Muscle recruitment and stone tool use ergonomics across three million years of Palaeolithic technological transitions

Abstract

Ergonomic relationships that minimise muscle activity relative to the creation of cutting stress underpin the design of modern knives, saws and axes. The Palaeolithic archaeological record, and the > 3 million years of technological behavior that it represents, is predominantly characterised by sharp stone implements used for cutting. To date, we do not know whether Palaeolithic hominins adhered to ergonomic principles when designing stone tools, if lithic technological transitions were linked to ease-of-use advances, or even how muscularly demanding different Palaeolithic tools are on an empirically defined relative basis.

Here, we report the results of an experimental program that examines how four key stone tool types, produced between ~ 3.3 million to ~ 40 thousand years ago, influence muscle activation in the hominin upper limb. Using standardized laboratory-based tests designed to imitate Pleistocene cutting behaviors, surface electromyography recorded electrical activity (amplitude) in nine muscles across the hand, forearm and shoulder of modern humans during the use of replica Lomekwian, Oldowan, Acheulean and Mousterian stone tools. Results confirm digit flexors and abductors, particularly the first dorsal interosseous and flexor pollicis longus, to be the most heavily recruited muscles during the use of all tool types. Significant differences in muscle activation are, however, identified dependent on the type of stone tool used. Notably, the abductor digiti minimi, flexor pollicis longus, and biceps brachii were highly activated during handaxe use, particularly when compared to the use of Oldowan and Levallois flakes. Results are discussed in light of current understanding on the origin of Lower and Middle Palaeolithic technologies, why specific tool types were produced over others during these periods, and the extent to which early hominins produced ergonomically designed tools.

1.0 Introduction

Hominins have relied on hand-held cutting-implements for over three million years. By facilitating access to food resources, providing a means to produce tools and clothing, and opening up new and otherwise inaccessible ecological niches, cutting-tools allowed Palaeolithic populations to spread throughout the Old World and colonize the vast interior of the Americas (Isaac, 1989; Ambrose, 2001; Eren, 2013; Dennell, 2017; Shea, 2017). Indeed, they were, and still are, essential for our survival.

Since the emergence of Palaeolithic archaeology as a discipline, people have sought to understand why one type or form of stone cutting-tool was produced over another (Boucher de Perthes, 1847; Evans, 1872; Ashton and McNabb, 1994; Key and Lycett, 2017a). Frequently these questions manifest themselves chronologically, with the observation that different stone technologies replaced and, presumably, were favored over other earlier types and forms (Isaac, 1969; Bar-Yosef, 1998; Ambrose, 2001; Foley and Lahr, 2003; Gowlett, 2009; Ollé et al., 2013; Shea, 2017). These technological and morphological transitions are often most clearly defined prior to the emergence of the Upper Palaeolithic.

The first flaked stone tool industry, the Lomekwian (Harmand et al., 2015), is currently known from a single 3.3 million-year-old locality in West Turkana, Kenya. Large flake implements (> 10 cm) with sharp edges suitable for cutting, produced through passive hammer and/or bipolar techniques, characterise these tools (Lewis and Harmand, 2016). By 2.6 Ma Oldowan stone technologies, associated with the production of flake cutting tools 3 - 5 cm in length and displaying the intentional production of sharp cutting edges (Toth, 1985; Roche, et al., 1999; Rogers and Semaw, 2009; Braun et al., 2019), come to dominate the archaeological record. Although these 'basic' flake tools continue to be produced throughout the Palaeolithic, the emergence of bifacially flaked large cutting tools (LCTs) during the Acheulean period (~1.75-0.3 Ma) represents a new level of investment and design intent in cutting technologies (Isaac, 1969; Goren-Inbar and Saragusti, 1996; Lycett and Gowlett, 2008; Semaw et al., 2009; Sharon, 2010; Wynn and Gowlett, 2018). Acheulean LCTs, principally characterized by handaxes and cleavers, are subsequently replaced as the foci of cutting technologies by Middle Palaeolithic (Mousterian) Levallois tools ~300 Ka (Moncel et al., 2011; Tron and Faith, 2013). Levallois flake tools, produced through predetermined hierarchical reduction strategies (Boëda, 1995; Brantingham and Kuhn, 2001; Eren and Lycett, 2012), vary in size (typically 3 - 15 cm in length [e.g. Tryon et al., 2006]) but characteristically display substantial lengths of effective cutting edge around their circumference (Brantingham and Kuhn, 2001; Eren and Lycett, 2016). Subsequent to the emergence of Late Middle and Early Upper Palaeolithic technologies there is increased complexity in the number of cutting-tool types produced, and finer chronological and geographic gradation between technological foci (Camps and Chauhan, 2011; Bicho et al., 2015).

68 Why Lower and Middle Palaeolithic hominins replaced one type or form of stone technology with
69 another has been discussed from diverse perspectives, in part due to the substantial variation that
70 exists in how and when these transitions occurred across the Old World. Previous research includes
71 investigation into hominin cognitive and anatomical capabilities (Wynn and Coolidge, 2004; Stout et
72 al., 2008; Faisal et al., 2010; Shipton, 2016; Key and Lycett, 2018; Key and Dunmore, 2018; Pargeter
73 et al., 2019), varying ecological contexts and the relevance of different tool-use performance
74 characteristics (McNabb, 2005; Shea, 2007; Rogers and Semaw, 2009; Shipton et al., 2013; Galán and
75 Dominguez-Rodrigo, 2014; Iovita, 2014; Key and Lycett, 2017b, 2017c; Bilbao et al., 2019), raw
76 material economic strategies (Brantingham and Kuhn, 2001; Muller and Clarkson, 2016; Lin et al.,
77 2018; Rezek et al., 2018), and population dynamics alongside the impact of socially mediated cultural
78 transmission mechanisms (Clark, 1987; Van Peer et al., 2003; Lycett et al., 2010; Moncel et al., 2012;
79 Lycett and Eren, 2013; Adler et al., 2014; Milhailovic and Bogicevic, 2017; Malinsky-Buller, 2016),
80 among others.

81 Equally, the idea that Lower and Middle Palaeolithic technological transitions coincided with
82 improvements to the ergonomic design of stone tools has been raised (e.g. Grosman et al., 2011; Eren
83 and Lycett, 2012; Wynn and Gowlett, 2018). That is, new stone technologies may have come to
84 dominate over previous alternatives because of their increased ease of use when held by the hand. No
85 studies have explicitly tested such hypotheses (although for tool production examples see Faisal et al.
86 [2010] and Key and Dunmore [2018]), but research concerning the evolution of the human hand
87 (Marzke and Shackley, 1986; Marzke, 1997; Rolian et al., 2011; Key and Lycett, 2018; Williams-
88 Hatala et al., 2018) or stone tool gripping strategies (Borel et al., 2016; Key et al., 2018a) has
89 indirectly examined tool-use ergonomics in different lithic technologies. Williams-Hatala et al. (2018),
90 for example, identified manual pressures incurred during percussive marrow extraction, a stone tool
91 behaviour likely to have occurred prior to 3.3 Ma, to be significantly greater than those observed
92 during flake and handaxe use. Meanwhile, Rolian et al. (2011) suggested that hominins were likely to
93 experience increased biomechanical stresses during Oldowan flake-tool use relative to larger stone-
94 cutting technologies (e.g. Lomekwian flakes, handaxes). There are, however, potential difficulties
95 aligning experimental data derived from modern humans with technological transitions enacted by
96 extinct hominins with (at times) distinct upper limb anatomy. Species with relatively small manual
97 dimensions (e.g. *Homo naledi, Australopithecus sediba*), for example, could have automatically
98 incurred increased musculoskeletal stresses when using larger tool types (Key and Lycett, 2018).

99 Archaeological studies often compare the functional performance of different Lower and Middle
100 Palaeolithic stone tool types and forms (e.g. Jones, 1981; Jobson, 1986; McCall, 2005; Prasciunas,
101 2007; Shea, 2007; Galán and Domínguez-Rodrigo, 2014; Key et al., 2016; Key and Lycett, 2017b;
102 Bilbao et al., 2019), but ergonomic considerations are almost exclusively based on subjective

103   observations by tool users or derived inferences. McNabb (2005: 292) provides a typically
104   characteristic and widely expressed example when stating 'at the most basic level the biface provides
105   a large cutting tool which is easier to hold [than a flake]. Its size allows the worker to maintain a
106   secure grip and apply continued pressure especially when the tool has become slippery as blood, fat
107   and other animal products adhere to the tool's surface during butchery'. Other works have inferred
108   there to be ergonomic design features in Palaeolithic technologies through morphological, usewear
109   and technological analyses of artefacts (e.g. Kleiniest and Keller, 1976; Phillipson, 1997; Tomka,
110   2001; Gowlett, 2006; Archer and Braun, 2010; Grosman et al., 2011; Eren and Lycett, 2012; Rots,
111   2013; Claud, 2015; Baena et al., 2016; Zupancich et al., 2016; Hardy et al., 2018; Wynn and Gowlett,
112   2018; Viallet, 2019). In many cases we agree with these statements and inferences, but to date these
113   hypotheses remain untested using empirical musculoskeletal data derived from experiments or
114   biomechanical modelling.

115   Electromyography (EMG), a technique which uses surface or intramuscular sensors to record
116   electrical activity (potential) during muscular contractions, is routinely applied during ergonomic
117   investigations of modern hand-held tools (e.g. Grant and Habes, 1997; Freund et al., 2000; Gazzoni et
118   al., 2016). Increased electrical activity, which indicates increased muscle force output achieved by an
119   increase in motor nerve firing (Milner-Brown et al., 1973), demonstrates muscles to be working
120   harder during the use of specific tool types or forms. Archaeological and anthropological research has
121   yet to widely incorporate EMG techniques; only the pioneering work of Hamrick et al (1998) and
122   Marzke et al. (1998) have done so in relation to stone tools. Marzke et al. (1998) used intramuscular
123   EMG to investigate electrical activity in 17 hand muscles during the production of replica Oldowan
124   flake tools. They identified the flexor pollicis brevis, flexor carpi ulnaris, first dorsal interosseous,
125   second flexor digitorum profundus and fifth flexor digitorum profundus to be heavily recruited and
126   essential for effective stone tool production. Hamrick et al (1998) investigated the use of flake stone
127   tools, but only did so for the flexor pollicis longus (FPL), and only compared flake tool use to
128   hammerstone use or 'fine manipulation' behaviours. They identified FPL electrical activity to increase
129   in line with resistance to the thumb's volar pad, but conclusions concerning which tool-use behavior
130   more heavily recruited the FPL were participant dependent. Despite requirements for additional EMG
131   tool-use investigations being noted at the time (Markze et al., 1998), no other studies have been
132   published (although also see Feuerriegel [2016]).

