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Defining and Determining Tool Users in the Hominid Record: Evolution of the Human Hand in Regard to Precision Gripping, and Tool Use through the Fossil Record and Comparisons to Chimpanzee Hand Structure and Use

Introduction

It is clear that the human hand is an essential, well-used instrument in human life. Human hands have built and shaped many aspects of our culture and community, helping us to define our lifestyles and ourselves. Yet how did the human hand become the powerful and versatile implement that it is today? As Susman (1994) summarizes, the Oldowan tool industry dates between 2.5 and 2.7 million years ago. Investigating man's development and use of stone tools (from this point on, simply referred to as "tools") throughout the hominid record may in fact lead to an understanding of the evolution of the hand. Tools appear to have been part of the hominid lineage for quite a while, and since the discovery of stone tools in association with *Homo habilis* in Olduvai Gorge (Leakey et al. 1964; Tobias 1965), there has been an assortment of hypotheses and studies surround the human hand. The debate regarding the development in the morphological features in the hand that are related to tool use considers discrete skeletal and muscular traits, as well as the idea that modern hand anatomy did not come about from tool use initially, and is merely an exaptation (Alba et al. 2003), and a result of the freeing of the hands due to bipedalism (Rolian et al. 2010).

This review takes literature regarding various *Australopithecus* and *Homo* species into consideration regarding morphological developments in the hand, while examining the methods used by various researchers to piece-together and define the many ways in which tools may impact human hands, and features in the hand that define a tool user. Varying hypotheses that have been developed and tested over the last 60 years, creating controversy while constantly being under pressure and change with new discoveries in the field.

Common Hand Grips

To begin to understand the unique features of the human hand that lead to tool manufacture, one must first distinguish the prehensile movements of the hand, which Napier (1956:902) defines as "…the movements in which an object is seized and held partly or wholly within the compass of the hand." After grasping an object, the stability of the hand in keeping hold of that object is important in any further manipulation of an object.

Power and precision grips

An object may be stabilized in the hand in two ways: a power grip or precision grip. In a power grip, the partially flexed fingers of the thumb create a clamp around the object. This is the grip used while holding a hammer, for example. The precision grip can be broadly defined as any grip that uses the thumb and at least one finger. Additionally, the palm itself may or may not merely be used as a prop (Marzke 1997). This grip consists of the object being held firmly between the flexors of the fingers and the thumb. Different objects, however, can lead to variations of these two grips. Positioning of the individual fingers and thumb helps define these types of grips as well. In precision gripping, the thumb acts as a clamp, helping to secure the object against the flexed fingers. In addition, the flexion and abduction of the fingers at the metacarpophalangeal joints helps to increase the span of the hand around the object being held. Even the positioning of the forearm is impacted during precision hand gripping; the hand help between the radial and ulnar deviation, while the wrist is dorsiflexed (Napier 1956). With the impression that precision grasping is directly related to tool use and perhaps manufacture, it seems relevant that the hand morphology seen in precision grips used by modern humans should serve as a method of comparison for earlier hominid species to diagnose tool use (Susman 1998). How were early humans using their hands, and can tool manufacture really be inferred by hand morphology?

Specialized precision grips in modern humans

There are two precision grips that appear to have been most useful in stone tool manufacture and use: the "pad-to-side" grip (as used when holding a key) and the "3-jaw chuck" grip (as used when holding a baseball) (Napier 1956). Humans today clearly use these grips on a regular basis, in that they would have been used in the basic tasks in hominid culture. The pad-to-side grip would have been useful in activities such as digging or probing, while the 3-jaw chuck grip would have been advantageous in stone throwing (Marzke 1983).

While humans show exceptional skillfulness in precision grip use, this is not to say that other primates do not use precision grips, but rather the precision grips used by chimpanzees, for example, may not be as diverse or multifarious as those used by humans. This is a result of the morphology of that organism's hand. Chimpanzees have often been observed using forms of precision grips and tools recurrently in their daily lives (e.g. termite "fishing", plucking grass), yet these activities do not necessarily encompass the sorts of precision grips needed for stone tool manufacture (Tobias et al. 1965).

Morphologies Diagnostic of Precision Grips in Humans

The use of precision grips in modern humans and extant primates is readily available for observation. However, researchers must turn to the fossil record to understand how the hominid hand came to be ideal for precision gripping, and thus tool making. A few authors have defined discrete morphological features as a means to determine whether or not an individual used or made tools.

Features defining the Oluvai hominids as tool users

Soon after the discovery of stone tools and hominid remains in Olduvai Gorge, it seemed apparent that this hominid must possess certain osteological features relating to tool use. Yet these diagnostic features seem minimal: (1) a fully opposable thumb with a broad distal phalanx, (2) broad distal phalanges of the other fingers (i.e. broad apical tufts), and (3) thumb/finger proportions that allow the thumb to oppose to the pads of all fingers. Of the few *H. habilis* hand bones that were found, which included a couple distal phalanges, proximal phalanges, a trapezium, capitate, and scaphoid, Napier (1962) concludes that these hominids fulfilled the first two diagnostic features. Without any metacarpals, however, it was impossible to determine a thumb/finger proportion.

