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The evolution of the hominin thumb and the influence exerted by the non-dominant hand during stone tool production

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ABSTRACT

Modern humans possess a highly derived thumb that is substantially stronger and more robust than the fingers. Previous hypotheses concerning the evolution of such traits have focused upon the manipulation of hammerstones during stone tool production and of stone tools during their use. To date there has been no research on the manipulative pressures exerted by the non-dominant (core-holding) hand during stone tool production and its potential influence on the evolutionary history of the thumb. Here we provide the first investigation into the frequencies of digit recruitment and the relative manipulative forces experienced in the non-dominant hand during stone tool production. Eight experienced knappers produced flake cutting tools under four distinct conditions while pressure sensors, secured to the volar pads of the thumb, index and middle fingers of the non-dominant hand, recorded manipulative forces. Results indicate that relative to the fingers, the thumb was recruited significantly more frequently and experienced significantly greater manipulative forces during core repositioning events and the securing of the core during flake detachments. Our results support the hypothesis that the robust thumb anatomy observed in the hominin lineage was selected for, at least in part, as a result of more frequent and greater manipulative pressures acting upon the thumb relative to the fingers on the non-dominant hand during stone tool production.

Introduction

The advent of modified stone technology at least 2.6 Ma (million years ago) (Semaw, 2000; Semaw et al., 2003) allowed Lower Palaeolithic hominins to more easily access previously unobtainable or highly problematic food sources. Subsequently, the hominin lineage became dependent upon stone tools for key aspects of survival and resource acquisition. Thus, the ability to effectively produce and use stone tools is hypothesized to have been a major selective force in our evolutionary history (Ambrose, 2001; Plummer, 2004; Domínguez-Rodrigo et al., 2014), particularly with regards to hominin hand anatomy (Marzke, 2013).

Modern humans (*Homo sapiens*) exhibit the most dexterous hand within extant primates, possessing a unique ability to use forceful precision grips (Napier, 1956, 1980; Marzke and Wullstein, 1996; Marzke, 1997; Diogo et al., 2012). Specifically, humans are able to forcefully manipulate objects between the distal aspects of the thumb and both the distal and lateral aspects of the opposing four fingers, an ability that is essential to both stone tool production and stone tool use (Marzke, 1997). Indeed, during stone tool production, hammerstones must be firmly gripped between the thumb and opposing fingers to withstand substantial impact forces that would otherwise dislodge the hammerstone from the hand (Marzke and Shackley, 1986; Marzke, 1997; Marzke and Marzke, 2000; Rolian et al., 2011; Williams et al., 2012). During stone tool use, tools must be firmly secured between the thumb and fingers to effectively transfer force through a tool's edge onto a worked material (Marzke and Shackley, 1986; Marzke, 1997; Marzke and Marzke, 2000; Tomka, 2001; Rolian et al., 2011; Key and Lycett, 2011, 2014; Key, 2013).

A number of derived anatomical features in the hand are thought to facilitate these strong precision grips and are traditionally considered advantageous for tool production and use. Recent reviews examining the evolution of the human hand emphasize the anatomical changes in the thumb and its key role in the exertion and resistance of manipulative force (Tocheri et al., 2008; Marzke, 2013). Indeed, the volar pad and apical tuft are largest in the human thumb, both within the hand and amongst extant primates (excluding *Papio*, although this has been ascribed to a loading regimen distinct from that of hominins; Marzke, 2013), suggesting a need to distribute greater forces over a larger surface

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area (Bimson et al., 1997; Susman, 1998; Mittra et al., 2007). The increased robusticity of the human first distal phalanx, relative to other extant apes, is also able to resist large forces (Shrewsbury et al., 2003). Similarly, trapeziometacarpal joint surface area and curvature in modern humans is suggestive of large joint stresses and manipulative forces exerted through the thumb (Marzke et al., 2010). Furthermore, unlike most other primates, humans possess a large and fully-formed flexor pollicus longus muscle belly that attaches to the distal phalanx and facilitates substantial flexion force in the distal aspect of the thumb (Hamrick et al., 1998; Marzke et al., 1998, 1999; Diogo et al., 2012). Altogether there are substantial morphological adaptations for the exertion and resistance of strong manipulative forces in the modern human thumb.

The evolution of this robust thumb anatomy has traditionally been explained through its recruitment during both stone tool production and stone tool use (Napier, 1980; Marzke and Shackley, 1986; Marzke, 1997, 2013; Hamrick et al., 1998; Marzke and Marzke, 2000; Tocheri et al., 2008). However, focus has recently shifted towards hypotheses that concentrate on the use of stone tools. Indeed, a key component of almost all stone tool grips is the application of the distal aspect of the thumb to one side of the tool, to secure it in the hand when opposing the fingers (Marzke and Shackley, 1986; Marzke, 1997). Thus, those individuals exhibiting an increased ability to effectively and efficiently grip, and therefore use, stone tools are thought to have an evolutionary advantage due to their increased ability to acquire food resources (Key and Lycett, 2011; Rolian et al., 2011).