133   Our understanding of tool-use ergonomics through the Lower-to-Middle Palaeolithic period, and how
134   they may have informed changes in technology are, therefore, limited. Here, we report the first large-
135   scale analysis of muscle activation during the use of multiple stone tool types spanning the Lower and
136   Middle Palaeolithic. Using surface electromyography (sEMG), we investigate nine muscle in the
137   upper limb of 30 modern humans while they use replica Lomekwian, Oldowan, Acheulean and

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138 Mousterian stone tools. Results provide the first data-driven ergonomic perspective on the invention

139 and persistence of multiple Lower and Middle Palaeolithic stone technologies.

140 **2. 0 Methods**

141 *2.1 Recording muscle activity*

142 During contraction, muscle fibers produce electrical signals through the propagation of intracellular

143 action potential (IAP). The electrical potential field generated by IAP in the outer fibers of muscles

144 can, in turn, be recorded by electrodes attached to the skin's surface (ionic current in the muscles is

145 converted into a flow of electrons in the electrode). Here, sEMG was employed to record electrical

146 activity at nine muscles sites on the dominant upper limb during stone tool use. Silver chloride (AgCl)

147 adhesive bipolar surface electrodes (24mm diameter) were attached to the skin relative to the

148 respective muscle belly according to international sEMG standards and SENIAM guidelines

149 (Hermens et al., 2000; Stegeman and Hermens, 2007). Signals for each electrode pair were amplified

150 using a gain of between 500 and 2000 V/V (participant dependent), sampled at 2048 Hz, and

151 converted to digital data using a 12-bit analog-to-digital converter (EMG-USB2+, OT Bioelettronica,

152 Torino, Italy; bandwidth 10-500 Hz). All signals were acquired in OT BioLab software.

153 The nine target muscles, their location, the site of sensor placement, and each muscle's movement

154 action are detailed in Table 1 and Figure 1. Investigated muscles include those important to stone tool

155 use and the unique manipulative capabilities of modern humans (e.g. flexor pollicis longus, abductor

156 digiti minimi), those essential to ours and other primates gripping capabilities and manual dexterity

157 (e.g. flexor pollicis brevis, flexor carpi radialis), and those associated with broader ranges of motion in

158 the upper limb (e.g. brachioradialis, biceps brachii) (Marzke et al., 1998; Diogo et al., 2012). Due to

159 the first dorsal interosseous', flexor pollicis brevis' and abductor digiti minimi's small size, electrodes

160 at these target sites were cut in half such that both could be placed above the muscle (Fig. 2).

161 The volume and characteristics of tissues (skin, subcutaneous fat etc.) separating muscle fibers from

162 electrodes have potentially large deforming and filtering effects on sEMG signals. We followed well-

163 established protocols to minimise these effects (Hermens et al., 2000; Farina et al., 2016; Merletti et

164 al., 2016). Prior to sensor attachment hair was removed from each site using a razor and cleaned using

165 70 % isopropyl alcohol swabs. Filtering effects are minimized by bipolar electrode spatial filtering,

166 however, additional controls included the standardization of electrode size, inter-electrode distances,

167 and their attachment being performed by the same experienced individual (IF). Crosstalk between

168 neighboring muscles is dependent on the target site, and is not likely to have had substantive impact

169 on recordings from large muscles or those isolated by other tissues. Following sensor positioning,

170 visual checks of each signal channel were performed to ensure absence of cross-talk when contracting

171 individual muscles. The flexor pollicis brevis experienced a degree of crosstalk from the abductor

172   pollicis brevis that could not be controlled for (although this is consistent for all participants and
173   tools). Finally, as far as was practical the experiment was conducted away from other electrical
174   sources to minimise interference potential. The amplifier was located behind participants and a
175   reference electrode was dampened with water and placed around the wrist of the non-dominant arm.

176   *2.2 sEMG data*

177   Muscular activity is recorded here as both a raw measure of amplitude, in this case the signal's root
178   mean square (RMS), and amplitude normalized as a percentage of that recorded during maximum
179   voluntary contractions (% MVC). Six MVC exercises were recorded from each participant prior to
180   tools being used, capturing MVC amplitude for each of the nine muscles under investigation here to
181   contextualise the RMS values reported for each muscle (Supplementary Online Material (SOM) Table
182   S1). Increases in amplitude of sEMG signals (i.e. signal strength) indicate the activation of additional
183   motor units, alongside modulation of IAP discharge rates (Fig. 3). The force created by muscles is
184   similarly dependent on motor unit recruitment and IAP discharge. In some muscles, such as those
185   controlling the fingers, the relationships between EMG amplitude and force can be considered linear
186   (Clancy et al., 2016; Enoka and Duchateau, 2016). Hence, RMS and % MVC can also provide
187   information about muscle contraction 'strength'.

188   Prior to RMS values being calculated, band pass filtering (double passed [zero-lag] 2nd order digital
189   Butterworth filter) between 10 Hz to 350 Hz was applied to all raw signals (Fig. 3). These standard
190   filtering parameters remove possible movement artefacts associated with whole body movement (not
191   the contraction of targeted muscles) and possible high frequency noise. RMS values were calculated
192   individually for 0.4 s time 'epochs' within each recorded sEMG signal, thus providing a degree of
193   smoothing to reduce signal variability (Fig. 3). For example, during a 30 second period 75 RMS
194   values would be calculated. Only RMS data that related to periods of stone tool-use were analyzed.
195   Digital videos were used to precisely define tool-use periods within data streams, or alternatively,
196   when participants rested, readjusted their body, or were waiting to start the task. A single individual
197   (AK) assessed all videos. In instances where participants briefly paused during the task, RMS values
198   from the period of cessation were removed from the analyzed data. On occasion, tools exerted
199   considerable pressure on the superior surface of the flexor pollicis brevis sensor due to the use of the
200   thenar eminence during five-jaw buttressed pad-to-pad grips, among others (very occasionally similar
201   pressures occurred at other target sites) (for grip descriptions see: Marzke, 1997; Key et al., 2018).
202   This resulted in signal clipping, saturation or motion artefact distortion (Fig. 3). If < 25 % of values in
203   a trial displayed these features then these portions were cut and the remaining data were used. If > 25 %
204   of data were distorted then the whole trial was discarded from the study. Hence, data sets for
205   individual target muscles can be below 30.

206

2.3 Stone tool assemblages and participants

208 Muscle activation was investigated during the use of four stone tool types (Fig. 4). These tools

209 span >3 million years of Plio-Pleistocene technological behavior, ranging from the earliest known

210 intentionally fractured Lomekwian flake technology through to Mousterian Levallois flakes (Fig. 3).

211 The four stone tool types utilized in this study are;

212   • Lomekwian large flake tools (LOM), as described by Harmand et al (2015).

213   • Oldowan flake tools (OLD), as outlined by Roche et al. (1999).

214   • Acheulean handaxes (ACH), as defined by Lycett and Gowlett (2008).

215   • Levallois flake tools (LEV), as described by Boëda (1995).

216 For each technology, 40 replica tools that conform to mass, size and shape ranges observed in the

217 archaeological record were produced (a random sample of 30 were used). Descriptive morphological

218 data for the utilized tool assemblages can be found in Table 2.

219 Palaeolithic stone tools display morphological fluidity within and between technological categories

220 and those utilized here broadly represent idealized forms that characterize their respective 'types'. The

221 present study therefore focuses on differences between types of stone tool, and not variation observed

222 within artefact classifications. Although there are multiple morphological and technological

223 differences between the tool types used here, key differences include their gross size, the presence or

224 absence of a 'globular butt' (c.f. Gowlett, 2006), the presence or absence of cutting edge scalloping,

225 and a tool's elongation and weight.

226 Each experimental subject (n = 30; 11 female, 19 male) was randomly assigned one tool from each of

227 the four assemblages, with these four tools being used in a randomly assigned order (both designated

228 using randomizer.org). Subjects were recruited from the student and staff population at the University

229 of Kent. All but two individuals had no prior training or education regarding Palaeolithic technologies,

230 and all were naïve of the aims of the experimental program (the majority were sports science graduate

231 students). The manual strength of participants was variable, with mean and standard deviation values

232 for pad-to-side pinch strength equalling 8.8 kg and 2.1 kg, respectively (recorded using a pinch

233 dynamometer). Informed consent was obtained prior to participation and all individuals received

234 nominal remuneration for their time (£10 [~$13]).

235 Inevitably, all participants display modern human (*H. sapiens*) upper limb anatomy. The replica tools

236 used in this experiment, however, represent artefacts produced by multiple hominin species across ~

237 three million years. Given that soft tissue anatomy is rarely preserved in the fossil record it is hard to

238 precisely define the accuracy with which results from this study can be applied to some hominin

239 species. We would contend that for most Middle-to-Late Pleistocene populations there is enough

240 evidence to suggest modern human-like manual capabilities and anatomy in these species (Marzke,

241 2013; Mersey et al., 2013; Ward et al., 2014; Kivell, 2015; Key and Lycett, 2018). Therefore, results

242 can likely be applied to these populations with reasonable accuracy. Late Pliocene and early

243 Pleistocene stone tool users, however, display more substantial anatomical differences compared to

244 modern humans. Although fossil evidence indicates these earlier species (e.g. *Au. afarensis*) to be

245 potential stone tool users (Marzke, 1983, 2013; Almécija and Alba, 2014; Feix et al., 2015; also see

246 Domalain et al., 2017), suggesting the muscular architecture essential for stone tool use to be present,

247 we would urge pragmatism in the application of our results to these species.