A single determining trait

Susman (1994) sets out to test the hypothesis that brain size is related to tool use, since the Oldowan tool industry had been associated with *H. habilis* due to this species' large cranial capacity (Leakey 1964; Tobias 1965). He states that, up until the time of this paper, there was limited understanding of what morphological traits in the hand really signified tool use. After comparing the proportion of the first metacarpal head width to shaft length in extinct hominids, modern humans, and extant apes, he found that tool users have significantly broader first metacarpal heads, aiding in opposability and precision grip capabilities. Overall, however, the author turns to the thumb and size of the metacarpal head as the single necessary feature needed to define a tool user. As Aiello (1994) interpreted, Susman's (1994) hypothesis involving a single diagnostic trait could imply that any robust-thumbed hominid could be a tool-user.

McGrew (1995) challenged Susman's (1994) hypothesis of a single, defining trait in human hand anatomy can define that individual as a tool-user, seeing as his studies on gorillas show that they have wide metacarpal heads compared to length, and do not use precision grips. Hamrick and Inouye (1995) responded with the same support regarding gorillas, questions the reliability of taking only a single trait into account in precision gripping. To support their argument, the authors reveal that gorillas have broad metacarpal heads, but are not capable of extensive precision grips. Susman (1998), however, stood by his claim, arguing that gorilla hands do not resemble early hominid hand remains, and gorillas may just be an exception in his analysis of broad metacarpal heads.

Marzke's (1997) eight diagnostic features

To help distinguish early hominids that may have been tool users, Marzke (1997) highlights eight morphological features that could be used to diagnose precision gripping capability in the hand in question. This discrete set of features was compiled based on tool replication by archaeologists, the comparison of various primates' manipulative actions, and analysis of chimp hand and wrist morphology. These discrete features are as follows:

(1) When examining the distal phalanges of humans compared to other great apes and primates, it is clear that the tips of the human fingers appear swollen. These extremely *broad apical (referred to as ungual in text) tufts* are distinctly human, allowing our fingers to have larger and more sensitive surface areas (Marzke 1997). Susman's (1979) comparative analyses of the great apes, including humans, also showed that humans tend to have proportionally larger tufts than the other apes.

(2) Among primates, humans have a distinctively *long thumb* (Aiello and Dean 1990). Such length allows the volar side, or palm side, of the thumb to assist in

various precision grips. Having a firmer and more accurate grip with the thumb helps the hand maintain great control of the object held (Marzke 1997).

(3) The *extensive development of the intrinsic muscles* of the thumb stands out as another prominent feature. In his comparative study on the muscles of hands among hominoids, Tuttle (1969) concludes that *Homo* had the largest total thumb musculature, which included the thenar eminance muscles and the adductor pollicis muscle. Other notable intrinsic muscles are the flexor pollicis longus (FPL), flexor pollicis brevis (FPB), and opponens pollicis (Marzke 1997). In addition, Susman (1979) states that the metacarpals of humans are distinct due to their well-developed muscle markings. Clearly, the musculature of the human hand is prominent, and can be noticeable in the fossil record due to distinct markings left from soft tissue attachment sites.

(4) The posture and position of the thumb plays a major role in allowing the hand to create precision and power grips (Napier 1956). Much of the force and flexion of the thumb comes from the *prominent flexor pollicis longus* muscle (FPL). In humans, this muscle has a large, prominent attachment side along the volar side of the distal phalanx of the thumb (Susman 1979). This powerful flexor of the thumb comes into play particularly during pinching and pad-to-side grips between the thumb and fingers (An et al. 1983). The FPL is a well-noted feature in the human hand. The strength and significance of the thumb is supported by the fact that the human hand contains three muscles that are often absent or reduced among the great apes: the flexor pollicis longus, flexor pollicis brevis, and the first palmar inerosseus muscle (Aiello 1994; Susman 1994). These muscles act as important flexors of the thumb, and help control and stablilize the movements of the thumb (Aiello and Dean 2002; Susman 1994). Susman (1994) has stated that humans are indeed the only primates that have a true FPL. In the fossil record, this is signified by the presence of a distinct pit or bony ridge on the distal pollical phalanx, which would have been this attachment site of the muscle. The placement of this insertion site at the distal end of the finger would have allowed greater leverage at the joint in regard to flexion.

(5) The torsion, or *radial orientation, of the third metacarpal* head allows some phalanx pronation during flexion, allowing it to oppose to the thumb. Such orientation allows more of the pad of the thumb to come in contact with that of the other fingers. Increasing this surface area contact with an object being held increases the force and power of a precision grip. This particular orientation in the third metacarpal is not seen among other hominoids (Susman 1979).

(6) Lewis (1977) notes a *marked asymmetry of the second metacarpal and fifth metacarpal heads* in the human hand. The two metacarpals appear to be mirror images of each other, in that the articular surface of the second metacarpal head extends radially into the volar side of the bone, while the articular surface of the fifth metacarpal head extends to the ulnar side, also along the volar aspect of the bone. Together, as the fingers are flexed, these articular extensions cause the index finger to pronate slightly and the pinky finger to supinate slightly, allowing all the fingers to come into as much contact as possible with an object being help. This phenomenon is clearly evidence in the 3-jaw chuck “baseball” grip, where the fingers appear to form to fit a round shape.

