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Hand biomechanics during simulated stone tool use

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ABSTRACT

Human radial digits have derived features compared with apes, with long robust thumbs, relatively larger joint surfaces, and hypertrophic thenar muscles. Here we test the hypothesis that these features evolved in the context of making and using stone tools, specifically for producing large gripping forces and for countering large joint contact stresses. We used portable force plates simulating early stone tools to: 1) document and compare the magnitude of external/internal forces and joint stresses in the radial digits during hardhammer percussion and flake use, and 2) examine how variation in digit morphology affects muscle and joint mechanics during stone tool use. Force and kinematic data were collected from a sample representing normal variation in digit morphology ($n = 25$). The effects of digit size/shape on digit biomechanics were evaluated using partial correlations, controlling for tool reaction forces and impact velocities. Results show that individuals with longer digits require relatively less muscle force to stabilize digital joints, and are exposed to relatively lower joint contact stresses during stone tool use, due in part to an increase in the robusticity of metacarpals and phalanges in humans relative to chimpanzees. These analyses further suggest that *Pan*- or australopith-like pollical anatomy presents serious performance challenges to habitual tool use. Our data support the hypothesis that evolutionary increases in thumb length, robusticity, and thenar muscle mass enabled *Homo* to produce more force and to tolerate higher joint stresses during tool use.

Introduction

The human hand presents many derived musculoskeletal traits relative to African ape hands (Lewis, 1989; Tocheri et al., 2008). Numerous features are hypothesized to be adaptations for making or using lithic technology, which first appears in the archaeological record about 2.6 Ma (Semaw, 2000). Most previous research on the evolution of the hand has focused on identifying differences in musculoskeletal anatomy between African ape and human hands and wrists, and making inferences about how these differences might have improved the ability to manufacture and use stone tools. Proposed adaptations for producing strong grips of the thumb against the lateral digits include a long robust thumb and relatively short fingers, robust metacarpals with asymmetrical heads, and hypertrophic intrinsic muscles (Marzke, 1997; Susman, 1998). These hypotheses of adaptation mostly assume that manufacturing and using stone tools applies large external forces to the hand, in turn requiring forceful grips, particularly between the thumb and radial digits (Marzke and Shackley, 1986). Ape-like hands are presumed to be less effective at generating high forces between the thumb and radial digits, and appear to be less able to tolerate the presumed high bone and joint stresses associated with the repeated use of stone tools (Susman, 1994; Marzke, 1997).

A problem with testing these hypotheses is the absence of published data on the magnitudes of external forces generated during the production and use of stone tools. Here, we address three major questions to assess whether or not external forces associated with early lithic technology present an adaptive challenge to early hominins. First, how large are the external forces generated by the production of flakes by hardhammer percussion, and the use of these flakes in butchering carcasses? Second, how do these external forces affect internal muscle and joint biomechanics during stone tool use? Third, what, if any, advantage(s) does the longer, more robust thumb and its hypertrophic musculature in modern humans, and inferred for some hominins, provide in resisting forces resulting from stone tool use, compared with the more gracile thumb of a chimpanzee-like hand?

We address these questions experimentally by integrating data on forces from custom-built portable force plates with kinematic data during simulations of stone tool making and use. Our primary goal is to document the magnitude of external and internal forces and joint stress in the thumb and index finger during simulated

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manipulative behaviors, particularly those that would have occurred frequently in the production and use of Oldowan tools; and to examine how variation in digit morphology, specifically thumb and finger length, relates to variation in internal muscle and joint mechanics during these behaviors.

Early stone tools, hands, and grips in humans

The earliest lithic assemblages, collectively known as the Oldowan industry, first appear around 2.6 Ma (Semaw, 2000). Some view the Oldowan as a uniform tradition that persisted relatively unchanged for over one million years (Semaw et al., 1997; Gabunia et al., 2001), others have suggested that it comprises two distinct lithic traditions: a Pre-Oldowan culture for assemblages in the late Pliocene (>2.0 Ma), and a developed Oldowan tradition in the early Pleistocene (reviewed in Stout et al., 2010). Regardless of the variation present in the Oldowan industry, one of its key characteristics, from the perspective of manufacture and use, is the employment of hammerstones to knock flakes off cores made of cryptocrystalline or microcrystalline rock (Plummer, 2004). Hardhammer percussion, which remains an important knapping technique in subsequent lithic industries, distinguishes hominin lithic technology from both non-lithic tool use and stone tool use by apes (reviewed in Toth and Schick, 2009). Hardhammer percussion in the Oldowan produced a variety of tool types including hammerstones, core forms (choppers, scrapers, and discoids), and flakes (Leakey, 1966, 1971). Microwear studies, experimental analyses, and ethnographic data have shown that flakes were most frequently used to cut meat, wood, and other materials, but that choppers were also sometimes used as cutting tools or for extracting marrow from long bones (Bunn, 1981; Toth, 1985; Schick and Toth, 1993).