2.3 Cutting task

249 Consistent with previous research (Prasciunas, 2007; Key and Lycett, 2017b, 2018; Bilbao et al.,

250 2019), the cutting task used modern industrially standardized materials so that conditions were

251 identical for each stone tool. This provided high levels of internal validity (Lycett and Eren, 2013) and

252 appropriately focused our investigation on differences between cutting implements and not the

253 worked material (Eren et al. 2016; Lin et al. 2018). Following Key et al. (2016), all stone tools cut

254 through a series of materials attached to a frame placed on the floor. A 70 x 180 cm aluminium frame

255 was custom built for the study and inclined on the floor at an angle of 15°-20° from vertical, such that

256 it lent away from participants when they knelt beside it (Fig. 1). The frame had five sections and four

257 unique cutting tasks. Before the use of each tool, individuals undertook practise cutting actions to

258 familiarize themselves with how best to resist cutting forces and grip the tool. Individuals were

259 required to use their dominant hand (self-reported) but were free to grip tools however they preferred.

260 The non-dominant hand could be used to secure and/or steady the cut materials. All subjects were

261 asked to perform the cutting task as quickly as possible, but were informed they must 'always remain

262 in full control of the tool, and use a slicing cutting motion' (i.e. no cleaving or uncontrolled hacking).

263 Subjects were first required to cut a 90 cm long 'S' shaped line, at a depth of 2 cm, into a slab of

264 pottery clay placed on a metal sheet secured by the aluminium frame (Fig. 1). Use of a stencil to

265 lightly mark the line on the clay's surface ensured each cut was identical. The second section required

266 subjects to cut through eleven 9-11 cm long segments of 4mm thick, heavy duty, polypropylene twine

267 arranged spherically and dissipating away from a central metal ring (Fig. 1). Five 16 cm segments of

268 the same twine, secured vertically, formed the third cutting task section. Segments four and five were

269 identical and consisted of ten 12 cm long twine segments secured horizontally. All twine segments

270 were secured using plastic hooks attached to metal eye bolts. Task duration varied between

271 participants and tool types, but typically took 1-3 minutes to complete. Subjects were given a 10-

272 minute rest between each tool use event.

273 While these tasks do not directly recreate Palaeolithic cutting activities, they do replicate cutting

274 motions consistent with butchery and woodworking activities (among others), enforce the use of

275 varied and dynamic cutting motions in a naturalistic kneeling position, and allow data collection in a

controlled and systematic manner. Moreover, differences between the present activities and some Palaeolithic cutting conditions are known, allowing material differences to be accounted for (Key et al., 2018b). To protect the hand and palmar sensors from damage a thin rubber glove was worn on the tool-using hand. Ethical approval was granted by the University of Kent School of Sports and Exercise Science (ref: prop 131_2016_17).

2.4 Statistical analysis

For every participant, mean RMS values were calculated for the nine target muscles during each tool use event (SOM Table S2). Due to signal strength variation and site dependent filtration / deforming effects on sEMG signals raw amplitude data (i.e. RMS) are not directly comparable between different target muscles. Hence, mean RMS values are used here to compare between activation levels for specific muscles dependent on the stone tool being used. Analysis of variance (ANOVA) tests were used to investigate which stone tools recruited individual muscles to a greater or lesser extent, as defined by mean RMS values, during the use of Lomekwian, Oldowan and Levallois flakes and Acheulean handaxes (α = .05). Tukey's honest significance difference (HSD) post hoc tests were used to identify where any significant differences may lie (α = .05).

MVC normalised amplitude values, where mean RMS values are expressed as a percentage of mean MVC RMS values (% MVC), facilitate comparison of recruitment levels between muscles during stone tool use events. This makes it possible to see, on a relative basis, which of the nine target muscles are recruited most heavily during stone tool use, and how this varies dependent on the type of tool being used. Percentile data is not continuous, often bounded (here, only by a lower threshold), and in some instances, data here were not normally distributed (revealed by Kolmogorov-Smirnov tests). In turn, Kruskal-Wallis tests were used to identify whether significant % MVC differences exist between muscles during the use of each tool type (α = .05). To identify where any significant differences may lie (if there are any), post hoc Mann-Whitney U tests were run between individual muscle's % MVC values.

Supplementary to the ANOVA tests comparing activation levels for individual muscles, dependent on the type of stone tool used, Kruskal-Wallis tests and post-hoc Mann-Whitney U tests using % MVC values were also performed. These repeat tests investigate the same question, but use normalised amplitude values to support those performed using RMS data. All data were analysed using PAST (version 3.25).

3.0 Results

3.1 Impact of tool type on muscle activation

ANOVA tests reveal sEMG signal amplitude to vary significantly for the abductor digiti minimi, dependent on the type of stone tool used (Table 3). This was consistent for both the clay and rope

cutting tasks. Post-hoc Tukey's HSD tests identified handaxes to display significant greater abductor digiti minimi RMS values relative to both Oldowan and Levallois flakes (SOM Table S3).

No other ANOVA tests between tool types returned significant differences in muscle RMS values at a 95% confidence interval (Table 3). Both the flexor pollicis longus and biceps brachii, however, displayed values approaching significance during the clay-cutting task. Post-hoc Tukey HSD tests using RMS data identified handaxes as displaying significantly greater values relative to Levallois flakes for the flexor pollicis longus during this task, but no significant differences between any tools for the biceps brachii (SOM Table S3). Supporting Kruskal Wallis tests performed using normalised % MVC data did, however, identify significant differences in flexor pollicis longus and biceps brachii activation dependent on the stone tool being used (SOM Table S4). The associated supporting post-hoc Mann Whitney U tests (using % MVC data) similarly only suggest significant differences in activation levels for the abductor digiti minimi, flexor pollicis longus and biceps brachii (SOM Table S5). All three muscles identified handaxes as requiring significant greater activation (% MVC) compared to Oldowan and Levallois flakes (SOM Table S5). The FLP also identified a significant difference between Levallois and Lomekwian flakes, while the BB displayed significant differences between Oldowan and Lomekwian flakes (Lomekwian flakes returned greater values in both cases). In sum, only abductor digiti minimi, flexor pollicis longus and biceps brachii activation was significantly affected by the type of stone tool used.

3.2 Relative muscle activation across the arm

Comparisons of muscle % MVC values using Kruskal Wallis tests, run independently for the four stone tool types and the two cutting tasks, returned significant differences in all instances (Table 4). The nine target muscles were, therefore, recruited to significantly different extents during the experimental task.

Post-hoc Mann-Whitney U tests elucidate these differences, and when combined with descriptive data reveal which specific muscles were used to a significantly greater or lesser extent (SOM Tables S2 and S6). The most heavily recruited muscles are responsible for flexion, adduction or abduction of the digits and in-hand manipulation. Of these, the first dorsal interosseous and flexor pollicis longus display the greatest % MVC values across all tool types in most instances, and are thus on a relative basis the most heavily recruited muscles investigated here. While there are differences dependent on the specific tool used or cutting task undertaken, the FDI and FPL were most often significantly greater than the FCR, B, BB, TB, and AD (SOM Table S6).

The flexor pollicis brevis was also heavily recruited, albeit usually to a lesser extent that the FDI and FPL (Fig. 5; SOM Table S1). Significant differences between the FPB and FCR, B, BB, TB, and AD are repeatedly observed, except during the rope-cutting task with the Levallois flake (SOM Table S6). The abductor digiti minimi is heavily recruited during the use of handaxes (Fig. 5; SOM Table S1),

345   particularly during the clay task, where % MVC values were significantly greater than those seen in

346   the FCR, B, BB, TB and AD (SOM Table S6). The two smaller flake types (Oldowan and Levallois)

347   recruit the ADM to a lesser extent (Fig. 5; SOM Table S1).

348   Muscles responsible for rotation and flexion of the hand at the wrist (flexor carpi radialis), flexion and

349   extension of the forearm (brachioradialis, biceps brachii, triceps brachii), and abduction of the

350   humorous (anterior deltoid) were less heavily recruited (Fig. 5; SOM Tables S2 and S6). In particular,

351   the biceps brachii and brachioradialis typically displayed the lowest % MVC values.

352   **4.0 Discussion**

353   Why Lower and Middle Palaeolithic hominins produced specific stone tool types for extended periods,

354   or invented alternatives for existing technologies, are fundamental questions that have been

355   investigated from diverse perspectives. Studies concerning manual-related aspects of these

356   technologies have grown in number and complexity in recent years. Still, we know little about how

357   ergonomic considerations influenced hominin stone tool production and use decisions. Here, we have

358   taken a first step towards empirically defining the upper limb ergonomics of Lower and Middle

359   Palaeolithic stone tool use.

360   *4.1 Impact of tool type on muscle activation*

361   Four types of stone tool were used in a standardized cutting task and their influence on electrical

362   activity (amplitude) in nine upper limb muscles was recorded. Significant differences in muscle

363   activation were identified between the four stone technologies. Foremost, abductor digiti minimi

364   amplitude was highly dependent on the type of tool used, with handaxes requiring significantly

365   greater activation levels, and therefore force outputs (Clancy et al., 2016; Enoka and Duchateau,

366   2016), relative to Oldowan and Levallois flakes. For the ADM then, handaxe use does not provide an

367   ergonomic advantage relative to their technological precursor, Oldowan flakes. Levallois flakes,

368   which come to prominence as characteristically 'Acheulean' handaxes start to occur less frequently in

369   the archaeological record, do however present a benefit relative to this larger, earlier technology.