(7) The seventh feature describes the *orientation of articulation of the trapezium and capitate with the second metacarpal*. This joint is unique from chimpanzees, in that the articulation faces away from the sagittal plane (Marzke 1997). This orientation allows the second metacarpal to abduct and pronate slightly during pad-to-side and 3-jaw chuck grips, and, like the previous feature, it provides a larger volar surface area for contact with an object being held. Finally, the orientation of the joint between the second metacarpal and capitate helps resist axial loads along the second metacarpal, helping to stabilize the hand, as the authors summarized from her own earlier study.

(8) The last diagnostic feature describes *spines along the volar side of the apical tufts* at the distal phalanges. In their study on the distal phalanges, Shrewbury and Sonek (1986) note that spines along the sides of the apical tufts are unique to humans among the primates. These spines serve as attachment sites for the radial and ulnar tuberspinous ligaments, supporting the pulp in the tip of the finger.

Proposed Stages of the Evolution of the Hominin Hand

The eight diagnostically hominid hand morphologies summarized by Marzke (1997) beg the question of how hominid hands became this way. Clearly these changes in design did not occur overnight. Marzke's (1997) and Tocheri et al.'s (1998) works suggest that the evolution of the human hand can be summarized in three stages, that denote morphological changes reflecting man's decrease in arboreality and increase in manipulative hand use via tools.

Stage 1

Generally, the first stage begins with the hand of our last common ancestor (LCA) with the African apes. The grip capability and morphology of these early hands would mostly resemble those seen in the hands of modern chimpanzee. For instance, this morphology would reflect the use of the pad-to-side precision grip tool behaviors seen in modern chimpanzees today (Marzke 1997). Tocheri et al. (2008) describes seventeen osteological features postulated to be present in the hand of the chimp-human LCA, based on characteristics shared by out-groups of the hominins, as well as homologies based on parsimony. These primitive features vary from the breadth of the apical tuft in the thumb, to the orientation of the joint between the second metacarpal base and the capitate. The authors also suggest eight muscular features that were likely present in the hand of the chimp-human LCA. For the purposes of this paper, the most noteworthy muscular feature is the absence (or possibly degenerate or merely ligament-like tendon slip) of the flexor pollicis longus muscle, which includes a tendinous insertion into the distal phalanx of the thumb.

Stage 2

The second stage encompasses the hand morphology of *Australopithecus afarensis* around 3 million years ago, which includes some derived features, overlapping with the second stage (Marzke 1997; Tocheri et al. 2008). The *Au. afarensis* specimens from Hadar has three of the eight features described by Marzke (1997). The first is "a cam-like projection on the volar radial side of the second metacarpal head and dorsal beveling of the articular surface" (105). This would have pronated the finger slightly as it was flexing. The second feature found in *Au. afarensis* is the orientation of the second metacarpal joints with the capitate and the trapezium away from the sagittal plane of the hand, which creates some "give" during pronation of the index finger. These australopithecine hands appear to have been capable of a firm pad-to-side and the 3-jaw chuck precision grips. Finally, the third feature seen in this hominid is a long thumb relative to finger length, which would have helped create stability and security during precision grips. The thumb may not have been long enough, however, to be useful in using smaller tools to shape a core. However, the trapeziometacarpal morphology does not appear to have been completely modern yet, which would have limited the control of objects.

In addition to the hominids found at Hadar, individuals at the Sterkfontein and Swartkrans sites represent the second stage in hominid hand evolution. At Sterkfontein, specimen STW 294 shows a broad apical tuft, as well as spines along the distal phalanges of other fingers. There also appears to be a well-developed insertion site for the FPL. At Swartkrans, individuals show human-like thumb features, signifying firm pad-to-side grip ability, and the distal pollical phalanx was significantly broad. A second thumb specimen suggests the presence of "an advantageous moment arm for metacarpo- phalangeal flexion/extension by the flexor pollicis brevis muscle" (Marzke 1997:106). This observation suggests stabilization in the thumb during pinch grips, giving these hominids evidence as hypothesized human-like precision-grip users.

Stage 3

The third stage describes the absence of arboreal-related morphologies in the hand, and the appearance of principally tool-using hands (Kivell et al. 2011). The remains of the *H. habilis* individuals at Olduvai exhibit this stage, with one of the most notable features being broad apical tufts, signifying precision pinch handling. In addition, in the hand of specimen OH 7 there is a broad articular surface along the trapezium, suggesting that this joint was able to take on large forces, which may have occurred during hammering in tool making while holding a stone in the cradle, or 3-jaw chuck grips (Trinkaus 1989). Susman (1998) summarize this stage as the beginning of dependence on manufacture and use of hafted tools. Eventually, smaller hafted tools and frequent use of precise pad-to-side grips would become more common leading up to the emergence of *H. sapiens* (Marzke 1997).

