from photographs versus directly on the bones, the same measurements were taken with calipers on the recent human sample. Error was found to be very low between methods (≈2.5%), and it was comparable to intra-observer error when multiple measurements were taken with calipers (≈2.6%), both <0.5mm for the MC1 breadths.

In order to assess the biomechanical implications of variation in opponens flange size across these samples, an additional measurement was taken to approximate the relevant moment arms on isolated MC1s. The maximum torque, or rotational force, that can be produced at a joint is theoretically determined by the physiological cross-sectional area (PCSA) of muscle acting across the joint and the muscle's effective mechanical advantage (EMA) (Gonzalez et al. 1997; Lieber and Boakes 1988; Narici et al. 1992; Zajac 1992). The effective or physiological cross sectional area (pCSA) = $(m/\varrho l)\cos\theta$, where m is muscle mass, ϱ is muscle density, l is fascicle length, and θ is pennation angle (Zajac 1992). Although pennation angle and fascicle length vary between muscle types, they are generally conserved within humans for a particular muscle (Yamaguchi et al. 1990; Narici et al. 1992; Albracht et al. 2008), and muscle density is known for vertebrate skeletal muscle (Méndez and Keys 1960). Therefore, when comparing pCSAs of the same muscle from individuals of the same species, the primary source of variation is the mass (and thus the volume) of the muscle. EMA is the ratio of the moment arm (r), defined as the perpendicular distance from the center of rotation (COR) of the joint to the line of action of the muscle force, to the load arm (R), defined as the perpendicular distance from the COR to the line of action of the external force. EMA thus estimates the relative amount of force a muscle must generate in response to an external load. For a given muscle volume, bony features that increase EMA will result in greater torque production.

Opposition at the CMC1 joint involves sequentially, abduction, flexion, and adduction of the MC1 in the saddle-shaped MC1 facet of the trapezium, which together result in axial rotation (pronation) of the pollex to produce palmar opposition to the ulnar digits (Kapandji 1982; Brand and Hollister 1999; Levangie and Norkin 2005). The COR for the flexion component of opposition is a line through the trapezium parallel to the body of the trapezium, and the COR for the abduction/adduction component of opposition is a line through the metacarpal base just distal to the dorsal and palmar beaks (Hollister et al. 1992). Rotation is defined by the degree of flexion/extension and abduction/adduction, and thus there is no independent COR for CMC1 pronation (Hollister et al. 1992).

The role of OP in prehension is complex, and it is active (to varying degrees) in most pollical postures during prehension, variably serving as an agonist, antagonist or synergist to the other thenar muscles (Close and Kidd 1969;

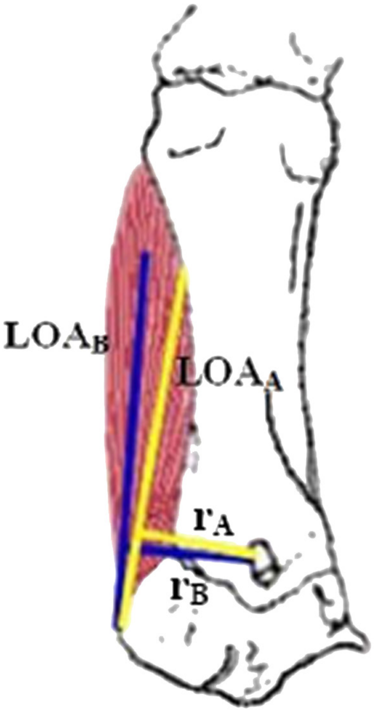

Figure 2. Biomechanical illustration of how increased breadth of the first metacarpal (MC1) results in greater moment arm length for opponens pollicis. LOA$_A$ and r$_A$ are the line of action and resulting moment arm for a narrow MC1, drawn to approximate measured dimensions for a recent modern human, and LOA$_B$ and r$_B$ are the line of action and resulting moment arm for a broad MC1, drawn to approximate measured dimensions for a Neandertal. LOA's are drawn as estimations of the average fiber direction for each. Illustration modified from Brand and Hollister (1999).

Cooney et al. 1985; Forrest and Basmajian 1965; Long et al. 1970). As an agonist it is particularly important for abduction and flexion of the thumb, although it also assists with adduction in the early stages of opposition.