370   The heavy recruitment of the ADM during handaxe use is not surprising. Indeed, Marzke et al. (1998)

371   reported high ADM activity in the non-dominant hand during stone tool production because of its

372   important role stabilising the fifth digit, and in turn, ulnarly located portions of cores. Marzke and

373   others also report that the fifth digit is only frequently recruited during the use of larger lithic

374   technologies (Marzke and Shackley, 1986; Key et al., 2018a), due to its ability, when abducted using

375   the ADM and flexed across the midpoint of the palm, to oppose the thumb and stabilise tools of this

376   size. There are also indications of larger tools increasing loading on the fifth digit (Williams-Hatala et

377   al., 2018), which in turn would place greater demands on the ADM. Combined, it is logical that the

use of handaxes, a technology substantially greater in size and mass than smaller flake tools, would result in high ADM activation.

Raw amplitude and MVC normalised data also reveal the flexor pollicis longus (FPL) to experience significantly greater activation during handaxe use compared to Levallois or Oldowan flakes. This indicates the first distal phalanx to be working harder to secure handaxes during cutting activities (Diogo et al., 2012). Again, then, the use of handaxes is not ergonomically beneficial relative to Oldowan or Levallois flakes and provides no ease-of-use advantages in terms of muscle activation. This finding corresponds with Williams-Hatala et al. (2018) who found pressure exerted and resisted by the first distal phalanx to be greater during handaxe use relative to small flake tool use. There are indications that Lomekwian flakes returned higher FPL activation levels relative to Levallois flakes, and thus may be more demanding to use. However, this was only significant during one cutting task using % MVC data, and we urge caution when interpreting this result.

Biceps brachii (BB) activation altered in a similar manner to the ADM and FPL; that is, handaxe use elicited significant increases in amplitude, relative the use of Oldowan or Levallois flakes. Again then, handaxes provide a disadvantage relative to smaller flake tools. The role of the BB during stone tool use is not well understood as it does not directly contribute to in-hand manipulation of tools. Our finding that BB activation varies dependent on the type of stone tool used is, however, consistent with this muscle contributing to the effectiveness of a stone tool's use. We predict variation in BB activation to result from the distinct cutting motions required by each technology. Indeed, ergonomic research concerning modern metal cutting tools confirms BB activation and force output to be affected by grip choice, body posture, and cutting direction during butchery behaviors (Grant and Habes, 1997; Pontonnier et al., 2012). A handaxe's longer cutting edge allows for greater and potentially more forceful cutting motions that more heavily activate the BB as the tool is drawn towards and across the worked material. Smaller flake tools are more likely to recruit the BB in a stabilizing role, with wrist flexion drawing the tool across a worked material. Lomekwian flakes returned higher BB amplitude values compared to Oldowan flakes during the clay task; perhaps for similar reasons as handaxes. Significance at $\alpha = .05$ was, however, only just achieved and differences were not as strong as those observed for handaxes.

At a broad level, the differences in ADM, FPL and BB activation observed here likely result from tool-type size variation. Handaxes are substantially heavier and larger than Oldowan and Levallois flakes, have longer scalloped cutting edges, and facilitate force application away from the hand which results in torsion (Gowlett, 2006, 2013); features that could cause muscles to work harder when gripping a tool or applying it to cutting tasks (Key, 2016). Previous studies, however, suggest the precision grips associated with flake tools to elicit greater stresses in the first digit (Rolian et al., 2011), and hand musculature more generally (Tomka, 2001), relative to larger tool types. This is, in

413 part, due to associated forces focusing on a few key manual areas (e.g. first volar pad, lateral side of

414 second digit), while larger tools more evenly distribute forces across additional palmar aspects of the

415 hand; as demonstrated by the recruitment of the ADM to secure handaxes. An inferred more secure

416 and evenly distributed grip underlines many of the positive ergonomic connotations associated with

417 handaxes (e.g. Jones, 1981; McCall, 2005; Shea, 2007; Toth and Schick, 2009; Grosman et al., 2011;

418 Key et al., 2016; Viallet, 2016). Our results are not contradictory; increased contact between the hand

419 and tool would distribute stresses more evenly across the hand and increase the security of grips.

420 Instead, our data suggest that despite this, muscles still have to work harder to secure handaxes in the

421 hand and apply them to worked materials when compared to flakes. The few differences identified

422 between Lomekwian flakes, which were of comparable size to handaxes, and the other three tool

423 types further suggests that the specific shape of handaxes (i.e. elongation, edge scalloping) may also

424 be playing a role. For example, their more obtuse edges relative to flake tools (Table 2) likely

425 increased force requirements during use (Key and Lycett, 2015). Although not explicitly tested here,

426 we suspect Middle Palaeolithic handaxes (e.g. Emery, 2010; Ruebens, 2013; Ashton and Scott, 2016)

427 to present similar muscular demands to their Acheulean counter parts; thus, being more demanding to

428 use relative to contemporary Levallois flakes.

429 Six muscles were not significantly affected by tool-type changes, despite the size, shape and

430 technological differences. This includes the first dorsal interosseous (DI) and flexor pollicis brevis

431 (FPB) which abduct the second proximal phalanx / adduct the first metacarpal and flex the first

432 metacarpal (respectively), allowing the thumb to forcefully oppose the fingers during stone tool grips.

433 For these muscles, all four tools appear to be similarly demanding. This may, in part, reflect a balance

434 between the demands of securing larger tools and the increased stresses on the first digit associated

435 with precision grips. It is interesting that requirements for the first metacarpal to oppose the fingers

436 remain relatively stable between tool types, despite the first distal phalanx being flexed with greater

437 force during handaxe use. The lack of any differences for the brachioradialis (B), flexor carpi radialis

438 (FCR), triceps brachii (TB) and anterior deltoid (AD) are less surprising. Their MVC % values are

439 substantially lower and any grip or cutting motion differences between tool types do not appear to be

440 substantial enough to affect activation levels in these muscles.

441 *4.2 Muscle activation across the arm*

442 Our data confirm muscles responsible for digit flexion and in-hand manipulation to be highly

443 activated during stone tool use. Expressed as a percentage of maximum voluntary contraction levels (%

444 MVC), mean values regularly exceeded 50 % for the first DI, FPL and FPB, while the ADM ranged

445 between 30 – 40%. This compares to the more frequent occurrence of 10 - 30 % of % MVC for the

446 other five investigated muscles. Differences between muscles were significant in many instances. The

447 muscles most heavily recruited during stone tool use are, therefore, those that secure tools within the
448 hand and not those responsible for larger ranges of motion associated with cutting actions.

449 Of those examined, the FPL and first DI are the most heavily activated muscles across all four
450 technologies. Lower and Middle Palaeolithic cutting-tool use would therefore have likely relied
451 heavily on these muscles, irrespective of the stone implement utilized. This is not surprising as the
452 FPL inserts into the base of the first distal phalanx and is responsible for its forceful flexion during
453 stone tool related grips (Marzke and Shackley, 1986; Marzke et al., 1998; Diogo et al., 2012). Our
454 data supports Hamrick et al. (1998), who demonstrated the FPL to be highly activated during flake
455 tool use, and corroborates previous research identifying high loading through the first distal phalanx
456 during flake and handaxe use (Marzke, 1997, 2013; Rolian et al., 2011; Key and Lycett, 2018;
457 Williams-Hatala et al., 2018). Moreover, the high FPL amplitude levels recorded here further
458 underlines the important and forceful role of the first digit during stone tool use, and lithic
459 technology's potential impact on the evolutionary trajectory of the hominin hand (Marzke, 1997, 2013;
460 Kivell, 2015).

461 The first DI is as heavily recruited as the FPL, and both are activated more than the FPB and ADM
462 (which are in themselves still highly activated). The high activation of the first DI is consistent with
463 previous studies that note its essential role in adducting the thumb and bringing it into opposition with
464 the fingers during stone tool use (Marzke et al., 1998; Marzke, 2013; Kivell, 2015). It is not that the
465 FPB and AMD are not vital to the effective use of stone tools. Rather, on a relative basis, the FPL and
466 first DI are the muscles most heavily recruited, those most likely to contribute to perceptions of 'ease-
467 of-use', and therefore the muscles most likely to influence tool design and use choices.

468 The FCR, B, BB, TB, and AD display much lower mean % MVC levels relative to those contributing
469 to the in-hand manipulation and gripping of tools. Again, this does not mean that they are not essential
470 for stone tool use; after all, you cannot draw a tool across a worked material without triceps. Rather,
471 these muscles are not heavily recruited relative to their potential activation levels and force output,
472 and therefore, can easily cope with the associated muscular demands. Muscles directly responsible for
473 gripping tools, particularly those responsible for flexion and adduction of the thumb (i.e. FPL and first
474 DI), are therefore most likely to contribute to the ergonomic limits and preferences influencing
475 Palaeolithic stone tool designs.

476 *4.3 Implications for technological change in the Lower and Middle Palaeolithic*

477 The Palaeolithic archaeological record does not often display geographically or chronologically
478 uniform technological transitions. Nor does any single explanatory hypothesis account for these
479 changes; although some variables are more relevant than others in specific circumstances. Constant
480 throughout, however, is the fact that stone tools were held by the hand. Ergonomic considerations

481 therefore had potential to influence technological transitions, tool preferences, and design features
482 throughout the Palaeolithic.

483 *4.4 Lomekwian to Oldowan transition, or, large flake use versus small flake use*

484 The Lomekwian is currently a relatively poorly understood period, requiring additional sites to better
485 define its chronological, geographical and technological boundaries (Harmand et al., 2015). The
486 Oldowan, however, is technologically well established and multiple sites indicate its origin ~2.6
487 million years ago in East Africa (Roche, et al., 1999; Rogers and Semaw, 2009; Braun et al., 2019).
488 From a tool-use perspective, the Lomekwian's distinctiveness (as it is currently understood) relates to
489 the large size of flake tools, which are often over 10cm in length. Although similarly large flakes are
490 on occasion found during the Oldowan (e.g. Leakey, 1971; Proffitt, 2018), mean tendencies are much
491 smaller and this difference requires explanation. Our data suggests there to be limited differences in
492 muscle activation during the use of these two flake sizes. There was a single instance of Lomekwian
493 flake's % MVC being significantly greater than the smaller Oldowan alternative, but it only just
494 reached significance ($p = .0452$) and was for the biceps brachii, one of the least heavily recruited
495 muscles examined here. We therefore do not interpret this as strong evidence of Oldowan flakes
496 displaying ergonomic benefits enough to prompt the invention and use of a new technology. Nor is
497 there evidence that the use of different sized flakes (up to a limit) during either period would have
498 substantially impacted muscle activation levels. Importantly, however, due to the duration of the
499 cutting task our results cannot consider fatiguing and it is still possible for one flake type to display
500 benefits over more extended durations.