Understanding Tool Manufacture

To understand which exact precision grips are needed or used in the manipulation and manufacture of tools, researchers must be creative and clever. Marzke (1997) suggests three potentially effective, albeit indirect, methods for determining such grips involved in tool making and use.

Experimental stone tool making by modern archaeologists

Regarding the first approach, Marzke (1997) discusses that in her earlier studies of the replication of Olduwan tools by modern humans, the pad-to-side grip between the thumb and index finger was used often, as well as the 3-jaw-chuck grip (as one would use when holding a baseball), and the cradle-precision grip (where the palm is facing up, and the thumb and all four index fingers are used to "cradle" the object being held). A strong pinching grip also appeared to be useful while hammering to help stabilize the stone receiving the blows from the hammer stone. In theory, researchers can use these observations to infer which precision grips are ideal for stone tool manufacture, specifically the grips that provide maximum stability and control, and minimal injury or discomfort. It appears that our earliest ancestral toolmakers have helped human hands become the powerful and precise instruments they are today. Marzke (1997) suggests that hominid hands first become accustomed to the use of raw materials as tools, followed by habitual manufacture and use of stone tools, leading to the morphological changes that have accumulated in the modern human hand.

Whittaker (1994) provides a very extensive analysis and discussion regarding flintknapping, explaining the history and describing everything concerning flintknapping techniques. The detailed accounts included from 19th century flintknapping observations help researchers today provide another glimpse into the tool-making behaviors that could have been utilized by our ancestors.

Besides empirical studies, flint-knapping and tool making has even become a hobby for some. Groups such as "The New Knappers Anonymous"[1] and even clubs at Universities[2] have become dedicated to recreating the art of early human tool manufacture. Perhaps by studying the workings of members of these groups could act as yet another resource in understanding early tool manufacture and its impact on modern hand morphology.

Susman (1998), however, notes flaws in archaeological replication experiments, clarifying the limitations of this method of study. When researchers observe modern humans replicate tools, they are only really examining how modern hominids may have made and used tools. Earlier morphological stages, and especially cognitive abilities, cannot truly be represented in modern human replication. Therefore, these studies may be subtly implying that the method of flintknapping, for example, is timeless, and therefore human ancestors were capable of this behavior regardless of specialized hand morphologies, and the varying hand morphologies of the fossil hominids.

Observations of today's stone tool makers

Anthropologists dream of being able to simply step back in time and watch how early hominids/hominins may have made and used stone tools. Toth et al. (1992) came close to this fantasy when they observed the Langda ax makers, who call themselves the Kim-Yal, in the highlands of New Guinea. The work of making hand axes in this culture reflects high status, and is learned only through lengthy apprenticeships between fathers and their sons. The "axes" can be classified as adzes, having an asymmetric, plano-convex shape. The authors refer to these tools as axes, merely because the Kim Yal uses them to chop wood and fell trees. A large, flawless stone that will break in a predictable matter (i.e result in a sharp edge) is

[1] http://www.reocities.com/knappersanonymous/index.html

[2] http://www.cas.sc.edu/anth/Flintknapping.html

chosen to make the ax. To harvest a piece of stone suitable for the ax, the worker swings two hammer stones against a lava boulder core, eventually producing about 10 blanks to carry back to the village for the ax making. The authors find the act of harvesting stone in this matter reminiscent of the manufacture of Acheulian hand axes. Toth et al. (1992) notes that an ax-worker would sit on his haunches, using his right hand for hammering and the blank he was working on in his left. In the process of shaping the ax, the worker would switch between hammer stones of different shapes and sizes for rough and fine flaking. Thus, it seems that slightly different pinch precision grips in the hammering-hand are utilized.

Pongid Relatives Making and Using Tools

Are advanced human hands really necessary for flaking and stone tool manufacture? By studying how our closes living primate relative use and create tools, researchers can better understand differences between human and ape hands and what may make human hands so well suited for tool manufacture. In the early 1990s, Nick Toth and colleagues taught a male bonobo named Kanzi to remove flakes from stone cores via free hand and hard hammer direct percussion after 18 months of training. At the time of the publication of this paper Kanzi, however, had only developed a "low degree of technical finesse" (Toth et al. 1992:89) in regard to the "degree of skill" criteria: flake angle, degree of decortication of cores, the size of flakes removed, and other qualitative features (e.g. hinge or step fractures). Therefore, it may be surmised that the quality of workmanship in tool making may have a direct link to the level of advancement in the morphology of the hand.

Chimpanzees have been observed using some precision grips while retrieving or holding food or other objects using the thumb and fingers (Marzke 1997). In some cases, as in grooming, chimpanzees seem to use a grip involving just the dorsal ends of the thumb and index finger for retrieving small objects. However, the authors noted that chimps seem unable to generate much force in a pinch grip involving the thumb and index finger. During tool making, Kanzi displayed this same issue, in that he had a hard time keeping a firm hold on the stone he was holding in the act of hammering. This can be seen in the short video of Kanzi using a hammer stone[3]; he seems to be holding the core with a gentle cradle grip in his left hand, and appears to lose his hold on it when forcefully striking the core with the hammer stone.

