Kent Academic Repository

Williams-Hatala, Erin Marie, Hatala, Kevin G., Gordon, McKenzie, Key, Alastair J.M., Kasper, Margaret and Kivell, Tracy L. (2018) *The manual pressures of stone tool behaviors and their implications for the evolution of the human hand.* Journal of Human Evolution, 119 . pp. 14-26. ISSN 0047-2484.

Downloaded from

https://kar.kent.ac.uk/66573/ The University of Kent's Academic Repository KAR

The version of record is available from

https://doi.org/10.1016/j.jhevol.2018.02.008

This document version

Author's Accepted Manuscript

DOI for this version

Licence for this version

CC BY-NC-ND (Attribution-NonCommercial-NoDerivatives)

Additional information

Versions of research works

Versions of Record

If this version is the version of record, it is the same as the published version available on the publisher's web site. Cite as the published version.

Author Accepted Manuscripts

If this document is identified as the Author Accepted Manuscript it is the version after peer review but before type setting, copy editing or publisher branding. Cite as Surname, Initial. (Year) 'Title of article'. To be published in *Title of Journal* , Volume and issue numbers [peer-reviewed accepted version]. Available at: DOI or URL (Accessed: date).

Enquiries

If you have questions about this document contact ResearchSupport@kent.ac.uk. Please include the URL of the record in KAR. If you believe that your, or a third party's rights have been compromised through this document please see our Take Down policy (available from https://www.kent.ac.uk/guides/kar-the-kent-academic-repository#policies).

The manual pressures of stone tool behaviors and their implications for the evolution of the human hand.

Erin Marie Williams-Hatala[a,b,*], Kevin G. Hatala [a,b], McKenzie Gordon [a], Alastair Key [c], Margaret Kasper [a], Tracy L. Kivell [c,d]

[a] *Department of Biology, Chatham University, 1 Woodland Rd., Pittsburgh, PA, 15232, USA*

[b] *Center for the Advanced Study of Human Paleobiology, The George Washington University, Washington, DC 20052, USA*

[c] *Animal Postcranial Evolution Lab, Skeletal Biology Research Centre, School of Anthropology and Conservation, University of Kent, Canterbury, Kent, CT2 7NZ, United Kingdom*

[d] *Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany*

*Corresponding author.

E-mail address: ewilliamshatala@chatham.edu (E.M. Williams-Hatala)

Key words: Hand evolution; Force; Stone tool use; Plio-Pleistocene; Lower Paleolithic.

ABSTRACT

It is widely agreed that biomechanical stresses imposed by stone tool behaviors influenced the evolution of the human hand. Though archaeological evidence suggests that early hominins participated in a variety of tool behaviors, it is unlikely that all behaviors equally influenced modern human hand anatomy. It is more probable that a behavior's likelihood of exerting a selective pressure was a weighted function of the magnitude of stresses associated with that behavior, the benefits received from it, and the amount of time spent performing it. Based on this premise, we focused on the first part of that equation and evaluated magnitudes of stresses associated with stone tool behaviors thought to have been commonly practiced by early hominins, to determine which placed the greatest loads on the digits. Manual pressure data were gathered from 39 human subjects using a Novel Pliance® manual pressure system while they participated in multiple Plio-Pleistocene tool behaviors: nut-cracking, marrow acquisition with a hammerstone, flake production with a hammerstone, and handaxe and flake use. Manual pressure distributions varied significantly according to behavior, though there was a tendency for regions of the hand subject to the lowest pressures (e.g., proximal phalanges) to be affected less by behavior type. Hammerstone use during marrow acquisition and flake production consistently placed the greatest loads on the digits collectively, on each digit and on each phalanx. Our results suggest that, based solely on the magnitudes of stresses, hammerstone use during marrow acquisition and flake production are the most likely of the assessed behaviors to have influenced the anatomical and functional evolution of the human hand.

Introduction

Stone tool behaviors are widely regarded as key innovations of the genus *Homo* that arguably gave early tool-using hominins significant competitive advantages relative to other organisms. They enabled early hominins to expand into new ecological and dietary niches (e.g., Unger et al., 2006; Braun et al., 2010), made possible multiple migration events out of Africa (e.g., Lycett and von Cramon-Taubadel, 2008), contributed to the reorganization and enlargement of the brain (e.g., Stout et al., 2008; McPherron et al., 2010), and influenced the evolution of the human hand and upper limb anatomy (e.g., Napier, 1962; Rhodes and Churchill, 2009; Roach and Richmond, 2015). In particular, Darwin (1871) was the first to propose a connection between stone tool behaviors and modern human hand morphology, and the discovery of hominin hand bones in association with Oldowan stone tools at Olduvai Gorge provided evidence in support of this association (Napier, 1962).

Hominins are known to have participated in a variety of stone tool behaviors—for example, nut-cracking (Goren-Inbar et al., 2002; Arroyo et al., 2016), flake production (Toth, 1985; Roche et al., 1999; Sharon, 2008), animal and plant tissue processing (Bunn, 1981; Domínguez-Rodrigo et al., 2001)—and these behaviors all involve different materials, different end goals, and different patterns of force and motion for the upper limb. Therefore, it is unlikely that each behavior exerted equal influence on the evolution of the modern human hand (Key and Lycett, 2017). Instead, a behavior’s likelihood of exerting a selective pressure on the hand is a function of the magnitude of stresses and hand/tool relationship associated with that behavior, the benefit received from it, and the amount of time spent performing it (Marzke, 1997; Rolian et al., 2011;

Key, 2016). The last of these criteria remains difficult to estimate, but experimental studies can provide some insight into the first three.

During manual behaviors, stone tool-related and otherwise, the internal stresses occurring at joint surfaces are many times higher than those expected given the external forces acting on the hand (Cooney and Chao, 1977; Chao et al., 1989). The stresses occurring at any one joint surface will vary depending on a variety of factors, including the joint angles, digit dimensions, internal muscle forces, and external loads (Rolian et al., 2011). For example, for any given joint angle and digit dimension, the internal forces at the first metacarpophalangeal joint are approximately five to six times greater than the associated external force experienced at the pollical distal phalanx, and those at the carpometacarpal joint are ~12 times higher (Cooney and Chao, 1977). The transition from a hand marked by small joint surfaces or longer fingers relative to the thumb length, as interpreted for many early australopiths (e.g., Green and Gordon, 2008; Lovejoy et al., 2009; but see Alba et al., 2003; Kivell et al., 2011; Almécija and Alba, 2014; Kivell, 2015) to a hand with larger joint surfaces and short fingers relative to a long thumb, as seen in later *Homo* (e.g., Lorenzo et al., 1999; Niewoehner, 2001; but see Kivell et al., 2015), is thought to reflect adaptive changes to meet the biomechanical demands of the high external forces involved in stone tool behaviors (Susman, 1994; Marzke et al., 1998; Rolian et al., 2011; Williams et al., 2012; Skinner et al., 2015; but see Weiss, 2012). The implication that high force, high stress behaviors will elicit a stronger selective response rather than repetitive, low stress behaviors (such as those associated with the development of osteoarthritis) is supported by evidence that the manual osteological dimensions of modern humans offer biomechanical advantages during hammer stone use (Rolian et al., 2011). From a bone functional adaptation perspective, there appears to be a minimum strain threshold to stimulate bone remodeling and modelling (Burr, 1985; Rubin and Lanyon, 1985; Frost, 1987), although there is much debate regarding the effects of variation in load magnitude, frequency and duration on bone form (for a review, see Bertram and Swartz, 1991; Kivell 2016). We recognize that selection was also influenced by the cost/benefit ratio of a particular behavior and the amount of time spent doing it (see above), and it is theoretically possible that selection was responding to low stress, repetitive behaviors. However, in the absence of known frequency of particular behaviors, we suggest that high force, high stress behaviors would elicit a strong selective response on hand morphology (Biewener, 1993; Kopperdahl and Keaveny, 1998).

By necessity, hypotheses citing stone tool behaviors in general as the primary selective pressure acting on hominin hands imply that all varieties of such behaviors impose similar biomechanical demands (e.g., manual loading patterns) and result in similar joint stresses. However, multiple lines of evidence suggest that loading of the hand varies substantially across different stone tool behaviors. Electromyographic studies report variable muscle recruitment patterns during stone tool use and stone tool manufacture behaviors, particularly in regard to the flexor pollicis longus (FPL) muscle (Hamrick et al., 1998; Marzke et al., 1998), the largest and most powerful thumb flexor. Furthermore, Marzke et al. (1998) found that recruitment levels of FPL varied with knapping skill level just within stone tool production itself. This observed variability in muscle recruitment patterns was indirectly supported by Key et al. (2017), who reported that experienced tool-makers used a variety of hammerstone grip strategies during knapping experiments.

Chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*) tool use offers further evidence of the unique demands imposed by various tool behaviors. Wild chimpanzees are well known for their adeptness at wielding hammerstones to crack open nuts (Whiten et al., 1999; Carvalho et al., 2008). Although bonobos rarely use tools in the wild (Hohmann and Fruth, 2003), at least one group of bonobos in a sanctuary includes adept nut-crackers who use a variety of different hammerstone grips (Neufuss et al., 2017). However, captive bonobos have shown limited success in using a hammerstone to produce flakes (Toth et al., 1993; Roffman et al., 2006). Together, these lines of evidence suggest that hand postures, loading regimes, and, by extension, biomechanical demands are distinct from one stone tool behavior to the next. To better understand the potential evolutionary influences of these behaviors, it is necessary to determine which of the stone tool behaviors impose the greatest loads on the human hand and thus are perhaps most likely to have exerted selective pressures on the evolution of modern human hand anatomy.

Although the variety of biomechanical strategies required to perform the suite of behaviors in which early hominins engaged is not often accounted for when discussing the selective pressures they applied to the human hand or human body in general (but see Hamrick et al., 1998), some researchers have tested specific behaviors in isolation (e.g., Marzke et al., 1998; Rolian et al., 2011; Williams et al., 2012; Key, 2016). However, due to the lack of necessary and comparable data across all possible behaviors, most researchers simply discuss the adaptive influence of ‘stone tool behaviors’ in general (e.g., Leakey et al., 1964; Susman, 1998; Kivell et al., 2011; Kivell, 2015). Neither option is entirely satisfactory; the former practice may remove the behavior from the larger biomechanical context of the organism (e.g., requirements of, or influences on the organism), while the latter groups together behaviors that are biomechanically dissimilar, such as nut-cracking, butchering and flake production. Both may mask important selective differences across behaviors, possibly leading researchers to overlook or misinterpret behavioral signals implied by paleontological and/or archaeological assemblages. Although it is difficult to demonstrate cause and effect relationships between stone tool behaviors and anatomical adaptations, understanding the biomechanical relationships between stone tools and the modern human hand may allow us to make more informed hypotheses about the influence of these behaviors on bony and/or soft tissue anatomy.