501 *4.5 Oldowan to Acheulean transition, or, small flake use versus handaxe use*

502 Flake tools of variable size continue to be produced during the Acheulean, however, after ~1.75 Mya
503 the production of handaxes is sustained and widespread across the Old World (Lycett and Gowlett,
504 2008). These large, bifacially flaked core tools represent a markedly more complex and demanding
505 (time, raw materials, cognition) technology relative to flakes. Our results suggest that the invention
506 and subsequent proliferation of handaxes is unlikely to be related to ease-of-use advantages during
507 cutting tasks. Rather, we provide evidence to the contrary, demonstrating handaxe use to be more
508 muscularly demanding relative to smaller flake tools. Relatively small 'Oldowan-like' flake tools
509 would, therefore, have been beneficial to use when cutting materials of a similar volume and
510 resistance to those examined here, promoting their production during the Acheulean. The invention
511 and prolonged production of handaxes, by multiple hominin species, therefore requires an alternative
512 explanation.

513 Functional advantages are still likely a primary cause underpinning the production of handaxes. These
514 tools are known to be particularly effective compared to flakes during heavy-duty cutting tasks (Jones,
515 1980, 1994; Toth, 1985; Toth and Schick, 2009; Galán and Domínguez-Rodrigo, 2014; Key and

15

516 Lycett 2017b), and the relative speed, reliability and efficacy of cutting behaviors has potential to be
517 more advantageous to hominins (in some situations) in spite of any ergonomic costs (during the clay
518 cutting task, for example, handaxes were 10-20% quicker than Oldowan and Levallois flakes).
519 Moreover, particularly resistant or extended cutting tasks, such as woodworking behaviors, were not
520 undertaken here. We think it likely that the increased cutting stress required to work hard materials
521 would result in fore- and upper arm muscles contributing proportionately greater forces, and being
522 more highly activated. Force transfer through the tool and onto the worked material would, in turn, be
523 more easily and comfortably facilitated by the greater tool-hand contact areas observed for handaxes
524 (Marzke and Shackley, 1986; Key et al. 2018a; Wynn and Gowlett, 2018). Further, we suspect that
525 rates of muscle fatiguing may differ between handaxes and smaller flake tools, with the former being
526 of greater benefit over extended duration. Within such contexts, handaxes still represent "an
527 ergonomically guided solution to the problem of producing a sturdy hand-held cutting tool" (Wynn
528 and Gowlett, 2018: 27). However, as with other recent studies, we also stress the potential influence
529 of multiple other factors in promoting handaxe production (Diez-Martín et al., 2015; de la Torre, 2016;
530 Key and Lycett, 2017b; Semaw et al., 2018; Wynn and Gowlett, 2018; García-Medrano et al., 2019;
531 Herzlinger and Goren-Inbar, 2019).

532 *4.6 Acheulean to Middle Palaeolithic transition, or, handaxe use versus Levallois flake use*

533 The Middle Palaeolithic transition is associated with the arrival of Levallois flakes, a variably sized
534 cutting technology (e.g. 3 - 15 cm in length) produced through predetermined hierarchical reduction
535 strategies (Boëda, 1995; Brantingham and Kuhn, 2001; Eren and Lycett, 2012). Although handaxes
536 continue to be produced during this period, Levallois technologies represent a widespread and
537 sustained phenomenon across the Old World that likely conveyed a benefit for hominins. Here we
538 demonstrate that Levallois flakes are ergonomically advantageous relative to handaxes when applied
539 to a range of cutting tasks, and thus may have been preferentially produced due to their lower
540 muscular demands and ease-of-use advantages. The context-specific functional benefits of handaxes
541 over 'basic' flake tools can, however, be similarly repeated for Levallois flakes; helping to explain the
542 sustained production of bifaces through the Middle Paleolithic (e.g. Reubens, 2013). However, there
543 is nonetheless a clear benefit to the use of Levallois flakes in some functional contexts. Our finding of
544 no difference in muscle activation between the Levallois and 'basic' (Oldowan) flakes is also
545 important. Indeed, the invention of Levallois flakes, and their production over more straightforward
546 alternatives, cannot be attributed to differences in their upper limb ergonomics (as revealed through
547 muscular activation). Alternative explanations must therefore continue to be emphasised (e.g. Eren
548 and Lycett, 2016; Shimelmitz et al., 2016; Malinsky-Buller, 2016).

549 *4.7 Further considerations*

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550   It is important to note that we have not investigated all stone tool types that emerged during the Lower

551   and Middle Palaeolithic. We focus on large flakes, 'basic flakes', handaxes and Levallois flakes

552   because they represent the technological foci of their respective periods and have consequently been

553   the focus of research seeking to explain changes in early human technological behavior. Attempts to

554   understand ergonomic-related behavioral changes across the Lower to Middle Palaeolithic should,

555   therefore, first start with these four technologies. Nonetheless, other stone tool technologies will likely

556   recruit muscles in variable ways and we cannot attest to how their production may have been affected

557   by tool-use ergonomics. In a similar regard, the tool types investigated here were not highly variable

558   in their shape or size. These additional factors and how they relate to ergonomic issues also require

559   future clarification.

560   The nine muscles investigated here have allowed assessment of muscular activity across the upper

561   limb of modern humans. Nonetheless, other muscles are linked to the effective use of stone tools

562   (Marzke et al., 1998; Diogo et al., 2012) and it has yet to be seen how their activation is affected by

563   the type of tool used. Moreover, in some respects the hominins responsible for using Lower and

564   Middle Palaeolithic technologies would have displayed upper limb anatomy distinct to the modern

565   humans in the present experiment (e.g. Niewoehner, 2001; Marzke, 2013; Mersey et al., 2013; Kivell,

566   2015; Tocheri et al., 2008; Domalain et al., 2017; Feuerriegel et al., 2019). It is not yet clear if the

567   ergonomic relationships observed here would be represented in an identical manner in these other

568   hominin species. For example, the more diminutive size of the *H. habilis* hand may have increased the

569   muscular costs of using a handaxe (relative to Oldowan flakes) for this species (Key and Lycett, 2018).

570   Modelling techniques (e.g. Domalain et al., 2017) combined with EMG data may provide one route to

571   investigate such phenomenon.

572   **5.0 Conclusion**

573   Here we have taken a first step in investigating the upper limb ergonomics of hand-held Lower and

574   Middle Palaeolithic stone tools. We use surface electromyography to demonstrate that activation

575   levels (and therefore force output) in three upper limb muscles, the abductor digiti minimi, flexor

576   pollicis longus and biceps brachii, are significantly influenced by the type of stone tool used during

577   cutting tasks. For each muscle, handaxes are more demanding to use relative to smaller Oldowan and

578   Levallois flake technologies. We argue that these differences could have promoted the production of

579   flake tools over handaxes in some functional contexts, across both the Acheulean and Middle

580   Palaeolithic.

581   Six of the muscles investigated, however, were not affected by tool type changes. Similarly, no

582   significant differences in muscle activation were observed between Oldowan flakes and Levallois

583   flakes, while Lomekwian flakes displayed no consistent differences with other tool types. Muscular

584   demands do not, therefore, decrease in-line with tool-type changes during the Lower and Middle

Palaeolithic periods. We therefore reemphasise the potential role of other factors in influencing technological transitions and tool production choices during this period, and stress that ergonomic factors alone cannot explain the tool use behaviors of early hominins.

Finally, we have demonstrated that across the four stone tool types investigated, muscles responsible for flexion, abduction and adduction of the digits and in-hand manipulation are heavily recruited, and significantly more so than those controlling for movement at the wrist, elbow or shoulder. It is these muscles, therefore, that work hardest during stone tool use and are most likely to be responsible for influencing tool-user 'ease-of-use' perceptions and stone tool ergonomic design features.

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References

Adler, D.S., Wilkinson, K.N., Blockley, S., Mark, D.F., Pinhasi, R., Schmidt-Magee, B.A., Nahapetyan, S., Mallol, C., Berna, F., Glauberman, P.J., Raczynski-Henk, Y., Wales, N., Frahm, E., Joris, O., MacLeod, A., Smith, V.C., Cullen, V.L., Gasparian, B., 2014. Early Levallois technology and the Lower to Middle Paleolithic transition in the Southern Caucasus. Science 345 (6204), 1609–1613

Almécija, S., Alba, D., 2014. On manual proportions and pad-to-pad precision grasping in *Australopithecus afarensis*. Journal of Human Evolution 73, 88–92

Ashton, N., McNabb, J., 1994. Bifaces in perspective. In: Ashton, N., David, A. (Eds.) Stories in Stone: Lithic Studies Society Occasional Paper No. 4, pp. 182–191

Ashton, N., Scott, B., 2016. The British Middle Palaeolithic. Quaternary International 411 (Part A), 62–76

Ambrose, S., 2001. Paleolithic technology and human evolution. Science 291 (5509), 1748–1753

Archer, W., Braun, D.R., 2010. Variability in bifacial technology at Elandsfontein, Western cape, South Africa: a geometric morphometric approach. Journal of Archaeological Science 37 (1), 201–209

615 Baena, J., Navas, C.T., Diaz, S.P., Bustos-Perez, G. Romagnoli, F. 2016. To grip or not to grip: an
616 experimental approach for understanding the use of prehensile areas in Mousterian tools. Boletin de
617 Arqueologia Experimental 11, 200–218

618 Bar-Yosef, O., 1998. On the nature of transitions: the Middle to Upper Paleolithic and the Neolithic
619 Revolution. Cambridge Archaeological Journal 8 (2), 141–163