More recently, Pouydebat et al. (2011) examined grip differences between humans and chimpanzees. Overall, the authors found that juveniles in both species use more digits when picking up an object than their adult counterparts. Regarding grips used, however, humans appear found to use precision grips to pick up large *and* small objects, while chimpanzees only use precision grips when picking up small objects, and power grips for large ones. The observation that chimpanzees use precision grips less often than humans may be due simply to the short length of chimpanzees' thumbs. It is not that the chimpanzee is unable to oppose his thumb to the fingers, but that the volar surface area of contact between the thumb and any finger is not as larger as it is in humans. Plus, chimpanzees are unable to apply

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[3] http://www.youtube.com/watch?v=1zsSH9UUQtQ

strong force through the thumb during precision grips, as humans are able to do (Marzke 1997).

The Chimpanzee and Human Hand Compared Regarding the FPL

A distinct difference between human and chimpanzee hands is that human hands are able to apply more force single-handedly in precision grips. As mentioned, Kanzi struggled to maintain a firm grip on the stone core he was hammering. Marzke et al. (1999) examined and compared the torque, the capability of a muscle to move a bone along a joint axis, in the muscles of human and chimp hands. The authors conclude that human thumb muscles do indeed exert greater torque forces, in fact as much as double than as observed in chimpanzee hands, based on the physiological cross-sectional area (PCSA) and moment arms of such muscles. In humans, the FPL comprises 22% of total thumb musculature, based on the PCSA, exhibiting the significance of this muscle in the human hand. The key to understanding how these muscular features and forces fit into hand evolution regarding the use and manufacture of tools is to study the skeletal configurations such as those involved in the moment arms and muscle use in the bones in the hand that articulate with the muscles in question. More specifically, developments must be made that utilize skeletal features that are affected by muscles used in tool manufacture.

While Marzke et al.'s (1999) study of muscle torque in human and chimpanzee hands reveals marked differences, it begs the question of what has caused such powerful developments in the human hand? An earlier study by Marzke et al. (1998) illustrates that this well-developed musculature was likely the result of stone tool manufacture and use. By using electromyography to study 17 muscles in the human hand while replicating Oldowan tool manufacture, the authors identified the muscles most often used in the motions associated with such tool manufacture. The study even consistency in the types of grips used by participants: the hammerstone was observed to be most often held in a 3-jaw chuck grip, while the core was held in a cradle grip, depending on the size of the core (smaller cores were held tightly between the volar surfaces of the fingers and thumb). The results show high activity levels of the intrinsic muscles of the thumb. Interestingly however, the FPL did not seem to be recruited often during tool manufacture in the non-dominant hand. This led to the hypothesis that fatigue during a strong pinch-grip involving the thumb, cause the worker to adjust his grip on the stone in a way that relaxes the FPL. However, the FPL does seem to be used often in other activities involving the user's dominant hand, such as holding a cylindrical stick for digging, as in actual tool use of the tools that had been made. This is also evidenced when observing the ax makers in New Guinea, who must firmly hold the wooden handle as they strap it to their ax (Toth et al. 1992).

Perhaps the FPL has developed prominently in the human hand due activities besides stone tool manufacture. Since the FPL may not be a good indicator of hard hammer percussion tool manufacture, Marzke et al. (1998) turned to the metacarpal regions of the thumb, index, and pinky fingers, and the intrinsic muscles associated with the palm. The muscles contract as the hand accommodates to hold varying sized hammerstones, in order to retain stability and resistance during repetitive hammering. Increased use of these fingers and muscles in tool manufacture may have led to prominent robusticity in the second and fifth metacarpals and large muscle stress markings on the hand bones.

Finally, Marzke et al. (1998) stresses that the morphological features utilized in the Oldowan tool manufacture as described in their study are features that would have needed to be in place already in the hands of early hominids that were habitual tool-users. Thus, if a fossil hominid hand lacks these skeletal and (implied) muscular features, then that hominid probably was not a habitual tool user, and in turn a hominid with those features is not necessarily a habitual tool maker.

What was the Pre-requisite for Tool Making?

Despite the various muscular and skeletal features examined and categorized, and methods of examining living primates as a means to understand hominid hand evolution and its relationship to tool making, there is little definite clarity on how "tool making" features came about. Tool making itself seems like a suitable driving force behind modern hand morphologies, but some studies question the real cause for the emergence of such morphologies.

"Tool making" features pre-dated tool-making, and just facilitated it

To test the hypothesis that manipulative activities in involving stone tool making are the selective force behind human hand proportions Alba et al. (2003) discusses the remains of *Au. afarensis*, as well as extant human and ape specimens. The authors reconstructed the afarensis hand and compared to those of gorilla, chimpanzee, and bonobo specimens. Particularly, the pad-to-pad precision grip was taken into consideration, since this grips effectiveness increases with a greater thumb/finger length proportion. Their results refute the hypothesis that human hand proportions are the result of selective pressures and adaptations to stone tool-use, since *Au. afarensis* pre-dates the earlier known stone-tool industry in the archaeological record. Results confirm that *Au. afarensis* proportions are higher than in chimps, and is in fact closer to modern human proportions, and therefore it appears that *Au. afarensis* was capable of pad-to-pad precision grips. *Au. afarensis* even had overall hand proportions similar to that of modern proportions, yet these morphologies predate the earliest known tool industries by 1 millions years! So, modern human hands probably didn't evolve as a result of tool-making (as far as proportions go), but some "tweaks" may have been the result of tool making. Hand proportions may have been an exaptation.