Here we investigate the pressures acting on the digits of the dominant hand during various stone tool behaviors for which there is evidence of hominin participation during the Plio-Pleistocene: nut-cracking, flake production, tissue-processing with flakes and hand axes, and marrow acquisition with a hammerstone (e.g., Toth, 1985; Blumenschine et al., 1991; Kimbel et al., 1996; de Heinzelin et al., 1999; Goren-Inbar et al., 2002; Bello et al., 2009; Braun et al., 2010; Arroyo and de la Torre, 2016). Based on the framework outlined above (i.e., the likelihood of selective prominence for manual behaviors is a function of load magnitude, benefit, and time), we focus on the first criterion, and use pressure data to evaluate which of the assessed behaviors are most likely to have influenced the evolution of human digits. In regard to the influence of load magnitude, we pose three questions: (1) are assessed stone tool behaviors characterized by a similar digital pressure distribution pattern (e.g., is pressure always highest on the third digit?); (2) which behavior(s) impose(s) the greatest overall biomechanical stress; and (3) if digital pressure distributions differ across behaviors, how are pressures distributed during the highest stress behaviors? Previous experimental research has shown much greater kinetic energy at the time of contact during human stone tool knapping (~7.37 J; Bril et al. 2010) than during nut-cracking (~0.4 J for walnuts, ~0.5 J for Brazil nuts in human adults; Bril et al., 2012) and thus we predict greater pressures on the digits during flake production. However, we have no expectations regarding how pressures might vary across the digits or compare across other behaviors tested in this study. We analyze manual pressures at three anatomical levels—the digits as a group, the digits, and the phalanges—to facilitate the development and evaluation of hypotheses regarding which regions of the digits are most likely to reflect adaptive responses to stone tool behaviors and to increase certainty that an evolutionarily important behavior is not overlooked. For example, a behavior that imposes the greatest loads on the digits collectively may not have been the behavior that placed the greatest loads on the thumb or the distal phalanges, both regions of the hand thought to have undergone significant selection in human evolution (e.g., Susman, 1988; Alba et al., 2003; Kivell et al., 2011; Almécija and Alba, 2014; Kivell, 2015; but see Rolian et al., 2010).

Methods

Participants

Pressure data were recorded on the dominant hand of 39 human subjects (36 females and 3 males) during the performance of behaviors for which there is evidence in the Plio-Pleistocene. The tested behaviors included cracking nuts with a hammerstone (Goren-Inbar et al., 2002; Arroyo and de la Torre, 2016), slicing animal tissue with a flake and a handaxe (Bunn and Kroll, 1986; Domínguez-Rodrigo, 1997), accessing the marrow cavity of a long bone with a hammerstone and a chopper (Blumenschine, 1995; Blumenschine and Pobiner, 2007), and making Oldowan-like flakes (Semaw, 2000; Braun et al., 2009; Stout et al., 2010). Participants ranged in age from 18 to 35 years old and all but two (one female and one male) were right handed. All subjects had no prior experience making or using stone tools. Although previous work has shown substantial interindividual variation in the kinematics of the upper limb during stone tool knapping within both novice and expert knappers (Rein et al., 2014), we include only novice participants to help reduce two confounding effects: (1) variation in skill for any given behavior among participants, and (2) variation in the skill possessed by a single participant among all tested behaviors. Data were collected from participants who provided informed consent under a protocol approved by the Institutional Review Board of Chatham University.

Experimental protocol

A Novel Pliance® manual pressure sensor system (novel GmBh, Germany) was used to record the pressures (i.e., normal force/area) acting at each sensor. The technology used in the Novel Pliance® system has been repeatedly validated in the Pedar® system, at pressures comparable to and higher than those associated with knapping (McPoil et al., 1995; Putti et al., 2007; Williams et al., 2012; Price et al., 2016). For example, Price et al., (2016) calibrated and validated the Pedar system for 20–600 kPa. The pressure-collection component of the system consists of 10 17 × 17 mm sensors (digits I–IV) and two 10 × 10 mm sensors (digit V) covered in a conductive woven textile. Each sensor feeds into a textile-based cable and all 12 of the cables are connected to a single unit, which is then connected to the Pliance-x electronic analyzer box. The analyzer box collects and transfers data to the computer. Sensors were placed on the palmar surface of the digits of the dominant hand, near the center of the proximal and distal phalanges of digits I, IV and V and the proximal, intermediate and distal phalanges of digits II and III (12 sensors in total; Table 1). The textile composition of the sensors (as opposed to a metallic wire based system as used in Williams et al., 2012) allows the sensors to experience high loads while being flexible and resistant to permanent bending or crimping damage.

The individual sensors were held in place on the palmar surfaces of each finger using double-sided tape and a Velcro strap that was attached to the edge of the sensor covering and wrapped around the dorsal aspect of the finger. Finger cots were placed over each digit and subjects wore a fitted rayon/cotton/rubber blend glove to further secure the sensors in place and to minimize the sensors' exposure to raw animal tissues during the tissue-processing behaviors. After the sensors were secured to the fingers, the sensor cables were positioned between adjacent digits and allowed to trail across the dorsal aspect of the hand before wrapping around to the anterior wrist where they were bundled together. Once bundled, the 12 cables were secured to the wrist using a Velcro strap and compression tape (Fig. 1).

Prior to data collection, a ‘mask’ was created for each subject within the Pliance® software to properly associate individual sensors with specific phalanges. Once the sensors were in place and secure, and the mask had been created, the participant was instructed to relax her or his hand to fully unload the sensors and the system was zeroed out to remove any potential loads exerted by the attachment apparatus.

Participants progressed through randomized sets of stone tool behaviors: using a hammerstone to make flakes from dacite, using a hammerstone to break into the marrow cavity of a cow tibia, cracking open each of four types of in-shell nuts (almonds, Brazil nuts, hazelnuts and macadamia nuts), and slicing tissue from a lamb shank using small and medium flakes and small and large handaxes knapped from British (Suffolk) flint by AK to standardized sizes (Table 2). For each behavior, a trial consisted of a single instance of the behavior. For example, during marrow acquisition, one trial consisted of one hammerstone strike against the tibia, and during tissue-processing, one trial consisted of a single longitudinal slice along the long axis of the lamb shank. All trials for a given behavior were completed before the participant proceeded to the next behavior. All pressure data were recorded at 200 Hz.

All knapping occurred with participants seated in a wooden chair (seat height ≈ 45 cm) and with a nodule of dacite held in place against one leg. Dacite (obtained from Neolithics.com) was selected for its generally fine-grained and uniform quality, which reduced the likelihood of inclusions or fractures and, in turn, made for more straightforward flake reductions for the novice knappers. Because participants were all novice knappers and to help avoid injury, each knapping session began with brief instructions on both flake removal and injury prevention. This was followed by a 10 min practice session, then data collection. Participants had the option of placing up to three leather pads (5 mm thick each) on their legs for protection. Each participant selected her or his hammerstone of choice from a selection of 10 hammerstones (< 1 kg each) and were free to switch hammerstones as desired. Tool production data were collected from 23 participants. Each performed 20 total trials and data analyses included those trials resulting in the production of flakes as well as those that failed to produce a flake. All tool use behaviors were conducted with novice participants seated on the ground in their preferred sitting position (the majority chose to sit either cross-legged or kneeling on both of their legs). During nut-cracking, participants were instructed to strike with sufficient force to break through the shell, but to refrain from smashing the internal nut. The four nut varieties were selected because their shells span a wide range of toughness values, as is true of the shells of nuts consumed by extant wild primates (Jennings and MacMillan, 1986; Lucas, 2004; Lucas et al., 2011). Toughness is the primary material property governing critical load to failure (Chai and Lawn, 2007a, 2007b), and as such will have a large influence on the strategies used when cracking the shells of different nut species. Nuts were inspected for shell integrity prior to testing and those with cracks or other signs of failure in the shells were discarded. All nut-cracking took place with the nut situated on a thick wooden cutting board (i.e., the anvil). Participants typically either held the nut in place on the anvil using the first and second digits of their non-dominant hand, or stabilized the nut alone on the anvil without further support from their non-dominant hand. They were allowed to select the hammerstone of their choice and to switch hammerstones as frequently as desired. Nut-cracking data were collected and included in the analyses from all 39 participants. Each participant cracked open or attempted to crack open 10 of each nut type. Nuts were discarded after being struck once, regardless of whether their shell was cracked open or not.

Marrow acquisition and tissue-processing took place on top of a cutting board placed on the ground. A cow tibia was selected for marrow acquisition because animals of a similar size (class 3; Brain, 1981), are commonly found in assemblages of fauna and stone tools, assumed to have been compiled by hominins (e.g., Klein, 1976; Clark and Plug, 2008). During the marrow acquisition phase, participants were instructed to attempt to access the marrow cavity but to refrain from exerting their maximum force to prevent injury, and to concentrate their strikes on the shaft of the bone rather than the epiphyses. Marrow acquisition data were collected and included in the analyses from all 39 participants. Each participant performed 20 trials (i.e., strikes) using the hammerstone of their choice and they were allowed to switch hammerstones as desired.

During the tissue-processing phase, the slicing protocol was the same for all tools: participants sliced the shank along the long axis in an uninterrupted stroke, constituting a single trial. Participants were instructed to refrain from using sawing motions and from starting and stopping during a single trial. Although this protocol differs from real butchery processes, the constraints were necessary to standardize the behavior thereby increasing the likelihood of recording data on the same experience (see limitations in the Discussion section). Tissue-processing data were collected from all 39 participants, but data from two were excluded due to a recording error. Each participant performed 10 trials (i.e., slices) each using four different tools: a small flake (mean length = 29.2 mm), a medium sized flake (mean length = 58.3 mm), a small handaxe (mean length = 119.7 mm) and a large handaxe (mean length = 168.4 mm). Participants were each given a tool with a fresh cutting edge (i.e., either the other side of a previously used tool or a tool with two fresh edges) and were required to use the same tool for all 10 trials.

Data analysis

Pressure data were extracted, formatted, and analyzed using a series of custom scripts written in the R programming language and environment (R Core Team, 2017). Each sensor collected pressure data (kPa) continuously throughout each trial at 200 Hz, resulting in hundreds of data points per sensor per trial. Therefore, the analyses presented here are concerned with peak pressures, which were defined in three different ways. First, we evaluated peak pressures in a sensor-by-sensor fashion. In these cases, peak pressures were the maximum recorded pressure on each individual sensor, within each trial. Second, we focused on digit-by-digit peak pressures. In these cases, peak pressure for each digit during each trial was calculated by summing the peak normal forces experienced by each sensor on a given digit, and then dividing by the total sensor area across that digit. Third, we evaluated cumulative pressures across all of the digits. Similar to the procedures used for digital analyses, within every trial peak normal force measurements across all sensors were summed and then divided by total sensor area.

Our analyses had to accommodate the fact that repeated measurements were taken of each subject performing each behavior. To account for this bias, we calculated the average peak pressures per sensor, per activity, per subject. In doing so, we eliminated within-subject and within-activity variation. Although this ultimately reduced the size of our data set, and meant that we were not explicitly examining within-subject variability, we felt that such an approach was justified in the context of the current study. Given that subject participants were not experienced in stone tool behaviors, central tendencies of their pressure distributions are arguably more applicable for understanding the general patterns by which subjects used their hands. Further, by simplifying the variance structures of the data set and subsequent model fits, the results are more directly interpretable.

