



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

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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.

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1. 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

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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 australopithecids (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 hammerstone use (Rolian et al., 2011). From a bone functional adaptation perspective, there appears to be a minimum strain threshold to stimulate bone remodeling and modeling (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; Blumenshine 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

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