Another potential explanation for the unique hand proportions and precision-gripping abilities seen in humans and not other apes is that once bipedalism became the main mode of locomotion, hominids were not, or minimally, using their hands for other activities, particularly locomotion. All primates use their hands for a number of activities, but the fact that humans really do not use their hands during locomotion paved the way for manual proportions that may have resulted from general non-locomotive abilities, and not just tool-making. Locomotion seems to exert stronger, perhaps more selective, forces on the hand among chimpanzees than their use of precision grips would. Thus, Alba et al. (2003) propose the hypothesis that the proportions of the human hand came about as a result of freeing up the hands after the adoption of bipedalism. The morphological changes seen in the hand today probably resulted from sole selective pressure coming from manipulative activities, like tool making. Why else would finger-length reduction be seen in the fossil record of hominids? If locomotion had still been causing selective pressure on the hands, finger length reduction would have been maladaptive for climbing and swinging. With regard to early hominids that may still have been utilizing arboreal locomotion, there may have been some climbing adaptations preserved. This is not to say that the australopithecines, for example, were not still living in the trees, but perhaps arboreality was no longer had a strong, selective place in their locomotion.

Tobias (1965) summarizes that earlier studies on apes suggest that bipedalism was not necessarily a pre-requisite for tool making. Tool making, therefore, may have a longer history than bipedalism in hominid evolution. He insists that all an animal needs to do to free his hands in order for tool making, and this can simply be accomplished by sitting upright. One is not obligated to stand while using a hammerstone – even humans sit while making stone tools, since this position helps stabilize the body. Perhaps the chimpanzee and human difference to focus on in regard to tool making is that locomotion. A human's transition from standing to walking does not necessarily interrupt the activity he may be doing; he may start knapping while sitting down, but can stand, walk and continue that activity if need be. Chimpanzees are not this fortunate, and relay on their arms during knuckle walking and arboreal locomotion.

Bipedalism and the freeing and forming the human hand

A recent study by Rolian et al. (2010) considers the evolution of the human hand from another perspective by comparing the phenotypic variation and "evolvability" of the digits of the hand and foot in humans and chimpanzees. Thus, if there is a relationship between the evolution of the fingers and toes, then genetic changes that resulted in phenotypic changes in the foot may have had a parallel impact on the morphology of the hand as well. The results show that there is a correlation in the blueprint, so to speak, preventing the foot and hand from evolving independently and reducing their phenotypic variation. It seems that in human evolution there was a strong selection for the restructure of the toes and foot. Features of the hand, like a longer thumb and more robust fingers, probably changed merely as a result of the strong forces acting on hominid feet.

While this studying concerning chimpanzees and modern humans provides some fascinating insight into the development of modern hands, there are limitations in applying these observations to the current hominid fossil record. There are not nearly enough complete fossil hand and foot remains from older species, but younger species, like the australopithecines, show some evidence of hand and foot proportion correlation. The most relevant conclusion suggests that the results of this study show that the selective pressure put on the toes as a result of bipedalism led to some of the morphological changes in the hand that associated with tool use and manufacture. In other words, bipedalism may have facilitated the stone tool technology among hominids. Hominid hand and foot proportions were essentially modern some time between 1.8 and 1.5 million years ago (Rolian et al. 2010).

This study by Rolian et al. (2010) may impact the phases in which researchers believe the evolution of tool use may have come about. Therefore, in the first stage of the development of modern hand morphology, which includes the australopithecines and perhaps some species prior, would have come about from strong selection for a more robust hallux, leading to more robust manual digits. This small change in the finger to thumb length ratio on australopithecines would have increased the efficiency of precision gripping (Alba et al. 2003).

Considering of all of this data in conjunction with earlier tool making related studies, perhaps it was bipedalism that was the precursor for the impact that stone tool making had as a contribution the evolution of our hands? Further, it may be hypothesized that it was after this progression from bipedalism to tool making that selections for minor re-adjustments in the structure of the hand to accommodate tool manufacture occurred.

Was precision gripping really even required for tool manufacture?

Early on in the debate, Napier (1962) questions the grip capabilities needed to make basic stone tools. The hand bones of the individuals discovered at Olduvai are described as robust (Leakey 1964; Napier 1962). Remains of juvenile phalanges appear to be in *sapiens* form, as well as the capitate bones. Interestingly, the distal phalanx of the thumb appears to have a deep insertion site for the FPL. Overall, however, the bones seem to resemble those of a gorilla rather than human, but have some human-like features, including the form of the metacarpal-phalangeal joint surfaces and broad tufts along the distal phalanges. These hand remains, according to the author, clearly came from a hominid (Napier 1962).