To address our first question of whether the different stone tool behaviors were characterized by similar distributions of pressure across the digits and how they differed, peak pressures from individual sensors were used. The peak pressures observed during each activity by each subject were adjusted because different subjects experienced different absolute magnitudes of pressures, and we were interested in analyzing consistency in distribution patterns. For each subject’s average peak pressure distribution during each activity (i.e., for each subject-activity pair), the pressures experienced across the sensors were normalized to a scale of 0 to 1, according to the following formula:

$$\mathrm{P}_{\mathrm{normalized}} = \frac{(\mathrm{P}_{\mathrm{observed}} - \mathrm{P}_{\mathrm{min}})}{(\mathrm{P}_{\mathrm{max}} - \mathrm{P}_{\mathrm{min}})}$$

Multivariate analysis of variance (MANOVA) was then used to determine the overall effect of behavior type on a multivariate response that included normalized peak pressures for each sensor, for each subject-activity pair.

Multiple steps were used to address our second question of which behaviors might impose the greatest biomechanical stress upon all of the digits. First, cumulative pressures across the digits were examined to identify which stone tool behaviors were associated with the highest magnitude pressure measurements. Analysis of variance (ANOVA), with post-hoc Tukey's honest significant difference (HSD) tests, was used to compare cumulative pressures across all behaviors. Following the ANOVA results that suggested there was high interindividual variation in pressure data, a linear mixed effects model was fit to the data to further investigate pressure variation across behaviors while accounting for subject identity as a random effect on cumulative pressure.

Next, to address our third question, more fine-scaled analyses were conducted to better understand the biomechanical differences across stone tool behaviors. MANOVA was used to determine the effect of behavior type on the raw magnitudes of (1) cumulative peak pressures on each digit and (2) peak pressures on each individual sensor. These analyses are pertinent to developing and evaluating hypotheses regarding which locations within the hand are likely to reflect anatomical adaptations to the biomechanics associated with stone tool behaviors and for evaluating which stone tool behaviors are the most likely to have exerted the strongest selective pressures on the anatomy of the human digits.

Results

Are different stone tool behaviors characterized by similar distributions of manual pressure?

Mean normalized peak pressure from each sensor across all participants for each activity is depicted in a heat map in Figure 2. Participants did not conform to a single pressure distribution pattern while performing the different stone tool behaviors investigated here; instead, behavior type had a significant effect on the multivariate overall pressure distribution (Pillai's Trace = 0.967, $p < 0.001$). A series of separate MANOVA analyses showed that behavior's effect was not uniform; a strong significant effect was observed during the various tissue-processing behaviors (Pillai's Trace = 0.949, $p < 0.001$), whereas all four nut-cracking behaviors resulted in statistically similar distributions (Pillai's Trace = 0.197, $p = 0.771$). This similarity did not, however, characterize percussive behaviors in general; a MANOVA analysis comparing pressure distributions during nut-cracking behaviors as well as marrow acquisition and flake production showed a strong significant behavioral effect (Pillai's Trace = 0.426, $p = 0.006$). This result was driven by variation in pressures on the second, fourth and fifth digits and no significant effects were present along the phalanges of the thumb and third digit.

Despite the overall differences, some consistencies in the normalized pressure distributions were present. Within each digit there was a tendency for the magnitude of the effect of behavior to correlate with the absolute magnitude of the load: behavior had a greater effect on those regions of the digit incurring the highest relative loads (typically the distal phalanges) and a lesser effect on the regions incurring the lowest relative loads (typically the proximal phalanges; Table 3, Fig. 2). The thumb was the exception to this pattern, being consistently relatively highly loaded regardless of the behavior. The results of the MANOVA analysis of percussive pressures support this hypothesis.

Which behaviors impose the greatest magnitude of manual pressure?

Analyses to determine which behavior(s) might impose the greatest biomechanical stress across the digits were conducted at multiple anatomical levels: the digits as a group, the individual digits, and the individual phalanges. Results were consistent across all three analytical levels: marrow acquisition and flake production consistently placed the greatest loads on all of the digits as a group (Fig. 3, Supplementary Online Material [SOM] Table S1), on individual digits (Fig. 4, SOM Table S2), and on the phalanges (Fig. 5, SOM Table S3).

Behavior had a highly significant effect on the cumulative raw pressures acting on the digits as a group ($p < 0.001$; Fig. 3). Post hoc pairwise comparisons showed that the use of hammerstones during flake production and marrow acquisition placed similarly ($p = 0.999$) high cumulative loads on the digits as a group, and both behaviors imposed significantly greater pressures than all other behaviors ($p \leq 0.05$), with two exceptions: pressures experienced while using a medium flake or large handaxe to slice tissue, which were not statistically different from pressures experienced during flake production ($p = 0.283$ and $p = 0.185$, respectively; Fig. 3). In addition, pressures experienced by the digits as a group while cracking hazelnuts were significantly smaller than those derived from medium flake or large handaxe use to slice tissue. All other post hoc pairwise comparisons of pressures acting on the digits as a group were not significantly different across the different behaviors.

The MANOVA results showed high variance within activities (Fig. 3), hinting at potentially high inter individual variation. To examine variation across activities in a more complete manner, a linear mixed effects model was fit to the data with total cumulative pressure as the response, behavior type as a fixed effect and subject identity as a random effect. This analysis could then include peak pressures from each trial for each subject rather than the average distributions per activity. The overall mean pressure for almond cracking was arbitrarily set as the reference behavior (intercept) of the mixed effects model and all other behaviors were contrasted with it. Cracking Brazil nuts did not involve significantly different pressures compared with almond cracking, cracking hazelnuts involved significantly lower pressures, and all other behaviors were associated with significantly higher total cumulative pressures (Table 4). Post hoc contrasts of all pairs of behaviors, with Holm-Bonferroni corrected p-values, showed that pressures imposed on the digits from cracking almonds, Brazil nuts and hazelnuts were significantly lower than pressures experienced during all other behaviors ($p < 0.001$). Pressures while cracking macadamia nuts were significantly greater than those while cracking any other variety of nut ($p < 0.001$). They were also greater than pressures experienced while using a small flake ($p < 0.001$) and similar to those while using a small handaxe ($p = 0.965$) but significantly lower than the pressures experienced during all other activities ($p < 0.001$).

When looking across the individual digits (i.e., accumulating data from sensors on the same digit), behavior also had a significant effect on pressure distribution (Pillai's Trace = 0.667, $p < 0.001$; Fig. 4). The strength of behavior's effect was greatest on the fourth digit, followed by the first, second, third and fifth digits (Table 5). Raw pressures tended to be higher on the radial side of the hand (i.e., digits I, II and III) relative to the ulnar side (i.e., digits IV and V) across all behaviors (SOM Table S2), meaning that the strength of the effect of behavior did not correlate with raw pressure, as was the case for normalized pressures.

Pressures while cracking almonds, Brazil nuts and hazelnuts again clustered together at the lowest end of the pressure range for the radial digits (though pressures tended to differ significantly only from marrow acquisition and flake production). However, on the ulnar side of the hand, these pressures were more similar to the pressures experienced during tissue processing behaviors. This was driven by a decrease in pressure on the fourth and fifth digits during tissue-processing behaviors rather than any substantial pressure increase on the same digits during nut-cracking. The comparatively low pressures on the fourth and fifth across nut-cracking and tissue-processing behaviors likely reflects the rarity with which these digits were in firm contact with the tool.

Post hoc Tukey HSD tests showed that among digits I through IV, hammerstone use during flake production and marrow acquisition exerted significantly greater pressures than all nut-cracking behaviors (minimum $p < 0.001$, maximum $p = 0.011$), apart from pressures experienced while cracking macadamia nuts compared with flake production ($p = 0.143$). Marrow acquisition and flake production also tended to impose significantly greater loads on digits I, III and IV than during tissue-processing behaviors (Fig. 4). The consistently high loads on the second digit across all behaviors reflected participants' tendency to grasp the flakes and handaxes primarily between their first and second or first, second and third digits, reserving the fourth and fifth to help steady the tool or not using them at all. Pressures were always lowest on digit V across all behaviors (20.69–75.83 kPa; SOM Table S2), with few statistical differences among the behaviors.

Behavior had a significant effect on pressure at the interphalangeal level, as it did at the other levels of analysis (Pillai's Trace = 1.134, $p < 0.001$). Similar to the distribution pattern of normalized pressures, the strength of behavior's effect was greater on those regions subject to higher loads (i.e., the distal phalanges; Table 6). Marrow acquisition consistently imposed greater loads on each phalanx compared with all other behaviors. This difference was significant across all phalangeal regions, apart from those of the fifth digit, compared with cracking almonds, Brazil nuts and hazelnuts. With few exceptions, flake production also exerted greater loads on each phalanx compared to all other behavior, however a consistent pattern regarding statistical significance was not present.

Discussion

Here we investigated manual pressure during Plio-Pleistocene stone tool behaviors to determine which behavior(s) exposed the digits of the dominant hand to the greatest magnitude of loads and thus were more likely to have influenced the evolution of human digit morphology. We addressed three questions: Are different stone tool behaviors characterized by similar distributions of manual pressure? Which behaviors impose the greatest magnitude of digital pressure? And, finally, what patterns of pressure distribution characterize the highest stress stone tool behaviors? In regard to the first question, we found that participants did not conform to a single pressure distribution pattern across all behaviors. In contrast, we found pressure experienced by the digits collectively and by the individual digits and phalanges varied significantly across the different Plio-Pleistocene tool behaviors.

Our finding that pressures experienced by the digits varied across the tested stone tool behaviors (Fig. 2) is, on one level, to be expected and indeed, our prediction that manual pressures would be lower during nut-cracking compared with flake production was supported. Subjects used tools of a wide range of sizes and shapes, including small flakes averaging 29.2–58.3 mm (Table 2) and hammerstones weighing 0.23 to ~1 kg, they had to utilize different kinematic approaches for various tasks (e.g., full arm swing versus more constrained extension at the wrist), and different magnitudes of force were required to successfully accomplish each behavior. Marzke and Shackley's (1986) discussion of the upper limb movements and grips used during various stone tool behaviors nicely contextualizes this result. Their participants exclusively used a grip known as a 'three jaw chuck' during Oldowan tool production and nut-cracking with small hammerstones, which relies on the first three digits of the dominant hand to grip the hammerstone. In contrast, while cutting with a small flake, the tool was grasped between the pollical distal phalanx and the lateral side of the second digit (Marzke and Shackley, 1986). Clearly, these postural and kinematics differences are likely to result in variations in manual pressure distributions.