Relative to adduction (and flexion), OP acts as the applied force in a class III lever with the COR adjacent to the CMC1 articulation, assuming that the resistance force is at or more distal to the metacarpophalangeal (MCP) joint. The moment arm (r) of opponens pollicis is the perpendicular distance from a line connecting its primary insertion on the distodorsoradial MC1 diaphysis and its origin on the trapezium, to its COR at the CMC1 joint.

Given that the muscle markings of both fossil and recent human MC1s for OP consist of variably rugose lines extending proximally from the MCP capsular attachment, fading out near midshaft, it is likely that the location of the maximum moment arm of the muscle is a relatively constant percentage of metacarpal length. With only skeletal remains preserved, the general similarity of the muscle markings across these samples (and hence the lack of data on the central fibers of the muscle), and the absence of trapezia for many of the fossil specimens, it is not possible to assess the relative moment arms of OP in adduction and flexion. In any case, the degree of radial projection of the OP flange, which has drawn repeated attention, would have a trivial effect on these moment arms, since it would displace the muscle largely perpendicularly to its line of action for these movements.

In contrast, the radial displacement of the OP insertion would shift the line of action for abduction radially relative to the COR of the joint, especially once the thumb is in partial opposition, and hence partially pronated. This would serve to increase its moment arm, and all else being equal, increase the EMA of OP in abduction (Figure 2). Radial displacement would have a greater effect on the more distal fibers of the OP, which would raise the average moment arm, as this is a function of the average line of action of all the muscle fibers. Since CMC1 pronation is a function of both abduction and flexion, increased effectiveness of OP in abduction will necessarily increase pronation effectiveness as well. The moment arm for OP in abduction cannot be measured directly from photographs of isolated MC1s, as an articulated trapezium would be required to estimate the origin of the muscle. However, the moment arm for OP in abduction should be directly correlated with the breadth of the shaft from the midline to its most projecting point radially (B_r). Thus, B_r serves as an indicator of the moment arm of OP in abduction and rotation.

To assess mechanical advantage, it is necessary to estimate the location of the applied load, which the muscles around a joint must counteract. With respect to abduction of the CMC1 joint, the applied load in advance of prehension will be the force of gravity acting at the center of mass of the digit. During prehension, the applied load will depend on the prehensile position and the object being held. With comparable prehensile behaviors, the applied load will be some function of the length of the digit, as it is very likely that Late Pleistocene and recent humans manipulated tools in proportionally similar ways. The total length of the thumb could not be calculated for the isolated MC1s; however, the summed lengths of the pollical phalanges to MC1 lengths are indistinguishable across similar Late Pleistocene and recent human samples (Trinkaus 2006; Trinkaus and Villemeur 1991). Thus, B_r will be used as an approximation of mechanical effectiveness for OP in abduction (and pronation), with the understanding that this reflects only part of the total mechanical effectiveness of the joint.

The long axis of the MC1 was defined as the line which bisects the maximum breadth of the trapezial facet proximally (B_b) and the metacarpal head distally (B_h) in palmar view (Figure 3). B_r was measured perpendicular to the long axis at 65% of maximum length. Most recent human MC1s have a smooth curvature along the radial surface, making it difficult to select a single point as the most radial extent, and 65% closely approximates the maximum development of the radial flange when it is present. Since B_r will vary with body size, comparisons were made of both B_r as an absolute value and scaled to MC1 length (as a proxy for body size). B_r was regressed against L, and raw residuals were

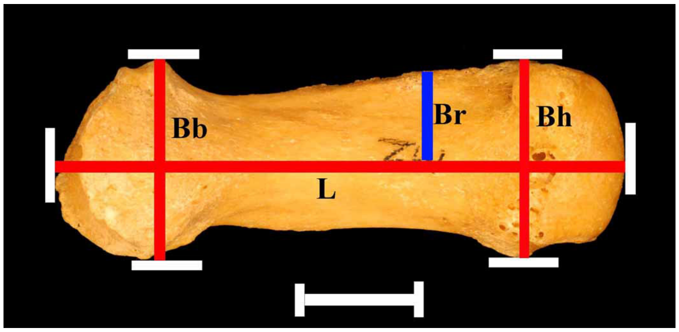

Figure 3. Measurement of the breadths of the base (B_b) and head (B_h), length (L), and the radial projection of the opponens pollicis insertion at 65% of L (B_r).

calculated from the reduced major axis (RMA) regression line through the recent human reference sample.