The identity of the Oldowan toolmakers remains unclear. The million-year span of the Oldowan overlaps the recorded time span of several species of *Australopithecus* and *Homo*. The oldest unequivocal *Homo* fossil, a maxilla from Hadar dated to 2.33 Ma, is nearly 300,000 years younger than the earliest stone tool evidence from Gona, Ethiopia (Kimbel et al., 1996; Semaw et al., 1997). Conversely, *Australopithecus africanus* remains from South Africa predate the oldest stone tools found there, precluding this taxon as the likely maker of the Oldowan technology (Kuman, 1998). Because robust *Australopithecus* fossils overlap Oldowan assemblages in East and South Africa, Susman (1988) has suggested that this genus was a stone tool maker/user. Others, however, have questioned whether or not these megadont hominins used stone tools for meat processing (Pickering, 2001). Although more than one species of hominin may have produced the Oldowan (Harmand, 2009), the taxa most likely to have made and used these stone tools are *Homo erectus sensu lato*, whose earliest appearance in Africa and Eurasia (1.9–1.7 Ma) overlaps the developed Oldowan, and *Homo habilis*, a somewhat less well defined species that may have existed between 2.3–1.4 Ma (Haeusler and McHenry, 2004; Spoor et al., 2007).

Further knowledge regarding the manufacture and use of early stone tools comes from comparative studies of tool use and manipulative behavior in humans and non-human primates (Marzke and Marzke, 2000). In addition to studies on cognitive and neurological aspects of knapping (e.g., Stout and Chaminade, 2007; Stout et al., 2008), there is much interest in different types of grips used in making and using tools, as these may correlate with derived aspects of hand morphology in humans and early hominins. John Napier's early studies on the opposability of thumbs and fingers in primates defined two broad categories of grips: 'precision grips,' in which an object is "pinched between the flexor aspects of the fingers and the opposing thumb" and 'power grips,' in which objects are squeezed mainly by the fingers, and are actively stabilized in the palm (Napier, 1956: 903, 1961). Napier noted that among hominoids, only human hands are capable of both types of grips, and attributed the inability to form precision grips in apes mainly to their disproportionately short thumbs and long fingers, and underdeveloped thenar and hypothenar musculature (Napier, 1960).

More recent analyses of manipulative behavior in primates have further modified this grip typology. Marzke and colleagues' studies of manipulative behavior in humans and non-human primates (e.g., Marzke, 1983; Marzke and Shackley, 1986; Marzke et al., 1992) found that when knappers replicate Oldowan tool types, they primarily use three types of precision grip. In the "three-jaw chuck," the palmar aspect of the thumb opposes a variably flexed third digit, and the index rests atop the object, which is partly buttressed against the second metacarpal. This modified precision grip is used for holding hammerstones during hardhammer percussion (Fig. 1A). The "two-jaw chuck," or key pinch grip, opposes the distal thumb pad to the side of the index finger. This grip is often used in handling flakes (Fig. 1B). Finally, cores were often manipulated using "cradle grips," in which the thumb and four fingers firmly pinch and maneuver large stone cores, exposing surfaces for flake removal by the hammerstone (Marzke, 1997; Fig. 1C).

Because these grips are all based on forceful opposition of the thumb to different aspects of the second and third fingers, Marzke (1997) suggested that the capacity of the thumb and radial digits to generate forceful grips would have been important for early stone

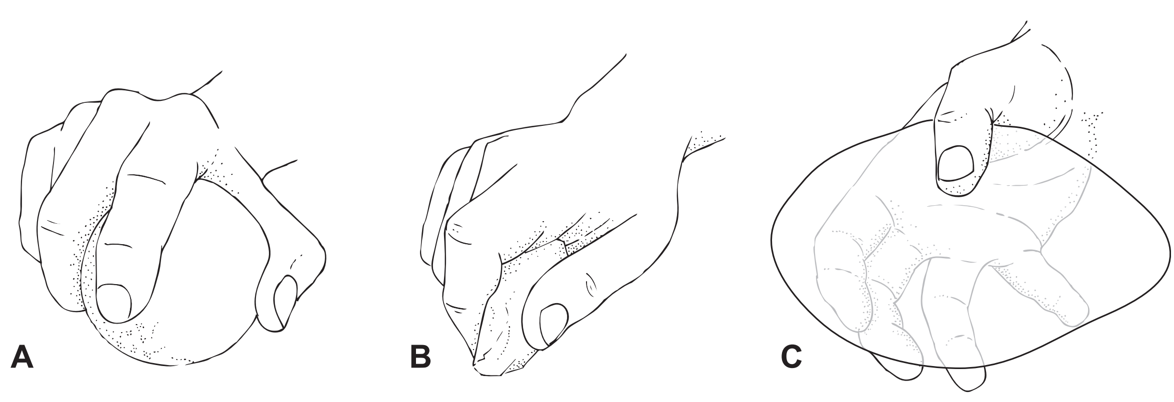

Figure 1. Types of enhanced precision grips used to wield Oldowan tools. A: Three-jaw chuck grip used to hold a hammerstone. B: Key pinch grip used to hold a flake. C: Cradle five-jaw grip used for large cores. Note the prominent role of the thumb in opposing the other digits.