Our results, however, suggest that such factors alone are insufficient to account for the observed variation, as illustrated by the differences in relative pressure distributions among percussive behaviors: despite participants using the same selection of hammerstones and gross similarities in the motions, behavior had a significant effect on the distribution of relative pressures in comparisons of nut-cracking, marrow acquisition and flake production (Pillai's Trace = 0.426, $p = 0.006$; Figs. 4 and 5). This was in sharp contrast to the strong statistical similarity among nut-cracking behaviors alone (Pillai’s Trace = 0.197, $p < 0.771$). These results suggest that the force needed to carry out a behavior—in these cases, load to failure of the bone, stone or nut—also influences the hand-tool pressure relationship and resulting distribution of relative pressures. It appears that during activities such as nut-cracking, when relatively low forces are required to cause material failure, a generic hand-tool posture that is not specialized to a specific high-loading condition can be used, resulting in a similar distribution of relative pressures across nut-cracking behaviors. However, more forceful activities, such as marrow acquisition and flake production, require specialization to maintain precise control of the hammerstone and to deliver the requisite forces while also avoiding injury.

This proposal is supported by the strong tendency for the strength of behavior’s effect to correlate positively with the relative magnitude of the load at a given sensor across all behaviors (Table 3). Thus, there was more variability in the relative pressures acting on the distal phalanges, which always experience the highest peak pressures, compared with the proximal phalanges and (generally) the intermediate phalanges. This pattern suggests that, regardless of which tool was being used, participants tended to stabilize the tool primarily with the distal phalanges and then adjusted the amount of force they applied at these phalanges according to the task at hand. Simultaneously, they tended to use the intermediate and proximal regions of the digits on a more limited basis, and at consistently low pressures. We found strong variability in relative pressures acting on the fourth and fifth distal phalanges in particular, which likely reflects the widely variable roles that these digital regions played across the various tool behaviors, as described above. At one extreme, these digits were consistently used and subject to the highest intra-digit pressures during nut-cracking, and at the other they were inconsistently used with the lowest inter sensor loads recorded during slicing with smaller cutting tools (Fig. 5).

The thumb was the exception to this pattern: despite the fact that loads on the pollical distal phalanx were significantly greater than those on the pollical proximal phalanx, behavior had a rather small effect on the relative loads acting on the distal phalanx, and a far stronger effect on the proximal phalanx (Table 3). In other words, the pollical distal phalanx tended to be subjected to the same relative loads (i.e., the greatest relative load), irrespective of behavior (Fig. 2). This illustrates the consistency in how the thumb was used: regardless of how the hand was oriented relative to the tool, the thumb acted as the stabilizing fulcrum or clamp against the tool or the other digits (Napier, 1956; Marzke, 1997). These results contrast with those of Key (2016), who found that stone carrying behaviors did not consistently result in heavy loading on the thumb, further emphasizing the important role of this digit during specific forceful stone tool use activities (such as those examined here). In regard to knapping, this is similar to results reported by Rolian et al. (2011), and in contrast to those reported by Williams et al. (2012), who reported that loads were highest on the second and third digits compared with the thumb. As suggested by Key and Dunmore (2015), the difference in these findings may reflect simple diversity in preferred hand postures during knapping, or it may be a result of the composition of the participant pools: novice tool makers were studied here and by Rolian et al. (2011), whereas Williams et al. (2012) studied only experienced tool makers.

Upon demonstrating that stone tool behaviors are not characterized by a single pressure distribution pattern, we examined the absolute loads to establish which behaviors placed the greatest biomechanical stress on the digits collectively and, by extension, may be more likely to have imposed a selective pressure on the digits. We first demonstrated that, at each anatomical level of analysis, behavior had a significant effect on absolute pressure magnitudes—cumulative pressures acting across the digits as a group ($p < 0.001$; Fig. 3), the individual digits (Pillai's Trace = 0.667, $p < 0.001$; Fig. 4), and the individual phalanges (Pillai's Trace = 1.134, $p < 0.001$; Fig. 5). Thus, both the relative pressures (i.e., normalized data) and the absolute pressures (i.e., raw data) acting at a given location are influenced by the behavior being performed, together strongly indicating that some behaviors may be more suitable candidates for those imposing selective pressures on the digits than others.

The two most striking results of the analyses of the absolute pressures imposed by the tool behaviors were (1) the clear distinction in the high pressures incurred by hammerstone use during marrow acquisition and flake production relative to all other assessed behaviors, and (2) the further distinction of low pressures during nut-cracking compared with all other behaviors. Our results revealed that relative to all other assessed behaviors, hammerstone use during marrow acquisition and flake production resulted in significantly higher pressures experienced by the digits as a group (Fig. 3). Similarly, marrow acquisition and flake production also imposed significantly greater loads on the radial four digits relative to nut-cracking behaviors (other than loads on digit II while cracking macadamia nuts compared with flake production). With the exception of loads acting on the second digit, marrow acquisition and flake production also tended to impose significantly greater loads on the digits compared with tissue processing behaviors. A similar pattern, although not always statistically significant, was found at the inter phalangeal level, such that peak pressures were generally highest during marrow acquisition and flake production, especially on the distal phalanges, compared to all other behaviors (Fig. 5).

On the radial four digits, hammerstone use during marrow acquisition and flake production consistently imposed significantly greater loads compared with the other tested behaviors on the distal phalanges. This was not consistently the case regarding the intermediate and proximal phalanges. Loads experienced at the distal phalanges have a larger contribution toward resultant joint stresses than do those experienced at the more proximal regions of the rays (Cooney and Chao, 1977). Thus, it is reasonable to argue that behaviors that concentrated loads on the distal phalanges would have been more influential from an evolutionary standpoint than those that concentrated loads on the intermediate and/or proximal regions.

In contrast to marrow acquisition and flake production, pressures experienced during nut-cracking behaviors, particularly when cracking almonds, Brazil nuts and hazelnuts, were generally far lower than pressures incurred during all other behaviors. This pattern was found in both pressures experienced by the digits as a group, where the differences were statistically significant, and among the three radial digits. Macadamia nuts were the exception to this pattern, such that pressures incurred by the digits as a group or by the individual digits were generally higher than other nut-cracking behaviors and most similar to pressures experienced during tissue-processing behaviors. The difficulty participants consistently had in cracking them resulted not from shell toughness but rather from their tendency to roll away when struck, due to their smooth, round shells. Thus, the higher loads seen while cracking macadamia nuts more likely reflect participants' use of high-force strikes in an attempt to prevent the nut from rolling away rather than what was needed to induce shell failure. Additionally, participants' lack of familiarity with nut-cracking behaviors likely also impacted their performance (Brill et al., 2010, 2012), both in regard to pressures experienced and their ability to successfully rupture the shell (see below).

Implications for the evolution of the human digits and hand

It is generally assumed that the modern human hand morphology is, at least in part, a byproduct of stone tool-related behaviors, and particularly a commitment to intensified use of these behaviors (e.g., Washburn, 1960; Napier, 1962; Marzke, 1997; Tocheri et al. 2008). Paleoanthropologists have reasoned that behaviors that involve higher load magnitudes or stronger muscle recruitment patterns, and which conferred a substantial benefit on the actor, such as the acquisition of high quality food items, were more likely to exert selective pressures on the evolution of human hand anatomy (e.g., Susman, 1994; Hamrick et al., 1998; Marzke et al., 1998; Rolian et al., 2011; Williams et al., 2012; Key and Dunmore, 2015). Our results suggest that hammerstone use during marrow acquisition and flake production would likely have resulted in the strongest selective pressures on the evolution of our hands (among the tool behaviors tested). The profound benefits early humans could have derived from their abilities to make and use sharp-edged stone tools have long been established, including increases in brain and body mass, territorial expansion, and advances in protective and predatory behaviors (e.g., Washburn, 1960; Aiello and Wheeler, 1995; Domínguez-Rodrigo et al., 2005; Shea, 2007; Ambrose, 2010; Shea and Sisk, 2010; Navarrete et al., 2011). It is thus fitting that the production of flakes is among the two behaviors that impose the greatest loads on the digits, making it even more likely to have elicited an adaptive response.

In comparison to stone tool making, marrow acquisition has received considerably less consideration in regard to the role it may have played in the evolution of the human digits and hand. However, our results demonstrate that pressures resulting from marrow acquisition can be as high as or even higher than those imposed by the production of stone flakes. The caloric benefits of marrow in the hominin diet are well established (Bunn, 1986; Bunn and Kroll, 1986; Blumenschine and Madrigal, 1993; Aiello and Wheeler, 1995; Milton, 2003). Furthermore, archaeological evidence demonstrates that hominins were potentially using hammerstones to access long bone marrow cavities as early as 3.39 Ma at Dikika, Ethiopia (McPherron et al., 2010; but see Domínguez-Rodrigo et al., 2011), contemporaneous with or even prior to the earliest evidence of stone tool production at 3.3 Ma (Harmand et al., 2015). Although there is currently no evidence that chimpanzees use hammerstones to access marrow cavities, rendering it premature to propose that the last common ancestor (LCA) of *Pan* and humans engaged in similar behaviors, chimpanzees are well known to use hammerstones to crack open nuts (Whiten et al., 2001; Carvalho et al., 2008) and those living in the Taï National Park in Côte d’Ivoire have been observed using sticks to pick marrow out of colobus monkey long bones (Boesch and Boesch-Acherman, 2000).

Bringing together our manual pressure results with archaeological evidence, we support Marzke et al.'s (1998) hypothesis that the biomechanical loads resulting from marrow acquisition with a hammerstone may have also been a primary cause of selection for greater stability and enhanced gripping abilities (e.g., a longer thumb relative to finger length; Alba et al., 2003; but see Rolian and Gordon, 2013, 2014) in early hominins' hands. Given the antiquity of the potentially percussed and cut-marked bones from Dikika, Ethiopia (McPherron et al., 2010; but see Domínguez-Rodriqo et al. 2011) and percussive and marrow acquisition behaviors in extant chimpanzees (Boesch and Boesch-Acherman, 2000; Carvalho et al., 2008), stone tool mediated marrow acquisition may have exerted selective pressures on hominin digital and hand anatomy just as early, if not even earlier, then those pressures related to flake production.

Our results also highlight that not all percussive behaviors may have been equally likely to generate a selective pressure on the digits. In contrast to flake production and marrow acquisition, the consistently low pressure experienced by the digits as a group during nut-cracking suggests that this behavior may not have generated strong selective pressures on digital morphology during human evolution. Chimpanzees do not show significant anatomical adaptations for manual manipulation or to withstand forces oriented in the same directions experienced by humans during percussive behaviors (Tocheri et al., 2005; Marzke et al., 2010; Rolian et al., 2011), so such adaptations would not be expected for purely nut-cracking hominins either. Recent analyses of Early Pleistocene anvils from Olduvai Gorge have demonstrated widespread percussive food processing activities by Lower Palaeolithic hominins, including potential evidence of nut-cracking (Sánchez Yustos et al., 2015; Arroyo and de la Torre, 2016; Arroyo et al., 2016). Assemblages of pitted hammerstones, anvils, and nut debris from the Early-Middle Pleistocene Acheulean site of Gesher Benot Ya'aqov (Israel) also provide early evidence of hominin nut-cracking behaviors (Goren-Inbar et al., 2002). Furthermore, a 4,300 year old chimpanzee nut-cracking site in Taï National Park (Mercader et al., 2007) and abundant documentation of chimpanzees in central and western Africa using hammerstones to crack open a variety of nut types (Whitesides, 1985; Whiten et al., 1999; Boesch and Boesch-Acherman, 2000; Carvalho et al., 2008) suggest that the *Pan-Homo* LCA may have also used hammerstones to crack open nut shells and access the internal nut meat (Haslam et al., 2009). Yet derived morphological features of the hand thought to be related to increased dexterity and/or manual loading are not known until *Australopithecus* (Tocheri et al., 2008), several million years after a potential nut-cracking LCA.