MC1 length is not an ideal measure of body size, despite its correlation with stature (Meadows and Jantz, 1992); however, there are similar MC1 to MC3 length proportions, and hand to arm length proportions, across these samples (Trinkaus 1983, 2006). Scaling the radial flange size to MC1 length therefore provides an estimation of variation in B_r, beyond the effects of variation in body size.

Descriptive statistics were calculated for each sample. Sample means and residuals were compared using ANOVA, with *post hoc* two-tailed pair-wise comparisons assuming unequal variances and Bonferroni adjustments to account for experiment wide error. Calculations were done using SPSS and NCSS.

RESULTS

Table 1 provides the measurements for the fossil specimens, and Table 2 includes descriptive statistics for L, B_h, B_b, and B_r for each sample, plus the residuals from the recent human RMA line. There are significant differences in B_b ($P<0.001$) and B_r ($P=0.008$) across the samples (see Table 2). *Post hoc* pair-wise comparisons for the two variables that were significant across the four samples demonstrated

TABLE 1. MEASUREMENTS OF LATE PLEISTOCENE HUMAN FIRST METACARPALS (MC1s)*.

		Length (L)	Base Breadth (B_b)	Head Breadth (B_h)	Radial Breadth (B_r)
Neandertals					
Amud 1	R	49.4	17.5	17.0	8.1
La Chapelle-aux-Saints 1	R	43.2	15.2	14.5	9.3
Feldhofer 1	L	45.9	16.7	16.1	9.4
La Ferrassie 1	R	48.7	18.9	16.7	8.3
La Ferrassie 2	R	39.8	13.9	13.9	7.6
Kebara 2	R	46.5	15.5	15.3	7.0
Kiik-Koba 1	L	43.9	17.5	16.4	8.0
Regourdou 1	L	43.2	15.9	15.3	8.0
Shanidar 4	L	44.0	15.7	15.4	7.3
Tabun 1	L	40.5	14.2	12.9	6.3
Mid Paleo Mod Humans					
Qafzeh 9	R	45.5	15.8	14.6	7.5
Skhul 5	R	45.5	17.2	14.8	7.5
Mid Upper Paleolithic					
Minatogawa 1	R	46.8	14.1	13.1	6.8
Minatogawa 2	L	40.8	14.1	12.2	6.4
Minatogawa 3	L	37.5	11.6	11.1	5.3
Pataud 4	L	43.1	14.6	12.6	4.9
Pataud 6	L	43.2	14.6	14.4	7.0
Pavlov 31	L	49.4	14.9	15.6	7.6
Sunghir 1	R	50.7	16.4	16.9	6.4

*in millimeters

TABLE 2. SUMMARY STATISTICS FOR THE METACARPAL 1 MEASUREMENTS (mean ± SD)*.

	Length (L)	Base Breadth (B_b)	Head Breadth (B_h)	Radial Breadth (B_r)	Radial Breadth Residual[2]	N
Neandertals	44.4 ± 3.3	16.0 ± 1.7	15.3 ± 1.3	7.8 ± 0.9	1.7 ± 1.1	10
Mid Paleo Mod Hum	45.5, 45.5	15.8, 17.2	14.6, 14.8	7.5, 7.5	1.0, 1.1	2
Mid Upper Paleolithic	44.7 ± 4.4	14.6 ± 1.6	14.0 ± 2.1	6.7 ± 1.4	0.2 ± 1.1	7
Recent Humans	47.2 ± 3.6	16.9 ± 1.4	15.1 ± 1.4	6.9 ± 1.0	0.0 ± 1.0	50
ANOVA P[1]	0.075	<0.001	0.100	0.008	<0.001	

* in millimeters

[1] The P-value from the ANOVA analysis across the four samples.

[2] The radial breadth residual is the raw residual from the reduced major axis regression line through the recent human sample distribution.

significant differences for B_r between the MUP and Neandertal samples (P=0.032), and between the MUP and recent human samples (P=0.003).

In absolute radial breadth, or projection of the OP flange, there were significant differences between each of the Middle Paleolithic samples and the two more recent samples (Figure 4; Table 3). However, it is not possible to separate the two MPMH MC1s from those of the Neandertals in this measure, since they fall well within the interquartile range of the latter sample.