620 Bicho, N., Merreiros, J., Cascalheira, J., Pereira, T., Haws, J., 2015. Bayesian modelling and the
621 chronology of the Portuguese Gravettian. Quaternary International 359-360, 499–509

622 Bilbao, I., Rios-Garaizar, J., Arrizabalaga, A., 2019. Relationships between size and precision of flake
623 technology in the Middle Paleolithic. An experimental study. Journal of Archaeological Science
624 Reports 25, 530–547

625 Boëda, E., 1995. Levallois: a volumetric construction, methods, a technique. In: Dibble HL, Bar-
626 Yosef O, editors. The Definition and Interpretation of Levallois Technology. Madison: Prehistory
627 Press. pp. 41–68

628 Borel, A., Cheze, L., Pouydebat, E., 2016. Sequence analysis of grip and manipulation during tool
629 using tasks: a new method to analyze hand use strategies and examine human specificities. Journal of
630 Archaeological Method and Theory 24 (3), 751–775

631 Boucher de Perthes J., 1847. Antiquités Celtiques at Antédiluviennes. Treuttel and Wurtz, Paris

632 Brantingham, P.J., Kuhn, S.L., 2001. Constraints on Levallois Core Technology: A Mathematical
633 Model. Journal of Archaeological Science 28 (7), 747–761

634 Braun, D.R., Aldeias, V., Archer, W., Arrowsmith, J.R., Baraki, N., Campisano, C.J., Deino, A.L.,
635 DiMaggio, E.N., Dupont-Nivet, G., Engda, B., Feary, D.A., Garello, D.I., Kerfelew, Z., McPherron,
636 S.P., Patterson, D.B., Reeves, J.S., Thompson, J.C., Reed, K.E., 2019. Earliest known Oldowan
637 artifacts at >2.58 Ma from Ledi-Geraru, Ethiopia, highlight early technological diversity. *PNAS,*
638 1820177116

639 Camps, M., Chauhan, P.R. 2011. Sourcebook of Paleolithic Transitions. Springer, New York

640 Clancy, E.A., Negro F., Farina, D., 2016. Single-channel techniques for information extraction from
641 the surface EMG signal. In: Merletti, R., Farina, D. (Eds.) Surface Electromyography: Physiology,
642 Engineering, and Applications. Wiley and Sons, Hoboken. pp. 91–125

643 Clark, J.D., 1987. Transitions: *Homo erectus* and the Acheulian: the Ethiopian sites of Gadeb and the
644 Middle Awash. Journal of Human Evolution 16 (7-8), 809–826

645 Claud, E., 2015. The use of biface manufacturing flakes: Functional analysis of three Middle
646 Paleolithic assemblages from southwestern and northern France. Quaternary International 361, 131–
647 141

648 Dennell, R. 2017. Human colonization of Asia in the late Pleistocene. Current Anthropology 58, 383–
649 396

650 Dibble, H.L., Bernard, M.C., 1980. A comparative study of basic edge angle measuring techniques.
651 American Antiquity 45 (4), 857–865

652 Diez-Martin, F., Yustos, P.S., Uribelarrea, D., Baquedano, E., Mark, D.F., Mabulla, A., Fraile, C.,
653 Duque, J., Diaz, I., Perez-Gonzalez, A., Yravedra, J., Egeland, C.P., Organista, E., Dominguez-
654 Rodrigo, M., 2015. The origin of the Acheulean: the 1.7 million-year-old site of FLK West, Olduvai
655 Gorge (Tanzania). Scientific Reports 5, 17839

656 Diogo, R., Richmond, B.G., Wood, B., 2012. Evolution and homologies of primate and modern
657 human hand and forearm muscles, with notes on thumb movements and tool use. Journal of Human
658 Evolution 63, 64–78

659 Domalain, M., Bertin, A., Daver, G., 2017. Was *Australopithecus afarensis* able to make the
660 Lomekwian stone tools? Towards a realistic biomechanical simulation of hand force capability in
661 fossil hominins and new insights on the role of the fifth digit. Comptes Rendus Palevol 16 (5–6), 572–
662 584

663 Enola, R.M., Duchateau, J., 2016. Physiology of muscle activation and force generation. In: Merletti,
664 R., Farina, D. (Eds.) Surface Electromyography: Physiology, Engineering, and Applications. Wiley
665 and Sons, Hoboken. pp. 1–29

666 Emory, K., 2010. A re-examination of variability in handaxe form in the British Palaeolithic. Ph.D.
667 Thesis, University College London

668 Eren, M.I. 2013. The technology of Stone Age colonization: an empirical, regional-scale examination
669 of Clovis unifacial stone tool reduction, allometry, and edge angle from the North American Lower
670 Great Lakes region. Journal of Archaeological Science 40 (4), 2101–2112

671 Eren, M.I., Lycett, S.J., 2012. Why Levallois? A morphometric comparison of experimental
672 'preferential' Levallois flakes versus debitage flakes. PLOS ONE 7(1), e29273

673 Eren, M.I., Lycett, S.J., 2016. A statistical examination of flake edge angles produced during
674 experimental lineal Levallois reductions and consideration of their functional implications. Journal of
675 Archaeological Method and Theory 23 (1), 379–398

676 Eren, M.I., Lycett, S.J., Patten, R.J., Buchanan, B., Pargeter, J., O'Brien, M.J., 2016. Test, model, and
677 method validation: the role of experimental stone artifact replication in hypothesis driven archaeology.
678 Ethnoarchaeology 8 (2), 103–136

679 Evans J., 1872. The Ancient Stone Implements, Weapons and Ornaments of Great Britain. Longmans,
680 Green and Co., London

681 Faisal, A., Stout, D., Apel, J., Bradley, B., 2010. The manipulative complexity of Lower Paleolithic
682 stone toolmaking. PLOS ONE 5 (11), e13718

683 Farina, D., Stegeman, D.F., Merletti, R., 2016. Biophysics of the generation of EMG signals. In:
684 Merletti, R., Farina, D. (Eds.) Surface Electromyography: Physiology, Engineering, and Applications.
685 Wiley and Sons, Hoboken. pp. 30–53

686 Feix, T., Kivell, T.L., Pouydebat, E., Dollar, A.M., 2015. Estimating thumb-index finger precision
687 grip and manipulation potential in extant and fossil primates. Journal of the Royal Society Interface
688 12 (106), 20150176

689 Feuerriegel, E., 2016. Biomechanics of the hominin upper limb: entheseal development and stone tool
690 manufacture. Ph.D. Thesis, Australian National University

691 Feuerriegel, E.M., Voisin, J.-L., Churchill, S.E., Haeusler, M., Mathews, S., Schmid, P., Hawks, J.,
692 Berger, L.R., 2019. Upper limb fossils of *Homo naledi* from the Lesedi Chamber, Rising Star System,
693 South Africa. *Paleoanthropology* 2019, 311–349

694 Freund, J., Takala, E.P., Toivonen, R., 2000. Effects of two ergonomic aids on the usability of an in-
695 line screwdriver. Applied Ergonomics 31 (4), 371–376

696 Foley, R., Lahr, M.M., 2003. On stony ground: lithic technology, human evolution, and the
697 emergence of culture. Evolutionary Anthropology 12, 109–122

698 Galán, A.B., Domínguez-Rodrigo, M., 2014. Testing the efficiency of simple flakes, retouched flakes,
699 and handaxes during butchery. Archaeometry 56 (6), 1054–1074

700 García-Medrano, P., Ollé, A., Ashton, N., Roberts, M.B., 2019. The mental template in handaxe
701 manufacture: new insights into Acheulean lithic technologic behaviour at Boxgrove, Sussex, UK.
702 Journal of Archaeological Method and Theory 26 (1), 396–422

703 Gazzoni, M., Afsharipour, B., Merletti, R., 2016. Surface EMG in ergonomics and occupational
704 medicine. In: Merletti, R., Farina, D. (Eds.) Surface Electromyography: Physiology, Engineering, and
705 Applications. Wiley and Sons, Hoboken. pp. 54–90

706 Goren-Inbar, N., Saragusti, I., 1996. An Acheulian biface assemblage from Gesher Benot Ya'aqov,
707 Israel: indications of African affinities. Journal of Field Archaeology 23 (1), 15–30

708   Gowlett, J.A.J., 2006. The elements of design form in Acheulean bifaces: modes, modalities, rules

709   and language. In N. Goren-Inbar & G. Sharon (eds): Axe Age: Acheulian Tool-Making From Quarry

710   to Discard, pp. 203–221. Equinox, London

711   Gowlett, J.A.J., 2009. The longest transition or multiple revolutions? Curves and steps in the record of

712   human origins. In M. Camps & P. Chauhan (eds): Sourcebook of Paleolithic Transitions, pp. 65–78.