The estimated caloric benefits of nut-cracking are enormous: Taï chimpanzees obtain more than 3,000 calories per day by consuming the nuts they crack (Boesch and Boesch Acherman, 2000) and maintain a 1:9 energy expenditure to calorie intake ratio (Günther and Boesch, 1993). This ratio is impressive given the toughness values of the nuts they consume. Boesch and Boesch-Acherman (2000) reported that cracking open a panda nut (*Panda oleosa*) necessitated the equivalent of dropping a 10 kg stone from a height of 120 cm. That this behavior has not led to the development of a digit and hand anatomy more similar to our own—marked by large joint surface areas (Rolian et al., 2011) and features contributing to robusticity and palmar stability (Marzke and Marzke, 1987; Susman, 1994; Marzke et al., 1998; Ward et al., 2014)—suggests that the loads and biomechanics associated with nut-cracking may be insufficient to induce an adaptive anatomical response, or that they may already be accommodated by chimpanzee digit and hand morphology.

It is important to consider the limitations present in the current study when applying these results to interpretations of the hominin fossil record. The pressure sensors quantify normal (i.e., vertical) force only, and thus forces acting in other planes that may vary depending on the tool and grip used, are not included in this analysis. Furthermore, pressure data were recorded from the palmar surfaces of the digits of the dominant hand and therefore these data do not account for loads acting on the medial and lateral sides of the digits or on the palm. Additionally, none of the participants in this study had any prior experience making or using Plio-Pleistocene tools. The selection of a novice population was deliberate to reduce the confounding effects of interparticipant variation in experience across all of the behaviors and inter-behavior variation in experience in a single participant. However, it is likely that the biomechanics presented here would change over time with practice (Bril et al., 2012; Rein et al. 2014). Thus, the data and the associated biomechanics and joint strains may represent a temporary phase in skill acquisition rather than a constant. On the other hand, it is a phase that all tool makers and users pass through and we cannot say whether digit selection was responding to a particular stage in development or the cumulative effects, and if so which stage that may be. Finally, we intentionally constrained the parameters of each behavior in an effort to standardize data collection and ensure comparable experiences across participants were being compared. Thus, we recognize that performing such behaviors in a natural context would likely invoke a greater range of variation in grip strategies, tool use/production techniques and manual pressures that are not captured in this study. However, as the first comprehensive study of manual pressures during a large variety of Plio-Pleistocene stone tool behaviors, these data provide the much needed comparative data to develop more informed hypotheses about the manipulative selective pressures that influence the evolution of human digit morphology.

Conclusions

Stone tool behaviors are not characterized by a single manual pressure distribution pattern: behavior has a strong effect on relative and absolute load distributions. Thus, in evaluations of behaviors likely to have exerted a selective response across the digits, it is insufficient to consider load distribution in the absence of load magnitude between behaviors (e.g., Williams et al., 2012; Key and Dunmore, 2015). When magnitude is taken into account, analyses of the digits as a group, of individual digits and of phalanges point to hammerstone use during marrow acquisition and flake production as the best candidates among the tested stone tool behaviors that may have exerted primary selective pressures on the evolution of the human digits.

Acknowledgments

We are grateful to those who volunteered to participate in this study. We thank the Editors and three anonymous reviewers for their comments that greatly improved this manuscript. This research was supported by a European Research Council Starting Grant 336301 (T.L.K., E.M.W.-H.), Chatham University, Wenner-Gren Foundation Grant 7995 (E.M.W.-H.), and the George Washington University’s Selective Excellence Fund

(E.M.W.-H.). A.K.’s research is supported by a British Academy Postdoctoral Fellowship (pf160022).

References

Aiello, L.C., Wheeler, P., 1995. The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. Current Anthropology 36, 199–221.

Alba, D.M., Moyà-Solà, S., Köhler, M., 2003. Morphological affinities of the *Australopithecus afarensis* hand on the basis of manual proportions and relative thumb length. Journal of Human Evolution 44, 225–254.

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

Ambrose, S.H., 2010. Coevolution of composite-tool technology, constructive memory and language: Implications for the evolution of modern human behavior. Current Anthropology 51, S135–S137.

Arroyo, A., De La Torre, I., 2016. Assessing the function of pounding tools in the Early Stone Age: a microscopic approach to the analysis of percussive artefacts from Beds I and II, Olduvai Gorge (Tanzania). Journal of Archaeological Science 74, 23–34.

Arroyo, A., Hirata, S., Matsuzawa, T., De La Torre, I., 2016. Nut cracking tools used by captive chimpanzees (*Pan troglodytes*) and their comparison with Early Stone Age percussive artefacts from Olduvai Gorge, PLoS One 11, e0166788.

Bello, S.M., Parfitt, S.A., Stringer, S., 2009. Quantitative micromorphological analyses of cut marks produced by ancient and modern handaxes. Journal of Archaeological Science 36, 1869–1880.

Bertram, J.E.A., Swartz, S.M., 1991. The ‘law of bone transformation’: a case of crying Wolff? Biological Reviews 66, 245–273.

Biewener, A.A., 1993. Safety factors in bone strength. Calcified Tissue International 53, S68–S74.

Blumenschine, R.J., 1995. Percussion marks, tooth marks, and experimental determinations of the timing of hominid and carnivore access to long bones at FLK *Zinjanthropus*, Olduvai Gorge, Tanzania. Journal of Human Evolution 29, 21–51.

Blumenschine, R.J., Madrigal, C., 1993. Variability in long bone marrow yields of East African ungulates and its zooarchaeological implications. Journal of Archaeological Science 20, 555–587.

Blumenschine, R.J., Pobiner, B.L., 2007. Zooarchaeology and the ecology of Oldowan hominin carnivory. In: Ungar, P. (Ed.), Evolution of the Human Diet: The Known, the Unknown and the Unknowable. Oxford University Press, Oxford, pp. 167–190.

Blumenschine, R.J., Whiten, A., Hawkes, K., 1991. Hominid carnivory and foraging strategies, and the socio-economic function of early archaeological sites [and discussion]. Philosophical Transactions of the Royal Society London B 334, 211–221.

Boesch, C., Boesch-Acherman, H., 2000. The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution. Oxford University Press, Oxford.

Brain, C.K., 1981. The Hunters or the Hunted? An Introduction to African Cave Taphonomy. University of Chicago Press, Chicago.

Braun, D.R., Harris, J.W.K., Levin, N.E., McCoy, J.T., Herries, A.I.R., Bamford, M.K., Bishop, L.C., Richmond, B.G., Kibunjia, M., 2010. Early hominin diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya. Proceedings of the National Academy of Sciences 107, 10002–10007.

Braun, D.R., Plummer, T., Ferraro, J.V., Ditchfield, P., Bishop, L.C., 2009. Raw material quality and Oldowan hominin toolstone preferences: evidence from Kanjera South, Kenya. Journal of Archaeological Science 36, 1605–1614.

Bril, B., Rein, R., Nonaka, T., 2010. The role of expertise in tool use: skill differences in functional action adaptations to task constraints. Journal of Experimental Psychology 36, 825–839.

Bril, B., Smaers, J., Steele, J., Rein, R., Nonaka, T., Dietrich, G., Biryukova, E., Hirata, S., Roux, V., 2012. Functional mastery of percussive technology in nut-cracking and stone-flaking actions: experimental comparison and implications for the evolution of the human brain. Philosophical Transactions of the Royal Society London B 367, 59–74.

Bunn, H.T., 1981. Archaeological evidence for meat-eating by Plio-Pleistocene hominids from Koobi Fora and Olduvai Gorge. Nature 291, 574–577.

Bunn, H.T., 1986. Patterns of skeletal representation and hominid subsistence activities at Olduvai Gorge, Tanzania and Koobi Fora, Kenya. Journal of Human Evolution 15, 673–690.

Bunn, H.T., Kroll, E.M., 1986. Systematic butchery by Plio/Pleistocene hominids at Olduvai Gorge, Tanzania. Current Anthropology 27, 431–452.

Burr, D.B., 1985. Bone remodelling in response to in vivo fatigue microdamage. Journal of Biomechanics 18, 189–200.

Carvalho, S., Cunha, E., Sousa, C., Matsuzawa, T., 2008. Chaînes opératoires and resource-exploitation strategies in chimpanzee *Pan troglodytes* nut cracking. Journal of Human Evolution 55, 148–163.

Chai, H., Lawn, B.R., 2007a. A Universal relation for edge chipping from sharp contacts in brittle materials: a simple means of toughness evaluation. Acta Materialia 55, 2555–2561.

Chai, H., Lawn, B.R., 2007b. Edge chipping of brittle materials: effect of side-wall inclination and loading angle. International Journal of Fracture 145, 159–165.

Chao, E., An, K.-N., Cooney, W. III, Linscheid, P., 1989. Biomechanics of the Hand. World Scientific, Singapore.

Clark, J.L., Plug, I., 2008. Animal exploitation strategies during the South African Middle Stone Age: Howiesons Poort and post-Howiesons Poort fauna from Sibudu Cave. Journal of Human Evolution 54, 886–898.

Cooney, W. III, Chao, E., 1977. Biomechanical analysis of static forces in the thumb during hand function. Journal of Bone and Joint Surgery 59, 27–36.

Darwin, C., 1871. The Descent of Man, and Selection in Relation to Sex. John Murray, London.

de Heinzelin, J., Desmond Clark, J., White, T., Hart, W., Renne, P.R., WoldeGabriel, G., Bevene, Y., Vrba, E.S., 1999. Environment and behavior of 2.5-million-year-old Bouri hominids. Science 283, 625–629.

Domínguez-Rodrigo, M., 1997. Meat-eating by early hominids at the FLK 22 *Zinjanthropus* site, Olduvai Gorge (Tanzania): an experimental approach using cut-mark data. Journal of Human Evolution 33, 669–690.

Domínguez-Rodrigo, M., Pickering, T.R., Bunn, H.T., 2011. Reply to McPherron et al.: Doubting Dikika is about data, not paradigms. Proceedings of the National Academy of Sciences 108, E117.

Domínguez-Rodrigo, M., Pickering, T.R., Semaw, S., Rogers, J.J. 2005. Cutmarked bones from Pliocene archaeological sites at Gona, Afar, Ethiopia: implications for the function of the world's oldest stone tools. Journal of Human Evolution 48, 109–121.

Domínguez-Rodrigo, M., Serrallonga, J., Juan-Tresserras, J., Alcala, L., Luque, L., 2001. Woodworking activities by early humans: a plant residue analysis on Acheulian stone tools from Peninj (Tanzania). Journal of Human Evolution 40, 289–299.

Frost, H.M., 1987. Bone "mass" and the "mechanostat": A proposal. Anatomical Record 219, 1–9.