Regression of B_r against L for the recent human sample provided a significant correlation (P_{slope}<0.001, Figure 5), and there is a highly significant difference across the four samples in the resultant residuals (see Table 2). *Post-hoc* pair-wise comparisons provide significant differences between the Neandertal sample and the MUP and recent human samples, and between the MPMH and recent human sample (see Table 3; Figure 6). Again, the two MPMH MC1s fall within the Neandertal interquartile range, even though they are moderately low within that range.

TABLE 3. *POST-HOC* PAIR-WISE TWO-TAILED T-TEST P-VALUES FOR RADIAL BREADTH VALUES AND RADIAL BREADTH RESIDUALS ACROSS THE FOUR SAMPLES, ASSUMING UNEQUAL VARIANCES.[1]

	MPMH	MUP	Recent Humans
Radial Breadth			
Neandertals	0.202	0.005**	0.010*
MPMH		0.018*	<0.001**
MUP			0.176
Radial Breadth Residual			
Neandertals	0.070	0.012*	<0.001**
MPMH		0.079	<0.001**
MUP			0.698

[1] *: P<0.05; **: P<0.01. Given the experiment-wide significance of these variables across the four samples, after a Bonferroni multiple comparison correction (see Table 2), further multiple comparison corrections are not employed here.

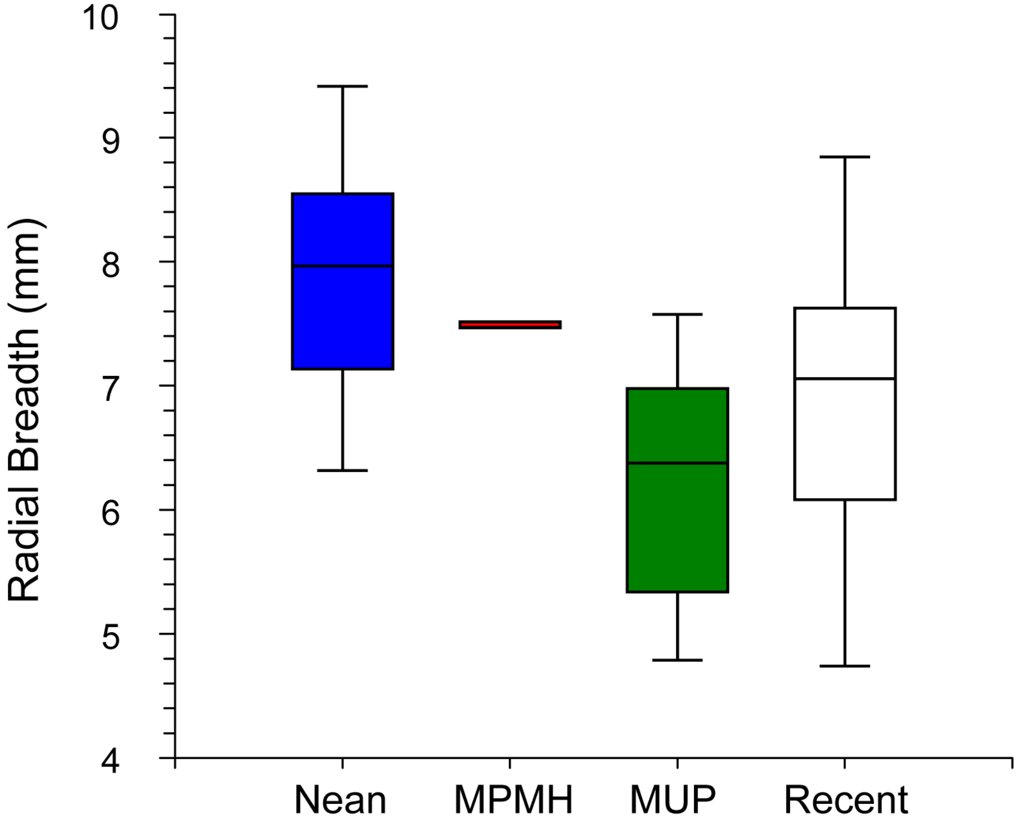

Figure 4. Box-plots of metacarpal 1 radial breadth (B_r) for Neandertals (Nean), Middle Paleolithic modern humans (MPMH), Mid Upper Paleolithic modern humans (MUP), and late Holocene humans (Recent).