At this time, the only diagnostic features associated with precision-gripping in the hand, as previously mentioned, were: a fully opposable thumb with a broad distal phalanx, broad distal phalanges of the other fingers (i.e. broad apical tufts), and thumb/finger proportions that allow the thumb to oppose to the volar pads of all fingers. On the basis of these characteristics, it was concluded that this hominid species was capable of tool use and manufacture. Further, stone tools had indeed been found in association with these hominid remains. Taking into account the potentially low level of intellectual ability that may have been present in H. habilis individuals, the crude, pebble tools making up the Oldowan tool industry would have been within the physical and mental capacity of these hominids, especially since it appears that advanced precision gripping would not have been needed as a pre-requisite to manufacture. Interestingly, Napier (1962) even acknowledges that an Oldowan stone tool was replicated using only a power grip!

Fitting Recent Discoveries in to the Mix

Although the readings and various studies discussed cover several species and hypotheses regarding hand evolution and precision gripping from the last 60 years, there is not way of avoiding the impact of new discoveries and changes in the known fossil record.

Ardipithecus ramidus

With the discovery and research done on the essentially complete *Ardipithecus ramidus*, the Lovejoy et al. (2009) state that *Ardipithecus* settles years of debate regarding human evolution.. This specimen, dated at approximately 4.4 million years old, predates the australopithecines. Interestingly, the These small changes include slight enlargement of the thumb, and a reduction in finger length; basically, the only change needed involved finger/thumb length proportions. In addition, the first metacarpal is large and robust, there is a noticeable insertion site for the FPL, and the trapezium's tuberosity projects towards the palm. The authors state that the hand remains of this specimen show that only small modifications needed to be done to the human hand to improve its function in tool making.

Australopithecus sediba

Yet as more hominid specimens are discovered, the understanding of the human hand must be re-evaluated. Recently, remains from two individuals were recovered from Malapa, South Africa. The female, known as Malapa Hominin 2 (MH2) remains consist of some of the forelimb bones from the right arm, as well as a nearly complete right hand and some of the bones from the left hand. Unfortunately, only a third metacarpal was found from the other individual, assumed to be a young male, called Malapa Hominin 1 (MH1) (Kivell et al. 2011). Do the hands of this new species, dated around 1.977 million years old, fit into the proposed hominid hand evolution?

In regards to Marzke's (1997) eight morphological features associated with precision gripping, the female MH2 *Au. sediba* specimen seems to possess several of these features: the distal pollical phalanx has an expanded apical tuft, a well developed ridge along the pollical apical tuberosity indicating a well developed FPL insertion site, a long thumb relative to the other fingers, strong development of some of the intrinsic muscles, and asymmetry of the metacarpal heads was noted. In contrast, the orientation of the trapezium and second metacarpal orientation lies more in the lateral than sagittal plane, and is therefore more similar to australopithecines. Also, the thumb and index finger of MH2 appear to have experienced loading frequencies more similar to that of the australopithecines (KIvell et al. 2011).

It is also apparent that there was poor development of the pollical intrinsic musculature, revealing that MH2's thumbs may not have been exposed to the same types of loading pressure as modern humans, and especially tool users. In addition, it really seems as though the hand structure of MH2 was moving away from arboreality, since the strong flexion ability in the hand suggests that this hand was well suited for firm precision gripping, while the gracile metacarpals would have been poor at resisting bending loads during arboreal locomotion. The *Au. sediba* individuals may have been simply in an interim phase between arboreality and manual abilities; the short, straight fingers seen in MH2 may have caused the flexor muscles of the thumb to retain the strength necessary for arboreal locomotion.

Overall, the upper limbs of these hominids suggest that they regulated utilized arboreal locomotion.

Finally, Kivell et al. (2011) stress the need to re-evaluate the defining hand features related to tool use, since the association of *H. habilis* with the Oldowon culture caused researchers to accept those hand characteristics as the diagnostic traits for a tool user. Yet upon examining MH2, *Au. sediba* individuals seem to have had more derived features than *H. habilis.* Thus, on this basis, *Au. sediba* could be considered a tool-user. Perhaps OH 7 and *H. habilis* was adapted to tool making in a different way than *Au. sediba*?

Concluding Remarks and Considerations

This collection of studies and papers illustrates the difficulty in really defining and pinpointing the correlation between tool use and the evolution of the hominid hand. As of today, the ultimate question concerns whether tool making itself was the driving force behind the morphologies researchers today link to tool use. On the other hand, the freedom of the human hand as a result of bipedalism may have facilitated tool use. Finally, can morphological features alone be the main form of diagnosing a tool user?

Are morphological features enough?

Another issue involves understanding what muscular and skeletal features in a fossil hand specimen can categorize it as coming from an individual that was using tools. Basically, is a discrete set of morphological traits enough to define a tools user? While Marzke (1997) and others set out to create such a list of traits, is that enough to completely understand whether or some someone was a tool user?