Goren-Inbar, N., Sharon, G., Melamed, Y., Kislev, M., 2002. Nuts, nut cracking, and pitted stones at Gesher Benot Ya'aqov, Israel. Proceedings of the National Academy of Sciences 99, 2455–2460.

Green, D.J., Gordon, A.D., 2008. Metacarpal proportions in *Australopithecus africanus*. Journal of Human Evolution 54, 705–719.

Günther, M.M., Boesch, C., 1993. Energetics of nut-cracking behaviour in wild chimpanzees. In: Preuschoft, H., Chivers, D.J. (Eds.), Hands of Primates. Springer, Vienna, pp. 109–129.

Hamrick, M., Churchill, S., Schmitt, D., Hylander, W., 1998. EMG of the human flexor pollicis longus muscle: implications for the evolution of hominid tool use. Journal of Human Evolution 34, 123–136.

Harmand, S., Lewis, J.E., Feibel, C.S., Lepre, C.J., Prat, S., Lenoble, A., Boes, X., Quinn, R.L., Brenet, M., Arroyo, A., Taylor, N., Clement, S., Daver, G., Brugal, J.-P., Leakey, L., Mortlock, R.A., Wright, J.D., Lokorodi, S., Kirwa, C., Kent, D.V., Roche, H., 2015. 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. Nature 521, 310–315.

Haslam, M., Hernandez-Aguilar, A., Ling, V., Carvalho, S., de la Torre, I., DeStefano, A., Du, A., Hardy, B., Harris, J., Marchant, L., 2009. Primate archaeology. Nature 460, 339–344.

Hohmann, G., Fruth, B., 2003. Culture in bonobos? Between-species and within species variation in behavior. Current Anthropology 44, 563–571.

Jennings, J.S., MacMillan, N.H., 1986. A tough nut to crack. Journal of Materials Science, 21, 1517-1524.

Key, A.J., 2016. Manual loading distribution during carrying behaviors: implications for the evolution of the hominin hand. PLoS One 11, e0163801.

Key, A.J., Dunmore, C.J., 2015. The evolution of the hominin thumb and the influence exerted by the non-dominant hand during stone tool production. Journal of Human Evolution 78, 60–69.

Key, A.J., Dunmore, C.J., Hatala, K.G., Williams-Hatala, E.M., 2017. Flake morphology as a record of manual pressure during stone tool production. Journal of Archaeological Science: Reports 12, 43–53.

Key, A.J., Lycett, S.J., 2017. Investigating interrelationships between Lower Palaeolithic stone tool effectiveness and tool user biometric variation: implications for technological and evolutionary changes. Archaeological and Anthropological Sciences DOI: 10.1007/s12520-016-0433-x

Kimbel, W.H., Walter, R.C., Johanson, D.C., Reed, K.E., Aronson, J.L., Assefa, Z., Marean, C.W., Eck, G.G., Bobe, R., Hovers, E., Rak, Y., 1996. Late Pliocene *Homo* and Oldowan Tools from the Hadar Formation (Kada Hadar Member), Ethiopia. Journal of Human Evolution 31, 549–561.

Kivell, T.L., 2015. Evidence in hand: recent discoveries and the early evolution of human manual manipulation. Philosophical Transactions of the Royal Society London B 370, 201501505.

Kivell, T.L., 2016. A review of trabecular bone functional adaptation: what have we learned from trabecular analyses in extant hominoids and what can we apply to fossils? Journal of Anatomy 228, 569–594.

Kivell, T.L., Kibii, J.M., Churchill, S.E., Schmid, P., Berger, L.R., 2011. *Australopithecus sediba* hand demonstrates mosaic evolution of locomotor and manipulative abilities. Science 333, 1411–1417.

Klein, R.G., 1976. The mammalian fauna of the Klasies River Mouth Sites, Southern Cape Province, South Africa. South African Archaeological Bulletin 31, 75–98.

Kopperdahl, D.L., Keaveny, T.M., 1998. Yield strain behavior of trabecular bone. Journal of Biomechics 31, 601–608.

Leakey, L.S., Tobias, P.V., Napier, J.R., 1964. A new species of the genus *Homo* from Olduvai Gorge. Nature 202, 7–9.

Lorenzo, C., Arsuaga, J.L., Carretero, J.M., 1999. Hand and foot remains from the Gran Dolina Early Pleistocene site (Sierra de Atapuerca, Spain). Journal of Human Evolution 37, 501–522.

Lovejoy, C.O., Simpson, S.W., White, T.D., Asfaw, B., Suwa, G., 2009. Careful climbing in the Miocene: the forelimbs of *Ardipithecus ramidus* and humans are primitive. Science 326, 70e1–70e8.

Lucas, P.W. 2004. Dental Functional Morphology: How Teeth Work. Cambridge University Press, Cambridge.

Lucas, P.W., Gaskins, J.T., Lowrey, T.K., Harrison, M.E., Morrogh-Bernard, H.C., Cheyne, S.M., Begley, M.R., 2011. Evolutionary optimization of material properties of a tropical seed. Journal of the Royal Society Interface, rsif20110188.

Lycett, S.J., von Cramon-Taubadel, N., 2008. Acheulean variability and hominin dispersals: a model-bound approach. Journal of Archaeological Science 35, 553–562.

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

Marzke, M.W., Marzke, R.F., 1987. The third metacarpal styloid process in humans: origin and functions. American Journal of Physical Anthropology 73, 415–431.

Marzke, M.W., Shackley, M.S., 1986. Hominid hand use in the Pliocene and Peistocene: evidence from experimental archaeology and comparative morphology. Journal of Human Evolution 16, 439–460.

Marzke, M.W., Tocheri, M.W., Steinberg, B., Femiani, J.D., Reece, S.P., Linscheid, R.L., Orr, C.M., Marzke, R.F. 2010. Comparative 3D quantitative analyses of trapeziometacarpal joint surface curvatures among living catarrhines and fossil hominins. American Journal of Physical Anthropology 141, 38–51.

Marzke, M.W., Toth, N., Schick, K., Reece, S., Steinberg, B., Hunt, K., Linscheid, R., An, K., 1998. EMG study of hand muscle recruitment during hard hammer percussion manufacture of Oldowan tools. American Journal of Physical Anthropology 105, 315–332.

McPherron, S.P., Alemseged, Z., Marean, C.W., Wynn, J.G., Reed, D., Geraads, D., Bobe, R., Béarat, H.A., 2010. Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. Nature 466, 857–860.

McPoil, T.G., Cornwall, M.W., Yamada, W., 1995. A comparison of two in-shoe plantar pressure measurement systems. The Lower Extremity 2, 95–103.

Mercader, J., Barton, H., Gillespie, J., Harris, J.M., Kuhn, S.L., Tyler, R., Boesch, C., 2007. 4,300-year-old chimpanzee sites and the origins of percussive stone technology. Proceedings of the National Academy of Sciences 104, 3043–3048.

Milton, K., 2003. The critical role played by animal source foods in human (*Homo*) evolution. The Journal of Nutrition 133, 3886S–3892S.

Napier, J., 1956. The prehensile movements of the human hand. The Journal of Bone and Joint Surgery 38, 902–913.

Napier, J., 1962. Fossil hand bones from Olduvai Gorge. Nature 196, 409–411.

Navarrete, A., van Schaik, C.P., Isler, K., 2011. Energetics and the evolution of human brain size. Nature 480, 91–93.

Neufuss, J., Humle, T., Cremaschi, A., Kivell, T.L., 2017. Nut-cracking behaviour in wild-born, rehabilitated bonobos (*Pan paniscus*): a comprehansive study of hand-preference, hand grips and efficiency. American Journal of Primatology 79, 1–16.

Niewoehner, W.A., 2001. Behavioral inferences from the Skhul/Qafzeh early modern human hand remains. Proceedings of the National Academy of Sciences 98, 2979–2984.

Price, C., Parker, D., Nester, C., 2016. Validity and repeatability of three in-shoe pressure measurement systems. Gait & Posture 46, 69–74.

Putti, A.B., Arnold, G.P., Cochrane, L., Abboud, R.J., 2007. The Pedar® in-shoe system: repeatability and normal pressure values. Gait & Posture 25, 403–405.

R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rein, R., Nonaka, T., Bril, B., 2014. Movement pattern variability in stone knapping: implications for the development of percussive technologies. PLoS One 9, e113567.

Rhodes, J.A., Churchill, S.E., 2009. Throwing in the Middle and Upper Paleolithic: inferences from an analysis of humeral retroversion. Journal of Human Evolution 56, 1–10.

Roach, N.T., Richmond, B.G., 2015. Clavicle length, throwing performance and the reconstruction of the *Homo erectus* shoulder. Journal of Human Evolution 80, 107–113.

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

Roffman, I., Savage-Rumbaugh, S., Rubert-Pugh, E., Ronen, A., Nevo, E., 2006. Stone tool production and utilizatio by bonobo-chimpanzees (*Pan paniscus*). Proceedings of the National Academy of Sciences 109, 14500–14503.

Rolian, C., Gordon, A.D., 2013. Reassessing manual proportions in *Australopithecus afarensis*. American Journal of Physical Anthropology 152, 393–406.

Rolian, C., Gordon, A.D., 2014. Response to Almécija and Alba (2014) – On manual proportions in *Australopithecus afarensis*. Journal of Human Evolution 73, 93–97.

Rolian, C., Lieberman, D.E., Hallgrimsson, B., 2010. The coevolution of human hands and feet. Evolution 64, 1558–1568.

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

Rubin, C.T., Lanyon, L.E., 1985. Regulation of bone mass by mechanical strain magnitude. Calcified Tissue International 37, 411–417.

Sánchez Yustos, P., Diez-Martín, F., Díaz, I.M., Duque, J., Fraile, D., Domínguez, M., 2015. Production and use of percussive stone tools in the Early Stone Age: Experimental approach to the lithic record of Olduvai Gorge, Tanzania. Journal of Archaeological Science: Reports 2, 367–383.

Semaw, S., 2000. The world's oldest stone artefacts from Gona, Ethiopia: their implications for understanding stone technology and patterns of human evolution between 2·6–1·5 million years ago. Journal of Archaeological Science 27, 1197–1213.

Sharon, G., 2008. Large flake Acheulian. Quaternary International 223–224, 226–233.

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

Shea, J.J., Sisk, M.L., 2010. Complex projectile technology and *Homo sapiens* dispersal into Western Eurasia. PaleoAnthropology 2010, 100–122.

Skinner, M.M., Stephens, N.B., Tsegai, Z.J., Foote, A.C., Nguyen, N.H., Gross, T., Pahr, D.H., Hublin, J.J., Kivell, T.L., 2015. Human-like hand use in *Australopithecus africanus*. Science 347, 395–399.

Stout, D., Semaw, S., Rogers, M.J., Cauche, D., 2010. Technological variation in the earliest Oldowan from Gona, Afar, Ethiopia. Journal of Human Evolution 58, 474–491.

Stout, D., Toth, N., Schick, K., Chaminade, T., 2008. Neural correlates of Early Stone Age toolmaking: technology, language and cognition in human evolution. Proceedings of the National Academy of Sciences 363, 1939–1949.