Therefore, in both the absolute comparison of radial breadth, or radial projection of the opponens pollicis flange from the MC1 longitudinal axis, across these Late Pleistocene and recent human samples, as well as the comparison of their distributions relative to the RMA regression line through the recent human reference sample, the primary distinction is between the two Middle Paleolithic samples (Neandertal and early modern human) and the more recent Mid Upper Paleolithic and late Holocene samples. Figure 2 illustrates how these differences result in an increased moment arm between recent modern humans and Neandertals.

DISCUSSION

Nearly all human grips require the pollex to oppose one or more digits (Levangie and Norkin 2005; Marzke et al. 1998; Napier 1956), and thus OP activity is central to human manipulative behaviors. OP is consistently recruited during both precision and power grips (Long et al. 1970; Maier and Hepp-Reymond 1995). In a precision grip OP does not act directly on the pollical phalanges, but it functions to stabilize the MCP joint during forceful pinching or squeezing of the digital pads (Maier and Hepp-Reymond 1995). In a power grip it assists with flexion and pronation of the pollex, and it resists forcible extension and lateral rotation (supination) of the thumb during manipulative movements that produce strong reaction forces through the thumb. Although OP is consistently recruited in both precision and power grips, greater forces are generated in a power versus a precision grip (Napier 1956), so the ability to produce large OP forces is of greater consequence in a power grip. In this context, the larger absolute and relative radial breadths of the two Middle Paleolithic samples, Neandertals and early modern humans, imply that these humans would have been more mechanically effective at generating and maintaining pollical grips than either the Mid Upper Paleolithic sample or the recent humans.

First metacarpals are rare for members of the genus *Homo* prior to the Late Pleistocene, consisting of a pair of immature diaphyses associated with KNM-WT 15000 that may be human, a largely complete one which probably derives from the genus *Homo* (SKX-5020), and one of ambiguous taxonomic attribution (SK-84) (Napier 1959; Susman 1988a,b; Trinkaus and Long 1990; Walker and Leakey 1993). The SKX-5020 MC1 in particular exhibits prominent radial development of the opponens pollicis insertion area, although it has not been possible to metrically assess its projection. The KNM-WT 15000 MC1s, if correctly identified, would have a clear OP insertion area, although it is not as prominent as the one on the developmentally similar La Ferrassie 3 Neandertal or those of the younger La Ferrassie 6 and Zaskalnaya 1 Neandertals (Heim 1982b; Vlček 1975). There is only one individual preserving the first metacarpal for the Early Upper Paleolithic, the Nazlet