Recent experimental work is consistent with this hypothesis, as individuals with larger, stronger grips are significantly more efficient during cutting tasks with flake stone tools than those with smaller/weaker grips (Key and Lycett, 2011). Furthermore, Rolian et al. (2011) demonstrated that simulated flake cutting required the constant application of low level forces through the thumb and that those individuals exhibiting longer digits, and therefore larger joint surfaces, experienced lower flexion forces and joint contact stresses. Thus, evolutionary forces may preferentially have selected for those individuals. Compared with the infrequent high forces acting on the thumb during hammerstone use, Rolian et al. (2011: 34) speculated that “flake use, not hard hammer percussion, placed a greater selective premium on hand morphology in Pleistocene hominins”, due to its constant low level force requirements. Similarly, Williams et al. (2012: 525) found that manipulative pressure experienced by the thumb during Oldowan tool production was not greater than either the second or third digits on the hammerstone-holding hand, and thus, robust thumb anatomy was not likely to have “evolved in response to elevated stresses compared with other regions of the hand during the making of stone tools”.

Rolian et al. (2010) have further suggested that the apomorphic human thumb may not have evolved as a result of any direct morphological selection but as a pleiotropic by-product of strong selection on the first pedal phalanx imposed by the evolution of bipedality. However, recent work has shown that whilst the human hallux is independently represented in the somatosensory cortex, unlike other primates humans retain a manual representation, a pattern present in extant catarrhine brains (Hashimoto et al., 2013). This led the authors to conclude that the hominin hand and foot did not share the parallel evolutionary history posited by the pleiotropy model. As such, the evolution of the robust modern human thumb is now principally explained through its relationship with lithic technology, and in particular the use of stone tools with the dominant hand.

Conversely, though the importance of the non-dominant (core-holding) hand during stone tool production has long been known (Marzke and Shackley, 1986; Marzke et al., 1998), it has received far less investigation in the literature than the dominant hand. Key findings have been limited to identifying the frequent use of a ‘Cradle Grip’ when knappers secure small cores during flake detachments (Marzke and Shackley, 1986), and the observation that muscles serving the thumb, index and fifth fingers are heavily recruited during such actions (Marzke et al., 1998). However, to date there has not been any research investigating concomitant aspects of these findings, such as the reduction of large cores, varied knapping positions, the recruitment frequencies of the thumb relative to other digits, or the manipulative pressures exerted by each digit, both during core securing and core repositioning actions. So, while it has been noted that a strong robust thumb on the core-holding hand is key to effective flake production (e.g., Marzke and Wullstein, 1996; Marzke, 1997), there has been comparatively little research quantitatively testing these predictions (cf. Marzke et al., 1998). As such, two of the principal manipulative actions undertaken during stone tool production, that of core securing and core repositioning, have been underrepresented in discussions relating to the evolution of the hominin hand, and specifically the evolution of hominin thumb robusticity.

Here we present the first direct investigation into the manipulative actions undertaken by the non-dominant hand during stone tool production. Specifically, we investigate the relative recruitment patterns of the thumb, index and middle fingers during core securing and repositioning actions, and record both the manipulative forces and the recruitment frequencies experienced by each digit. Using eight highly skilled knappers with pressure sensitive pads secured to the volar pads of the first, second and third digits, we test the hypothesis that during the production of basic flake tools, the thumb on the non-dominant, core-holding hand experiences both significantly higher manipulative forces and greater frequency of use than either the second or third digits on the same hand.

Materials and methods

Participants

Due to the need to have accurate referents for hominins that habitually engaged in stone tool production and for the data to be collected under natural conditions, unimpaired by the novelty or anxiety of sensors being attached, only skilled/experienced participants were selected. Subsequently, only individuals who are able to habitually and consistently produce handaxes and had been knapping for at least three years were asked to take part. This ‘threshold’ also controlled for the influence of knapping skill variation. From the 11 initially identified within the UK above this ‘threshold’, eight were able to take part. Descriptive information for each participant is available in Table 1. Informed consent was obtained prior to participation and all individuals were offered personal protective equipment.

Core reductions

Each participant was required to undertake the reduction of two large English flint nodules, with each being knapped under two distinct conditions (Fig. 1). All flint was sourced from Ingham, Suffolk, with the 16 nodules used weighing 11.8–20.4 kg and measuring 26.0–32.9 cm in length, 17.5–34.1 cm in width and 9.9–21.7 cm in depth. All nodules were selected by one of the authors (AJMK) on the basis of lack of fractures, suspected internal homogeneity (i.e., few chalk inclusions) and fine grain silica.

The first reduction undertaken was initiated on the floor with the participant kneeling next to the core, before (at a point chosen