Susman, R.L., 1988. Hand of *Paranthropus robustus* from Member 1, Swartkrans: fossil evidence for tool behavior. Science 240, 781–784.

Susman, R.L., 1994. Fossil evidence for early hominid tool use. Science 265, 1570–1573.

Susman, R.L., 1998. Hand function and tool behavior in early hominids. Journal of Human Evolution 35, 23–46.

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

Tocheri, M.W., Razdan, A., Williams, R.C., Marzke, M.W. 2005. A 3D quantative comparison of trapezium and trapezoid relative articular and nonarticular surface areas in modern humans and great apes. Journal of Human Evolution 49, 570–586.

Toth, N., 1985. The Oldowan reassessed: A close look at early stone artifacts. Journal of Archaeological Science 12, 101–120.

Toth, N., Schick, K.D., Savage-Rumbaugh, E.S., Sevcik, R.A., Rumbaugh, D.M., 1993. *Pan* the tool-maker: investigations into the stone tool-making and tool-using capabilities of a bonobo (*Pan paniscus*). Journal of Archaeological Science 20, 81–91.

Unger, P., Grine, F.E., Teaford, M.F., 2006. Diet in early *Homo*: A review of the evidence and a new model of adaptive versatility. Annual Review of Anthropology 35, 209–228.

Ward, C.V., Tocheri, M.W., Plavcan, J.M., Brown, F.H., Manthi, F.K., 2014. Early Pleistocene third metacarpal from Kenya and the evolution of modern human-like hand morphology. Proceedings of the National Academy of Sciences 111, 121–124.

Washburn, S.L., 1960. Tools and human evolution. Scientific American 203, 62–75.

Weiss, K.M., 2012. Agnotology. Evolutionary Anthropology 21, 96–100.

Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.E., Wrangham, R.W., Boesch, C., 1999. Cultures in chimpanzees. Nature 399, 682–685.

Whitesides, G.H., 1985. Nut-cracking by wild chimpanzees in Sierra, Leone, West Africa. Primates 26, 91–94.

Williams, E.M., Gordon, A.D., Richmond, B.G., 2012. Hand pressure distribution during Oldowan stone tool production. Journal of Human Evolution 62, 520–532.

Figure captions

Figure 1. Dorsal (left) and palmar (right) views of the sensor and cable placement and the attachment apparatus.

Figure 2. Heat map showing the distribution across the digits of normalized pressures. The lowest normalized pressures acting at each sensor are shown in blue, the highest normalized pressures acting at each sensor are shown in red (refer to the scale on the

right). The highest normalized pressures tended to act on digit I and lowest normalized pressures tended to act on the digit V. Otherwise, there was considerable variation in the distribution. An a priori example of similarity is provided at the left. Abbreviations: HA = handaxe; see Table 1 for sensor abbreviations.

Figure 3. Boxplots displaying the raw cumulative pressures acting on the hand during the tested behaviors. The center line represents the sample median. The box boundaries display the interquartile range (25–75%), and whiskers extend to the farthest data points that are within 1.5 times the interquartile range from either the lower or upper bound of the box. Dots represent extreme outliers, defined as points more than 1.5 times the interquartile range from the central 50% of the data.

Figure 4. Heat map showing the distribution of raw pressures among the digits. The lowest absolute pressures acting along each digit are shown in blue, the highest absolute pressures acting along each digit are shown in red (refer to the scale on the right). Across all behaviors, absolute pressures were highest on digit I and lowest on digit V. Marrow acquisition and flake production tended to impose significantly greater loads on the digits compared with other tested behaviors. Abbreviations: HA = handaxe.

Figure 5. Heat map showing the distribution of raw pressures among the phalanges. The lowest absolute pressures acting along each sensor are shown in blue, the highest absolute pressures acting along each sensor are shown in red (refer to the scale on the right). Pressures tended to be highest on the distal phalanges and marrow acquisition and flake production tended to impose significantly greater loads on each phalangeal segment compared with other tested behaviors. Abbreviations: HA = handaxe; see Table 1 for sensor abbreviations.

Figure 1

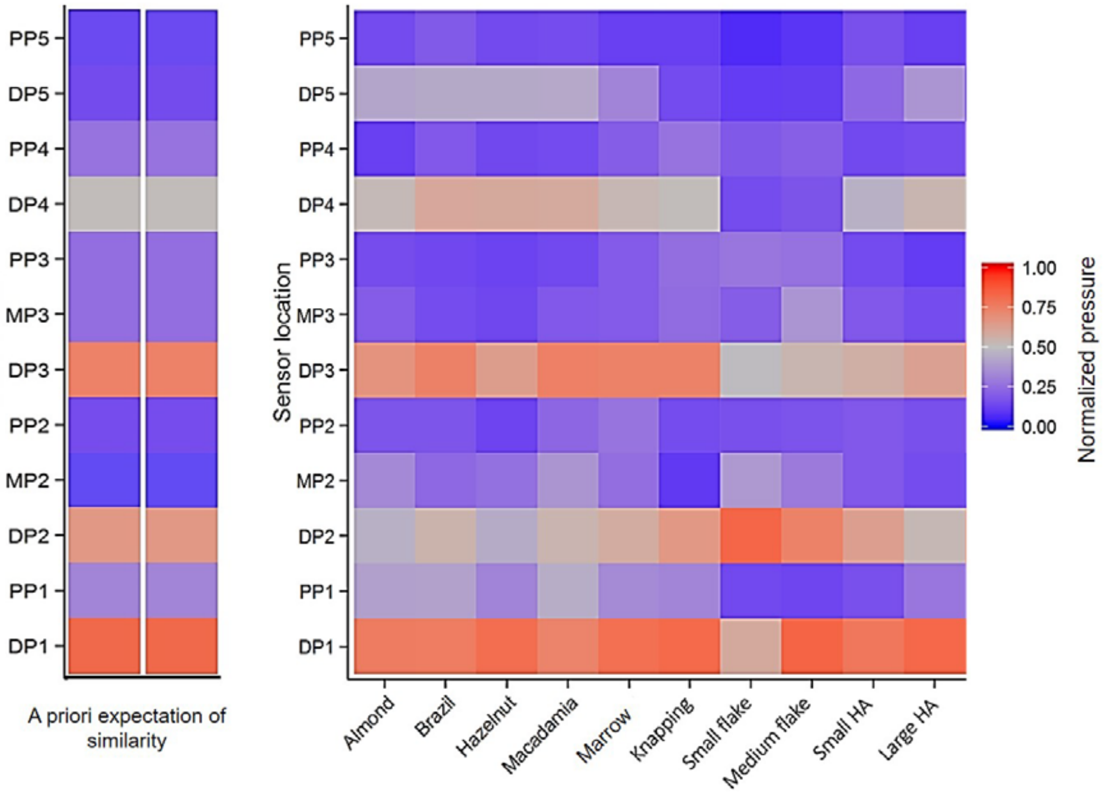
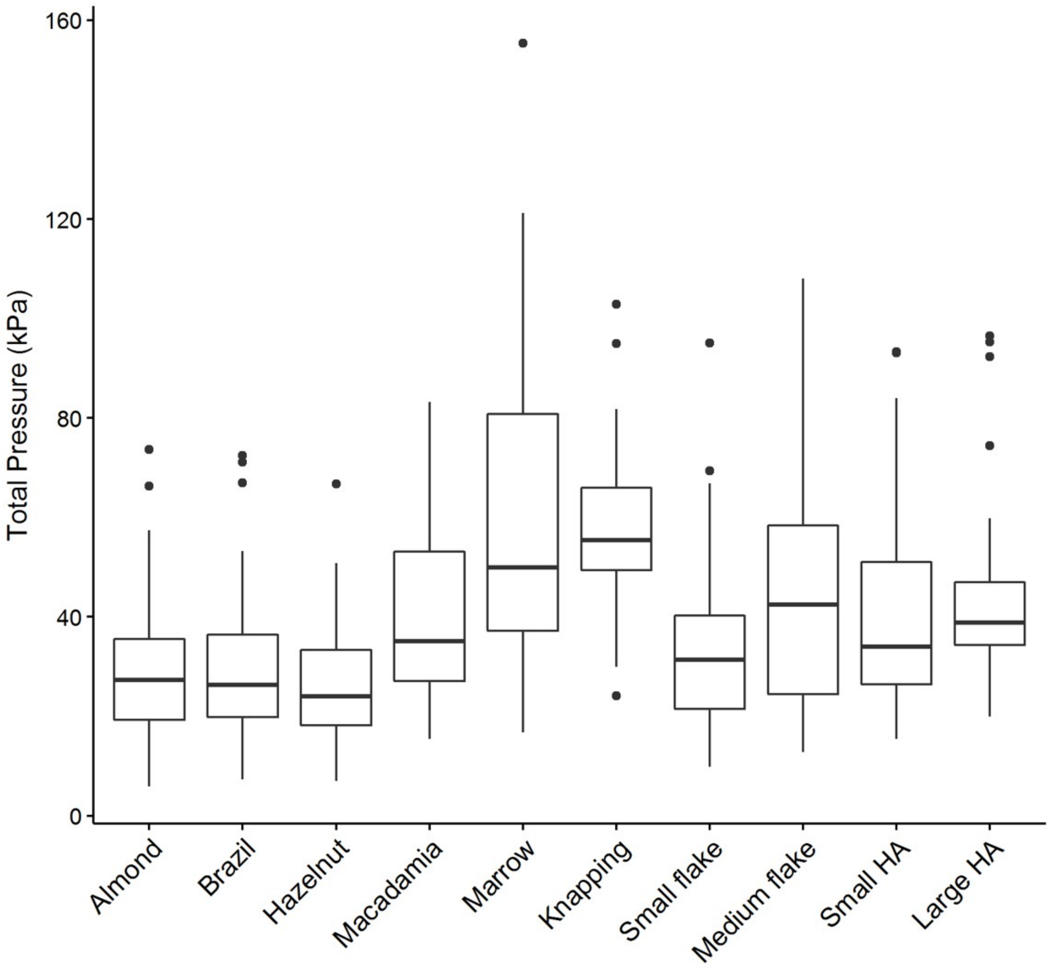
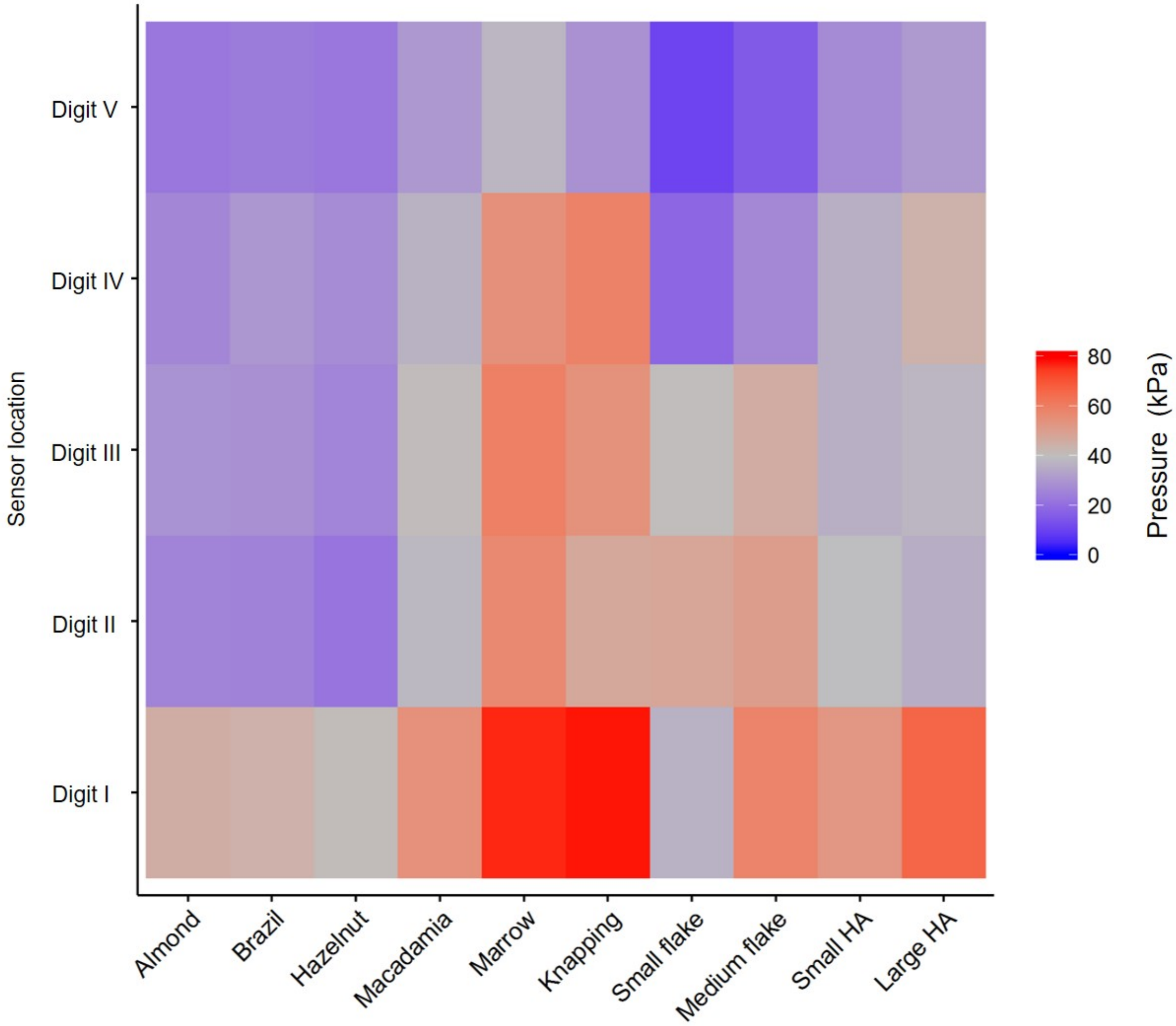