713   Springer, New York

714   Gowlett, J.A.J., 2013. Elongation as a factor in artefacts of humans and other animals: an Acheulean

715   example in comparative context. Phil. Trans. R. Soc. B. 368, 20130114

716   Gorsman, L., Goldsmith, Y., Smilansky, U., 2011. Morphological analysis of Nahal Zihor handaxes: a

717   chronological perspective. PaleoAnthropology 2011, 203–215

718   Grant, K.A., Habes, D.J., 1997. An electromyographic study of strength and upper extremity muscle

719   activity in simulated meat cutting tasks. Applied Ergonomics 28 (2), 129–137

720   Hamrick, M.W., Chirchill, S.E., Schmitt, D., Hylander, W.L., 1998. EMG of the human flexor pollicis

721   longus muscle: implications for the evolution of hominid tool use. Journal of Human Evolution 34 (2),

722   123–136

723   Hardy, B.L., Moncel, M.-H., Despriee, J., Courcimault, G., Voinchet, P., 2018. Middle Pleistocene

724   hominin behaviour at the 700ka Acheulean site of la Noira (France). Quaternary Science Reviews 199,

725   60–82

726   Harmand, S., Lewis, J.E., Feibel, C.S., Lepre, C.J., Prat, S., Lenoble, A., Boes, X., Quinn, R.L.,

727   Brenet, M., Arroyo, A., Taylor, N., Clement, S., Daver, G., Brugal, J.-P., Leakey, L., Mortlock, R.A.,

728   Wright, J.D., Lokorodi, S., Kirwa, C., Kent, D.V., Roche, H., 2015. 3.3-million-year-old stone tools

729   from Lomekwi 3, West Turkana, Kenya. Nature 521, 310–315

730   Hermens, H. J., Freriks, B., Disselhorst-Klug, C., Rau, G., 2000. Development of recommendations

731   for SEMG sensors and sensor placement procedures. Journal of Electromyography and Kinesiology

732   10 (5), 361–374

733   Herzlinger, G., Goren-Inbar, N., 2019. Beyond a cutting edge: a morpho-technological analysis of

734   Acheulian handaxes and cleavers from Gesher Benot Ya'aqov, Israel. Journal of Paleolithic

735   Archaeology 3, 33–58

736   Iovita, I., 2014. The role of edge angle maintenance in explaining technological variation in the

737   production of Late Middle Paleolithic bifacial and unifacial tools. Quaternary International 350, 105–

738   115

739   Isaac, B. 1989. The Archaeology of Human Origins: Papers by Glynn Isaac. Cambridge University
740   Press, Cambridge

741   Isaac, G., 1969. Studies of early culture in East Africa. World Archaeology 1 (1), 1–28

742   Jobson, R.W., 1986. Stone tool morphology and rabbit butchery. Lithic Technology 15, 9–20

743   Jones, P., 1980. Experimental butchery with modern stone tools and its relevance for Palaeolithic
744   archaeology. World Archaeology 12 (2), 153–165

745   Jones, P.R., 1981. Experimental implement manufacture and use; a case study from Olduvai Gorge,
746   Tanzania. Phil. Trans. R. Soc. B. 292, 189–195

747   Jones, P., 1994. Results of experimental work in relation to the stone industries of Olduvai Gorge. In:
748   Leakey MD (ed) Olduvai Gorge: Excavations in Beds III, IV and the Masek Beds 1968–1971.
749   Cambridge University Press, Cambridge

750   Key, A.J.M., 2016. Integrating mechanical and ergonomic research within functional and
751   morphological analyses of lithic cutting technology: Key principles and future experimental directions.
752   Ethnoarchaeology 8 (1), 69–89

753   Key, A.J.M., Dunmore, C.J., 2018. Manual restrictions on Palaeolithic technological transitions. PeerJ
754   6, e5399

755   Key, A.J.M., Lycett, S.J., 2017a. Form and function in the Lower Palaeolithic: history, progress, and
756   continued relevance. Journal of Anthropological Sciences 95, 67–108

757   Key, A.J.M., Lycett, S.J., 2017b. Reassessing the production of handaxes versus flakes from a
758   functional perspective. Archaeological and Anthropological Sciences 9 (5), 737–753

759   Key, A.J.M., Lycett, S.J., 2017c. Influence of handaxe size and shape on cutting efficiency: a large
760   scale experiment and morphometric analysis. Journal of Archaeological Method and Theory 24 (2),
761   514–541

762   Key, A.J.M., Lycett, S.J., 2018. Investigating interrelationships between Lower Palaeolithic stone tool
763   effectiveness and tool user biometric variation: implications for technological and evolutionary
764   changes. Archaeological and Anthropological Sciences 10 (5), 989–1006

765   Key, A.J.M., Proffitt, T., Stefani, E., Lycett, S.J., 2016. Looking at handaxes form another angle:
766   assessing the ergonomic and functional importance of edge form in Acheulean bifaces. Journal of
767   Anthropological Archaeology 44, 43–55

768   Key, A.J.M., Merritt, S.R., Kivell, T.L., 2018. Hand grip diversity and frequency during the use of
769   Lower Palaeolithic stone cutting-tools. Journal of Human Evolution 125, 137–158

770   Key, A., Young, J., Fisch, M.R., Chaney, M.E., Kramer, A., Eren, M.I., 2018. Comparing the use of

771   meat and clay during cutting and projectile research. Engineering Fracture Mechanics 192, 163–175

772   Kivell, T.L., 2015. Evidence in hand: recent discoveries and the early evolution of human manual

773   manipulation. Phil. Trans. R. Soc. B. 370, 20150105

774   Kleindienst, M.R., Keller, C.M., 1976. Towards a functional analysis of handaxes and cleavers: the

775   evidence from Eastern Africa. Man 11 (2), 176–187

776   Leakey, M.D., 1971. Olduvai Gorge. Excavations in Beds I & II 1960 – 1963. Cambridge University

777   Press

778   Lewis, J.R., Harmand, S., 2016. An earlier origin for stone tool making: implications for cognitive

779   evolution and the transition to *Homo*. Phil. Trans. R. Soc. B 371 (1698), 2015.0233

780   Lin, S.C., 2018. Flake selection and scraper retouch probability: an alternative model for explaining

781   Middle Paleolithic assemblage retouch variability. Archaeological and Anthropological Sciences 10

782   (7), 1791–1806

783   Lin, S.C., Rezek, Z., Dibble, H.L., 2018. Experimental design and experimental inference in stone

784   artifact archaeology. Journal of Archaeological Method and Theory 25 (3), 663–688

785   Lycett, S.J., von Cramon-Taubadel, N., Gowlett, J.A.J., 2010. A comparative 3D geometric

786   morphometric analysis of Victoria West cores: implications for the origins of Levallois technology.

787   Journal of Archaeological Science 37 (5), 1110–1117

788   Lycett, S.J., Eren, M.I., 2013. Levallois economics: an examination of 'waste' production in

789   experimentally produced Levallois reduction sequences. Journal of Archaeological Science 40 (5),

790   2384–2392

791   Lycett, S.J., Eren, M.I., 2013. Levallois lessons: the challenge of integrating mathematical models,

792   quantitative experiments and the archaeological record. World Archaeology 45 (4), 519–538

793   Lycett, S.J., Gowlett, J.A.J., 2008. On questions surrounding the Acheulean 'tradition'. World

794   Archaeology 40 (3), 295–315

795   Malinsky-Buller, A., 2016. Lost and found: Technological trajectories within Lower/Middle

796   Paleolithic transition in Western Europe, North of the Pyrenees. Quaternary International 409 (Part B),

797   104–148

798   Marzke, M.W., 1983. Joint functions and grips of the *Australopithecus afarensis* hand, with special

799   reference to the region of the capitate. Journal of Human Evolution 12 (2), 197–211

800 Marzke, M.W., 1997. Precision grips, hand morphology, and tools. American Journal of Physical
801 Anthropology 102 (1), 91–110

802 Marzke, M.W. 2013. Tool making, hand morphology and fossil hominins. Philosophical Transactions
803 of the Royal Society B 368, 20120414

804 Marzke, M.W., Shackley, M.S., 1986. Hominid hand use in the Pliocene and Pleistocene: evidence
805 from experimental archaeology and comparative morphology. Journal of Human Evolution 15 (6),
806 439–460

807 Marzke, M.W., Toth, N., Shick, K., Reece, S., Steinberg, B., Hunt, K., Linscheid, R.L., An, K.-N.,
808 1998. EMG study of hand muscle recruitment during hard hammer percussion manufacture of
809 Oldowan tools. American Journal of Physical Anthropology 105 (3), 315–332

810 McCall, G.S., 2005. An experimental examination of the potential function of Early Stone Age tool
811 technology and implications for subsistence behaviour. Lithic Technology 30 (1), 29–43

812 McNabb, J., 2005. Hominins and the Early-Middle Pleistocene transition: evolution, culture and
813 climate in Africa and Europe. In: Head, M.J., Gibbard, P.L. (Eds.) Early-Middle Pleistocene
814 Transitions: The Land-Ocean Evidence. Geological Society, London. pp. 287–304

815 Merletti, R., Botter, A., Barone, U., 2016. Detection and conditioning of surface EMG signals. In:
816 Merletti, R., Farina, D. (Eds.) Surface Electromyography: Physiology, Engineering, and Applications.
817 Wiley and Sons, Hoboken. pp. 54–90

818 Mersey, B., Jabbour, R.S., Brudvik, K., Defleur, A., 2013. Neanderthal hand and foot remains from
819 Moula-Guercy, Ardeche, France. American Journal of Physical Anthropology 152 (4), 516–529

820 Mihailovic, D., BogiCevic, K., 2017. Technological changes and population movements in the Late
821 Lower and Early Middle Paleolithic of the Central Balkans. In: Harvati, K., Roksandic, M. (Eds.)
822 Paleoanthropology of the Balkans and Anatolia. Springer, Dordrecht. pp. 139–152

823 Milner-Brown, H. S., Stein, R. B., Yemm, R., 1973. Changes in firing rate of human motor units
824 during linearly changing voluntary contractions. Journal of Physiology 23 (2), 371–390.

