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

Keywords: Surface electromyography; lithic function; Lower Palaeolithic; Levallois; cutting efficiency; muscle activity

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.

34 **1.0 Introduction**

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

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

48 The first flaked stone tool industry, the Lomekwian (Harmand et al., 2015), is currently known from a
49 single 3.3 million-year-old locality in West Turkana, Kenya. Large flake implements (> 10 cm) with
50 sharp edges suitable for cutting, produced through passive hammer and/or bipolar techniques,
51 characterise these tools (Lewis and Harmand, 2016). By 2.6 Ma Oldowan stone technologies,
52 associated with the production of flake cutting tools 3 - 5 cm in length and displaying the intentional
53 production of sharp cutting edges (Toth, 1985; Roche, et al., 1999; Rogers and Semaw, 2009; Braun
54 et al., 2019), come to dominate the archaeological record. Although these 'basic' flake tools continue
55 to be produced throughout the Palaeolithic, the emergence of bifacially flaked large cutting tools
56 (LCTs) during the Acheulean period (~1.75-0.3 Ma) represents a new level of investment and design
57 intent in cutting technologies (Isaac, 1969; Goren-Inbar and Saragusti, 1996; Lycett and Gowlett,
58 2008; Semaw et al., 2009; Sharon, 2010; Wynn and Gowlett, 2018). Acheulean LCTs, principally
59 characterized by handaxes and cleavers, are subsequently replaced as the foci of cutting technologies
60 by Middle Palaeolithic (Mousterian) Levallois tools ~300 Ka (Moncel et al., 2011; Tron and Faith,
61 2013). Levallois flake tools, produced through predetermined hierarchical reduction strategies (Boëda,
62 1995; Brantingham and Kuhn, 2001; Eren and Lycett, 2012), vary in size (typically 3 - 15 cm in
63 length [e.g. Tryon et al., 2006]) but characteristically display substantial lengths of effective cutting
64 edge around their circumference (Brantingham and Kuhn, 2001; Eren and Lycett, 2016). Subsequent
65 to the emergence of Late Middle and Early Upper Palaeolithic technologies there is increased
66 complexity in the number of cutting-tool types produced, and finer chronological and geographic
67 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

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

207 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.

248 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

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

281 *2.4 Statistical analysis*

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

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

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

306 **3.0 Results**

307 *3.1 Impact of tool type on muscle activation*

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

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

312 No other ANOVA tests between tool types returned significant differences in muscle RMS values at a
313 95% confidence interval (Table 3). Both the flexor pollicis longus and biceps brachii, however,
314 displayed values approaching significance during the clay-cutting task. Post-hoc Tukey HSD tests
315 using RMS data identified handaxes as displaying significantly greater values relative to Levallois
316 flakes for the flexor pollicis longus during this task, but no significant differences between any tools
317 for the biceps brachii (SOM Table S3). Supporting Kruskal Wallis tests performed using normalised %
318 MVC data did, however, identify significant differences in flexor pollicis longus and biceps brachii
319 activation dependent on the stone tool being used (SOM Table S4). The associated supporting post-
320 hoc Mann Whitney U tests (using % MVC data) similarly only suggest significant differences in
321 activation levels for the abductor digiti minimi, flexor pollicis longus and biceps brachii (SOM Table
322 S5). All three muscles identified handaxes as requiring significant greater activation (% MVC)
323 compared to Oldowan and Levallois flakes (SOM Table S5). The FLP also identified a significant
324 difference between Levallois and Lomekwian flakes, while the BB displayed significant differences
325 between Oldowan and Lomekwian flakes (Lomekwian flakes returned greater values in both cases).
326 In sum, only abductor digiti minimi, flexor pollicis longus and biceps brachii activation was
327 significantly affected by the type of stone tool used.

328 *3.2 Relative muscle activation across the arm*

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

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

341 The flexor pollicis brevis was also heavily recruited, albeit usually to a lesser extent than the FDI and
342 FPL (Fig. 5; SOM Table S1). Significant differences between the FPB and FCR, B, BB, TB, and AD
343 are repeatedly observed, except during the rope-cutting task with the Levallois flake (SOM Table S6).
344 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 humerus (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

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

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

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

406 At a broad level, the differences in ADM, FPL and BB activation observed here likely result from
407 tool-type size variation. Handaxes are substantially heavier and larger than Oldowan and Levallois
408 flakes, have longer scalloped cutting edges, and facilitate force application away from the hand which
409 results in torsion (Gowlett, 2006, 2013); features that could cause muscles to work harder when
410 gripping a tool or applying it to cutting tasks (Key, 2016). Previous studies, however, suggest the
411 precision grips associated with flake tools to elicit greater stresses in the first digit (Rolian et al.,
412 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

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*

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

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

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

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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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