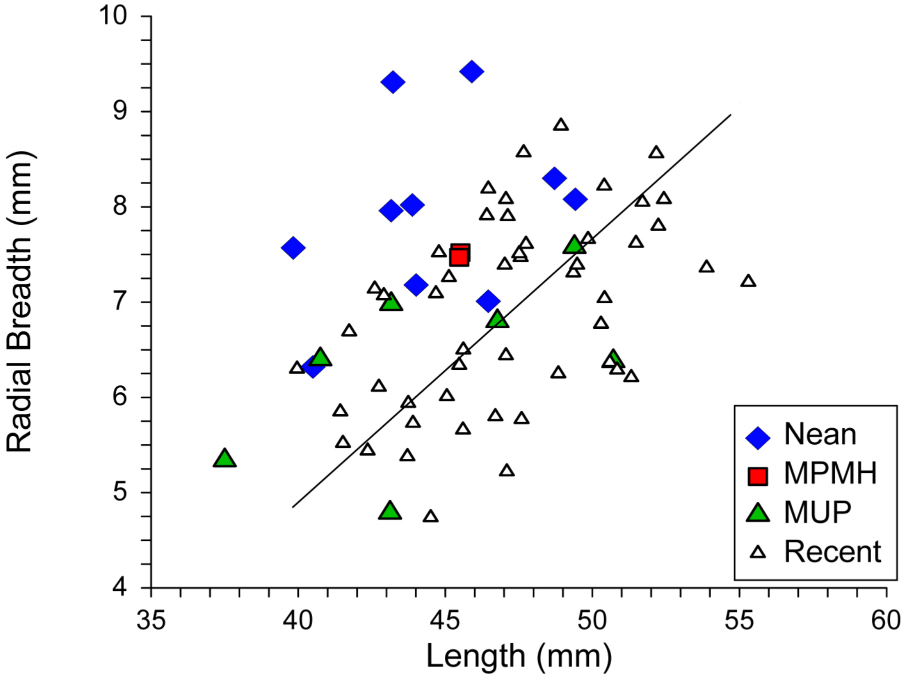

Figure 5. Bivariate plot of metacarpal 1 radial breadth versus length for Late Pleistocene and recent human. The line is the reduced major axis (RMA) regression line through the recent human sample. Sample abbreviations as in Figure 3. The two MPMH specimens have almost identical values, and hence their points are superimposed.

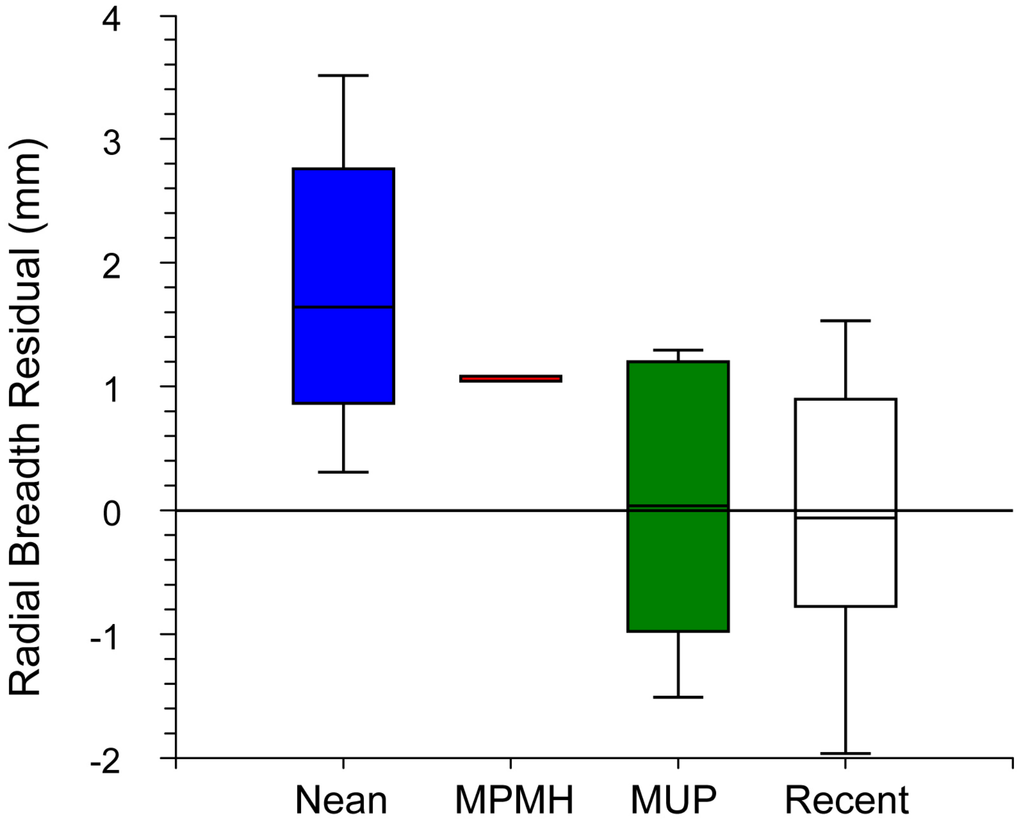

Figure 6. Box-plots of the residuals from the reduced major axis (RMA) line through the recent human sample for the Late Pleistocene and recent human samples. Abbreviations as in Figure 3.

Khater 2 partial skeleton (Crevecoeur 2008). Metric data for its opponens pollicis radial position are unavailable, but it appears to lack the radial projection present in the MPMH and especially Neandertal MC1s, conforming more to the pattern seen in the Mid Upper Paleolithic. From these two specimens, SKX-5020 and Nazlet Khater 2, it is likely, but needs to be confirmed, that the primary contrast in opponens pollicis flange development is between Middle Paleolithic and earlier members of the genus *Homo*, on the one hand, and Upper Paleolithic and more recent humans on the other hand.