825 Moncel, M.-H., Moigne, A.-M., Sam Y., Combier, J., 2011. The emergence of Neanderthal technical
826 behaviour: new evidence from Orgnac 3 (Level 1, MIS 8), Southeastern France. Current
827 Anthropology 52 (1), 37–75

828 Moncel, M.-H.,, Moigne, A.-M., Combier, J., 2012. Towards the Middle Palaeolithic in Western
829 Europe: the case of Orgnac 3 (southeastern France). Journal of Human Evolution 63 (5), 653–666

830 Muller, A., Clarkson, C., 2016. Identifying major transitions in the evolution of lithic cutting edge
831 production rates. PLOS ONE 11 (12), e0167244

832   Niewoehner, W.A., 2001. Behavioral inferences from the Skhul / Qafzeh early modern human hand
833   remains. PNAS 98 (6), 2979–2984

834   Ollé, A., Mosquera, M., Rodriguez, X.P., de Lombera-Hermida, A., Garcia-Anton, M.D., Garcia-
835   Medrano, P., Pena, L., Menendez, L., Navazo, M., Terradillos, M., Bargallo, A., Marquez, B., Sala,
836   R., Carbonell, E., 2013. The Early and Middle Pleistocene technological record from Sierra de
837   Atapuerca (Burgos, Spain). Quaternary International 295, 138–167

838   Pargeter, J., Khreisheh, N., Stout, D., 2019. Understanding stone tool-making skill acquisition:
839   experimental methods and evolutionary implications. Journal of Human Evolution 133, 146–166

840   Phillipson, L., 1997. Edge modification as an indicator of function and handedness of Acheulian
841   handaxes from Kariandusi, Kenya. Lithic Technology 22 (2), 171–183

842   Pontonnier, C., Dumont, G., de Zee, M., Samani, A., Madeleine, P., 2012. Cutting force and EMG
843   recordings for ergonomic assessment of meat cutting tasks: influence of the workbench height and the
844   cutting direction on muscle activation. Proceedings of the 11th Biennial Conference On Engineering
845   Systems Design And Analysis, 00762797

846   Prasciunas, M.M., 2007. Bifacial cores and flake production efficiency: an experimental test of
847   technological assumptions. American Antiquity 72 (2), 334–348

848   Proffitt, T., 2018. Is there a developed Oldowan A at Olduvai Gorge? A diachronic analysis of the
849   Oldowan in Bed I and Lower-Middle Bed II at Olduvai Gorge, Tanzania. Journal of Human Evolution
850   120, 92–113

851   Rezek, Z., Dibble, H.L., McPherron, S.P., Braun, D.R., Lin, S.C., 2018. Two million years of flaking
852   stone and the evolutionary efficiency of stone technology. Nature Ecology and Evolution 2, 628–633

853   Roche, H., Delagnes, A., Brugal, J.-P., Feibel, C., Kibunjia, M., Mourre, V., Texier P.-J., 1999. Early
854   hominid stone tool production and technical skill 2.34 Myr ago in West Turkana, Kenya. Nature 399,
855   57–60

856   Rogers, M.J., Semaw, S., 2009. From nothing to something: the appearance and context of the earliest
857   archaeological record. In: Camps, M., Chauhan, P.R. (Eds.) Sourcebook of Palaeolithic transitions:
858   Methods, Theories, and Interpretations. Springer, New York. pp. 155–171

859   Rolian, C., Lieberman, D.E., Zermeno, J.P., 2011. Hand biomechanics during simulated stone tool use.
860   Journal of Human Evolution 61 (1), 26–41

861   Rots, V., 2013. Insights into early Middle Palaeolithic tool use and hafting in Western Europe. The
862   functional analysis of level IIa of the early Middle Palaeolithic site of Biache-Saint-Vaast (France).
863   Journal of Archaeological Science 40 (1), 497–506

864   Ruebens, K., 2013. Regional behaviour among late Neanderthal groups in Western Europe: a
865   comparative assessment of late Middle Palaeolithic bifacial tool variability. Journal of Human
866   Evolution 65 (4), 341–362

867   Semaw S., Rogers M., Stout D., 2009. The Oldowan-Acheulian transition: Is there a "Developed
868   Oldowan" artifact tradition?. In M. Camps & P. Chauhan (eds): Sourcebook of Paleolithic Transitions,
869   pp. 173–193. Springer, New York

870   Semaw, S., Rogers, M.J., Caceres, I., Stout, D., Leiss, A.C., 2018. The early Acheulean ~1.6-1.2 Ma
871   from Gona, Ethiopia: Issues related to the emergence of the Acheulean in Africa. In: Gallotti, R.,
872   Mussi, M. (Eds.) The Emergence of the Acheulean in East Africa and Beyond. Springer Nature,
873   Cham. pp. 115–128

874   Sharon, G., 2010. Large flake Acheulian. Quaternary International 223–224, 226–233

875   Shea, J., 2007. Lithic technology, or, what stone tools can (and can't) tell us about early hominin diets.
876   In P.S. Ungar (ed): Evolution of the Human Diet: The Known, the Unknown, and the Unknowable, pp.
877   212–229. Oxford University Press, Oxford.

878   Shea, J., 2017. Occasional, obligatory, and habitual stone tool use in hominin evolution. Evolutionary
879   Anthropology 26, 200–217

880   Shimelmitz, R., Weinstein-Evron, M., Ronen, A., Kuhn, S.L., 2016. The Lower to Middle Paleolithic
881   transition and the diversification of Levallois technology in the Southern Levant: Evidence from
882   Tabun Cave, Israel. Quaternary International 409 (Part B), 23–40

883   Shipton, C., 2016. Hierarchical organization in the Acheulean to Middle Palaeolithic transition at
884   Bhimbetka, India. Cambridge Archaeological Journal 26 (4), 601–618

885   Shipton, C., Clarkson, C., Pal, N.J., Jones S.C., Roberts, R.G., Harris, C., Gupta, M.C., Ditchfield.
886   P.W., Petraglia, M.D., 2013. Generativity, hierarchical action and recursion in the technology of the
887   Acheulean to Middle Palaeolithic transition: A perspective from Patpara, the Son Valley, India.
888   Journal of Human Evolution 65 (2), 93–108

889   Stegeman, D., Hermens, H., 2007. Standards for surface electromyography: The European project
890   Surface EMG for non-invasive assessment of muscles (SENIAM). Enschede: Roessingh Research and
891   Development, 108–112.

892   Stout, D., Toth, N., Schick, K., Chaminade, T., 2008. Neural correlates of Early Stone Age
893   toolmaking: technology, language and cognition in human evolution. Phil. Trans. R. Soc. B 363,
894   1939–1949

895 Tocheri, M., Orr, C.M., Jacofsky, M.C., Marzke, M.W., 2008. The evolutionary history of the
896 hominin hand since the last common ancestor of *Pan* and *Homo*. Journal of Anatomy 212 (4), 544–
897 562

898 Tomka, S.A., 2001. The effect of processing requirements on reduction strategies and tool form: a
899 new perspective. In: Andrefsky J. (Ed.) Lithic Debitage: Context, Form, Meaning. The University of
900 Utah Press, Salt Lake City. pp. 207–225

901 de la Torre, I., 2016. The origins of the Acheulean: past and present perspectives on a major transition
902 in human evolution. Phil. Trans. R. Soc. B, 371, 20150245

903 Toth, N., 1985. The Oldowan reassessed: a close look at early stone age artifacts. Journal of
904 Archaeological Science 12 (2), 101–120

905 Toth, N., Schick, K., 2009. The importance of actualistic studies in early Stone Age research: some
906 personal reflections. In K. Schick & N. Toth (Eds.), The Cutting Edge: New Approaches to the
907 Archaeology of Human Origins. Gosport: Stone Age Institute Press. pp. 267–344

908 Tryon, C.A., Faith, J.T., 2013. Variability in the Middle Stone Age of Eastern Africa. Current
909 Anthropology 54 (8), 234–254

910 Tryon, C.A., McBrearty, S., Texier, P.-J., 2006. Levallois lithic technology from the Kapthurin
911 Formation, Kenya: Acheulian origin and Middle Stone Age diversity. African Archaeological Review,
912 22 (4), 199–229

913 Van Peer, P., Fullagar, R., Stokes, S., Bailey, R.M., Moeyersons, J., Steenhoudt, F., Geerts, A.,
914 Vanderbeken, T., De Dapper, M., Geus, F., 2003. The Early to Middle Stone Age transition and the
915 emergence of modern human behaviour at site 8-B-11, Sai Island, Sudan. Journal of Human Evolution
916 45 (2), 187–193

917 Viallet, C., 2016. Bifaces used for percussion? Experimental approach to percussion marks and
918 functional analysis of the bifaces from Terra Amata (Nice, France). Quaternary International 406,
919 174–181

920 Ward, C.V., Tocheri, M.W., Plavcan, J.M., Brown, F.H., Manthi, F.K., 2014. Early Pleistocene third
921 metacarpal from Kenya and the evolution of modern human-like hand morphology. PNAS 111 (1),
922 121–124

923 Williams-Hatala, E.M., Hatala, K.G., Gordon, M., Key, A., Kasper, M., Kivell, T.L., 2018. The
924 manual pressures of stone tool behaviors and their implications for the evolution of the human hand.
925 Journal of Human Evolution 119, 14–26

926   Wynn, T., Coolidge, F.L., 2004. The expert Neanderthal mind. Journal of Human Evolution 46 (4),
927   467–487

928   Wynn, T., Gowlett, J.A.J., 2018. The handaxe reconsidered. Evolutionary Anthropology 27 (1), 21–29

929   Zupancich, A., Lemorini, C., Gopher, A., Barkai, R., 2016. On Quina and demi-Quina scraper
930   handling: preliminary results from the late Lower Paleolithic site of Qesem Cave, Israel. Quaternary
931   International 398, 94–102

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941   **Figure 1**: The full array of sensors attached to the arm of a participant (A, B). Figure C depicts a
942   participant as they use a handaxe to cut the vertically secured twine segments midway through the
943   task. All sections of the cutting task are displayed in Figure D.

944   **Figure 2:** Sensors attached above the first dorsal interosseous, highlighting their shape when cut in
945   half to fit above a target muscle.

946   **Figure 3:** An example of two sEMG signals with amplitude variation at 0.4 second epochs (A), the
947   same signals after band pass filtering between 10 Hz to 350 Hz is applied (B), then again expressed as
948   each signal's root mean square (RMS) (C). An example of signal clipping and motion artefact
949   distortion during a flexor pollicis brevis signal recording can be seen in figure D.

950   **Figure 4**: Examples of the replica Lomekwian (A), Acheulan (B), Levallois (C) and Oldowan (D)
951   tools used in this experiment, alongside the full assemblage of 30 Acheulean handaxes. All other
952   complete assemblages are available in SOM Figure S1. The scale bar is 10 cm (A, B, C, D) or 30 cm
953   (E) long.

954   **Figure 5:** Maximum voluntary contraction percentage (% MVC) values for each of the nine target
955   muscles during the clay-cutting task. Differences can be observed between each muscle dependent on

956   the type of stone tool being used, despite the task being identical in each instance. Activations over

957   100% may be possible where the muscle was incompletely activated during the static MVC exercise

958   and a higher activation occurred during the experimental task.

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