When a species in the hominoid fossil record appears to have traits diagnostic of advanced precision grip capabilities it does not mean that specimen can automatically be considered a tool user, as exemplified in the case of *Oreopithecus bambolii*. According to Moyá-Solá et al. (1999) *O. bambolii*, a Miocene ape estimated to have lived about 8 million years ago, shows morphological features in the hand that reflect precision gripping capabilities. Firstly, the hand of the specimen IGF 11778 is relatively short compared to its hypothesized body weight. Even more intriguing is the long length of the thumb in *O. bambolii*, which the authors find to be within the range of human thumb/index finger proportions. The joint orientation of the second metacarpal and capitate also seems to follow to follow the hominid pattern for precision gripping, in that *O. bambolii*'s appears to face away from the sagittal plane and is perpendicular to the facet for the third metacarpal. Finally, in two *Oreopithecus* distal pollical phalanges, there seems to be a deep, rough insertion site for the flexor pollicis longus muscle. The authors felt that the *Oreopithecus* hand could provide a model to compare all hominid hands, which could push back the timeline for hominid hand evolution and raise even more questions regarding the selective pressures for modern human hand morphology.

Overall, it seems outlandish to assume that this Miocene ape was a tool user, illustrating that traits alone are not enough to define a tool user. Controversy quickly followed Moyá-Solá et al.'s (1999) work, and Susman (2004) attacked the paper, insisting that there was no clear evidence for an FPL insertion site, metacarpal and phalangeal measurements were incorrect due to incorrect bone identifications, and that the length of the specimen's hand actually falls within modern ape range. Finally, he points out that the apical tufts on the distal phalanges of *Oreopithecus* do not match the broad pattern of modern humans'. Clearly, the interpretation of any fossil interpretation must be accepted with caution.

Free hands, bipedalism, and basic tools

In reality, freed hands may have been enough to initiate tool use; precision grips may not have been necessary. Even Napier (1962) notes that the Oldowan tool industry is basic enough that it could have been accomplished using only power grips. Therefore, while Kanzi's Oldowan tools making skills lacked the finesse modern human hands have when making such tools, it does not mean that the tools Kanzi created could not have been useful in some way (Toth et al. 1992). This is not to saw that bipedalism automatically led to all morphological features associated with tool use, but that this merely initiated the changes needed to make the use of raw materials easier for early hominids (Rolian et al. 2010). Once these hominids began using basic stone tools, as described in the proposed Stage 1 of hominid hand evolution (Marzke 1997), increased use and manipulation may have just refined the human hand in accordance to the selective pressures caused by an increased dependence on tool use and the precision grip in daily life.

Compiling hypotheses as a means of understanding hand evolution

Bipedalism may have been the driving force behind initial hand proportion changes, as in the robusticity of the metacarpals (especially the thumb) and thumb and finger length (Rolian et al. 2010). Finally, tool use itself throughout ones life can manipulate the appearance and morphological characteristics of individual bones, helping them be more suited for tool use and loading pressures experienced on a habitual basis (Marzke et al. 1998). Thus, the use of diagnostic morphological features, such as those described by Marzke (1997), as a means of characterizing a tool user should still be acknowledged, since these incorporate some of the more specific, specialized features needed to make precision gripping as effective as possible. The most inclusive and apparent reasoning behind the evolution of the human hand and precision gripping appears to be a compilation of locomotor changes and manipulative behaviors of early humans.

Limitations to this Review

Although this paper encompasses much of the works over the last years regarding the evolution of the human hand and tool use, it is important to note than several areas of study were not taken into consideration. Clearly, this debate regarding hominid hand evolution in relation to tool use is complex; simple assumptions or ideas can take on a ripple effect, which was hopefully avoided in this paper.

Other primates for consideration

Firstly, chimpanzees were often the species utilized for comparison, since they are our closest living relatives. Studies of other dexterous primates, however, may provide meaningful insight into primate hand use and evolution. Studies, particularly involving capuchin monkeys, shed light on the relationship between cognition and manipulative abilities (e.g Vevers and Weiner 1963; Jalles-Filho and Teixeira da Cunha 2008).

Cognition

As Alba et al. (2003) state: "According to some authors [e.g. Napier 1956], even though anatomical traits might permit prehensile actions suitable for certain behaviors such as stone tool- making, it is the brain with its associated cognitive abilities that, in ultimate terms, governs their execution." (250). Sometimes simply having something is not enough, since that individual may need the proper cognitive ability to use a tool, or even his own hands, in a way that utilizes the precision grip capabilities he may possess.

The fossil record

Finally, it is important to take into consideration that mere lack of available hominid hand fossil remains for extensive study regarding hand evolution. Napier (1962) even noted this, stating that the fossil record lacked pollical metacarpals, which are clearly critical to understanding the development of the human thumb. The discoveries and publications regarding *Au. sediba* and *Ardipithecus* are just a couple examples of how theories on hand evolution must themselves evolve as researchers are exposed to more material. Hopefully, as time goes by and research continues, more findings of hominid hand remains will be located, helping to slowly whittle down and ideally completely clarify our understanding of the extent of the interaction between tool manufacture and hominid evolution.

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