PP5
DP5
PP4
DP4
PP3
MP3
DP3
PP2
MP2
DP2
PP1
DP1
A priori expectation of similarity
Sensor location
Almond
Brazil
Hazelnut
Macadamia
Marrow
Knapping
Small flake
Medium flake
Small HA
Large HA
1.00
0.75
0.50
0.25
0.00
Normalized pressure

Figure 2



Total Pressure (kPa)
160
120
80
40
0
Almond
Brazil
Hazelnut
Macadamia
Marrow
Knapping
Small flake
Medium flake
Small HA
Large HA

Figure 3



Digit V
Digit IV
Digit III
Digit II
Digit I
Sensor location
Almond
Brazil
Hazelnut
Macadamia
Marrow
Knapping
Small flake
Medium flake
Small HA
Large HA
80
60
40
20
0
Pressure (kPa)

Figure 4

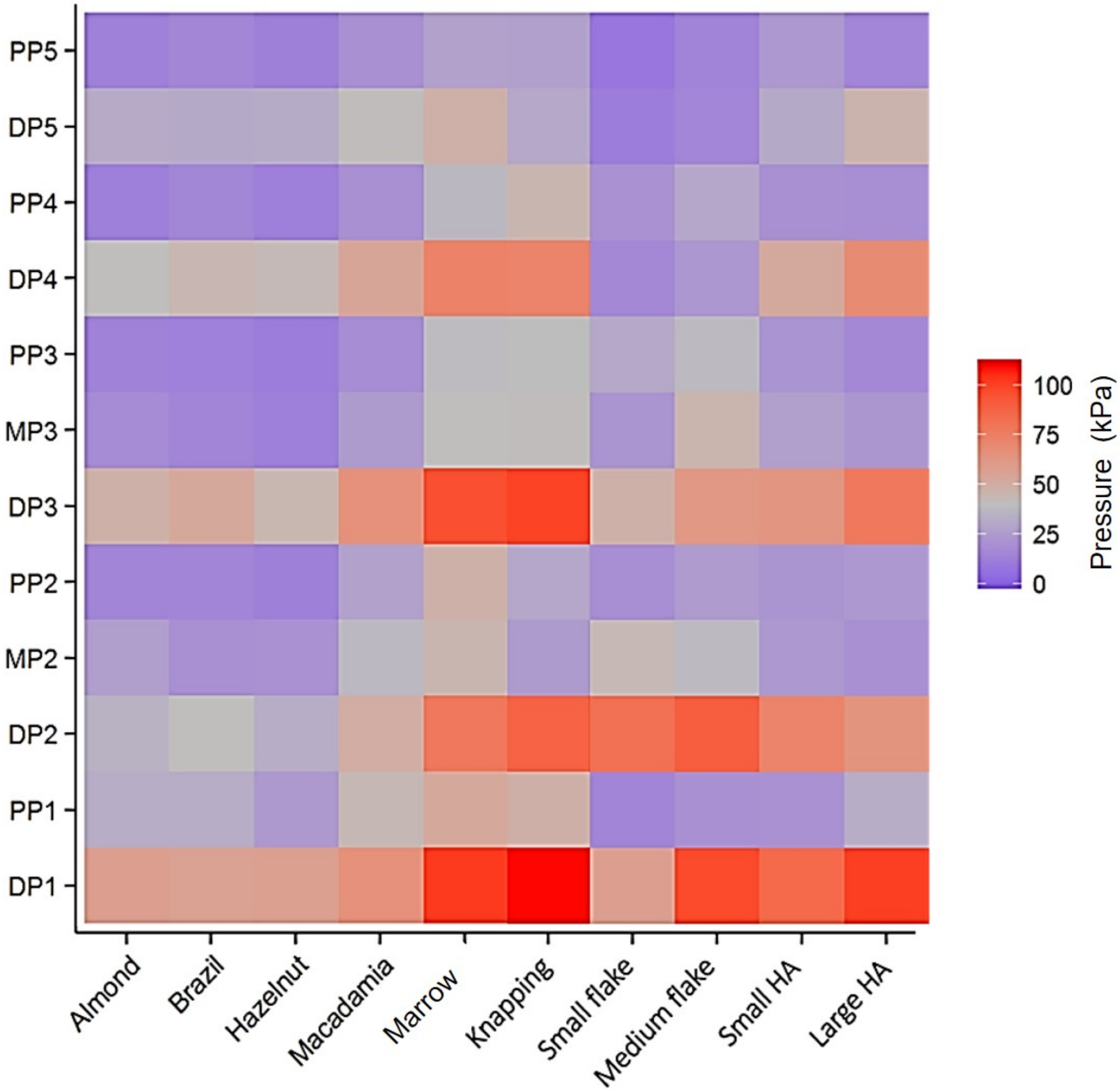

PP5
DP5
PP4
DP4
PP3
MP3
DP3
PP2
MP2
DP2
PP1
DP1
Almond
Brazil
Hazelnut
Macadamia
Marrow
Knapping
Small flake
Medium flake
Small HA
Large HA
Pressure (kPa)
100
75
50
25
0

Figure 5

Table 1 Sensor placement.

Phalanx	Abbreviation
First distal phalanx	DP1
First proximal phalanx	PP1
Second distal phalanx	DP2
Second middle phalanx	MP2
Second proximal phalanx	PP2
Third distal phalanx	DP3
Third middle phalanx	MP3
Third proximal phalanx	PP3
Fourth distal phalanx	DP4
Fourth proximal phalanx	PP4
Fifth distal phalanx	DP5
Fifth proximal phalanx	PP5

Table 2 Descriptive stone tool metrics

Tool		Mean	SD	CV
Small flake	Mass (g)	5.6	1.5	26.7
	Length (mm)	29.2	0.5	1.8
Medium flake	Mass (g)	29.8	7.1	23.7
	Length (mm)	58.3	1.4	2.4
Small handaxe	Mass (g)	235.4	59.2	25.2
	Length (mm)	119.7	8.5	7.1
Large handaxe	Mass (g)	756.7	229.3	30.3
	Length (mm)	168.4	18.9	11.2

Abbreviations: CV = coefficient of variation (%); SD = standard deviation.

Table 3 Relationships between activity and normalized pressure distributions.

Sensor	F-value	*p* (>F)
DP1	2.583	0.007
PP1	7.749	< 0.001
DP2	7.741	< 0.001
MP2	4.883	< 0.001
PP2	1.313	0.229
DP3	4.291	< 0.001
MP3	3.429	< 0.001
PP3	4.137	< 0.001
DP4	18.24	< 0.001
PP4	1.993	0.039
DP5	10.080	< 0.001
PP5	1.890	0.052

See Table 1 for sensor abbreviations.

Table 4

Linear mixed effects model fit to cumulative digital pressure.[a]

	Value	SE	t-value	*p*-value
Intercept	29.621	2.888	10.257	0
Brazil	0.568	1.036	0.548	0.584
Hazelnuts	-2.664	1.035	-2.573	0.010
Macadamia	10.605	1.035	10.244	0
Marrow	29.641	0.903	32.843	0
Knapping	20.648	1.012	20.401	0
Small flake	5.157	1.045	4.933	0
Medium flake	16.153	1.045	15.452	0
Small handaxe	11.339	1.045	10.846	0
Large handaxe	15.084	1.045	14.428	0

[a] Degrees of freedom = 4146.

Table 5

Relationships between behavior and absolute inter-digital pressure distributions.

Sensor	F-value	*p* (>F)
Digit 1	11.405	< 0.001
Digit 2	9.152	< 0.001
Digit 3	7.614	< 0.001
Digit 4	11.895	< 0.001
Digit 5	6.901	< 0.001

Table 6

Relationships between behavior and absolute inter-sensor pressure distributions.

Sensor	F value	*p* (>F)
DP1	9.671	< 0.001
PP1	8.610	< 0.001
DP2	10.87	< 0.001
MP2	4.599	< 0.001
PP2	5.641	< 0.001
DP3	9.838	< 0.001
MP3	5.966	< 0.001
PP3	7.179	< 0.001
DP4	13.661	< 0.001
PP4	8.460	< 0.001
DP5	6.134	< 0.001
PP5	5.003	< 0.001

See Table 1 for sensor abbreviations.