It is tempting to make correlations between these OP inferences and the characteristics of the associated technologies. There is abundant evidence for hafting in both Neandertal and early modern human associated Middle Paleolithic assemblages (Boëda et al. 1999; Hardy et al. 2001; Mazza et al. 2006; Meller 2003; Shea 1991; Villa et al. 2009). However, there is a shift towards more complex and probably more frequent composite tools in the earlier Upper Paleolithic (EUP and MUP) (e.g., Bar-Yosef 2002; Bar-Yosef and Kuhn 1999; Knecht 1993; McBrearty and Brooks 2000; Shea 2006), implying more habitual use of tools which would have reduced the muscular forces required for the same technological tasks. At the same time, attempts to document a difference in the behavioral implications of the Middle Paleolithic assemblages associated with Neandertals versus early modern humans in southwest Asia (e.g., Shea 1991, 2006) have provided little more than subtle frequency shifts between these assemblages. In this context, the general correlation of reducing OP EMA with technological changes across the Middle to Upper Paleolithic transition appears reasonable.

The shift in OP radial projection does not, however, fully correlate with indications of muscularity and strength elsewhere in the upper limb. In particular, there is a suite of distributional contrasts between the upper limb remains of Middle Paleolithic modern humans and Neandertals, which are consistent with indicating reduced muscularity and/or effective mechanical advantage in the MPMH sample. These differences include scapular breadth, pectoralis major insertion size, radial tuberosity average position, radial diaphyseal curvature, carpal palmar tuberosity size and projection, trapezio-metacarpal articular shape, pollical phalangeal length proportions, manual phalangeal articular dimensions, and distal phalangeal tuberosity size (Hambücken 1993; Niewoehner 2001; Trinkaus 1983, 2006; Trinkaus and Churchill 1990; Trinkaus and Villemeur 1991; Walker et al., 2011). It is true that the OP radial projection of the two MPMH MC1s is less than the average projection among the Neandertals, and neither Qafzeh 9 nor Skhul 5 has the prominent and rounded OP flange evident on some of the Neandertals (e.g., Amud 1, La Ferrassie 1 and 2, Kiik-Koba 1, and Regourdou 1). Yet, these two MPMH specimens are at the top of the MUP range of variation and among the recent humans with the most projecting OP insertion area.

In contrast, the reduction in OP effectiveness inferred for the Mid Upper Paleolithic humans, and probably for the one known Early Upper Paleolithic individual preserving MC1s, correlates with a general reduction in muscularity and mechanical effectiveness among these early modern humans relative to the Neandertals (Churchill and Rhodes 2006; Crevecoeur 2008; Trinkaus 1983, 2006; Trinkaus et al. 2006; Trinkaus and Villemeur 1991).

Similarly, the hypothesis that Neandertals are adapted for forceful manipulation has been put forward as an explanation for relatively flatter TMC joints in most Neandertals (and earlier *Homo*) as compared with early and recent modern humans, as an adaptation to habitually large axial joint reaction forces (Trinkaus 1989; Niewoehner 2001; Marzke et al. 2010). It has also been argued that increased MC3 styloid process projection and obliquely rather than parasagitally oriented MC2 capitate facets observed in early modern humans may have been better adapted to obliquely oriented loads (Niewoehner et al. 1997; Niewoehner 2001). Yet, more recent observations that MC3 styloid processes scale allometrically in Late Pleistocene humans (Trinkaus et al. 2010) raise questions about this inference. Moreover, it remains unclear how capitate-metacarpal articular variation relates to habitual load levels through the hand.

CONCLUSION

A metric reassessment of the mechanical implications of the frequently large and projecting opponens pollicis flanges on the Neandertals, in the context of Late Pleistocene early modern humans and recent humans, indicates that the primary contrast is between the Middle Paleolithic and the more recent human samples. Despite a series of contrasts in other functional aspects of the upper limb between Neandertals and Middle Paleolithic modern humans, which imply less habitual manipulative force generation in the latter, there does not appear to be a meaningful difference in opponens pollicis mechanical effectiveness between these two samples. There is, however, a consistent reduction in mechanical opponens pollicis effectiveness in earlier Upper Paleolithic modern humans, which correlates with the overall reduction in upper limb muscularity and technological elaborations.

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