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CHEIRIDIAL GENETICS AND TOOL USE AMONG LATER HOMINIDS

ABSTRACT: There is still uncertainty about which species made the earliest known stone tools and what are the minimum biological attributes for stone tool manufacture. According to the “Morphocentric View”, the details of hand anatomy will tell us which fossil species made stone tools; according to the “Neurocentric View”, brain size and structure are the determining factors. Here, we espouse the Neurocentric View, and test it using information about the genetics of the hands and feet. We find that over 91% of the genes which affect the toes also affect the fingers, suggesting that evolution of hominid hands is tied to the evolution of our feet which are adapted for bipedalism. This and other evidence leads us to the conclusion that we must be cautious when using details of hand morphology to understand the origin and development of lithic technology.

KEY WORDS: Hominid fingers and toes – Pleiotropy – Neurocentric – Morphocentric – Stone tools

INTRODUCTION

The earliest stone tools are dated at 2.5 Ma BP (Semaw *et al.* 1997 [36]), but there are no fossil hominids associated directly with them. This leaves open the question: who made the earliest tools? Without clear associations between fossils and artefacts, answers to this question have tended to rest on opinions of what is necessary to make a hominid a tool user. Darwin (1871) wrote that, “[to] chip a flint into the rudest tool, or to form a barbed spear or hook from a bone, demands the use of a perfect hand...”. Susman (1988) made this idea more specific when he wrote, “The new [hand] fossils are direct evidence by which to assess the manual dexterity of *Paranthropus robustus* and thus to judge the potential for tool behavior in the ‘robust’ australopithecines”. Elsewhere (Susman 1989) he wrote, “The fossil hand bones of *Paranthropus*...reveal a precision grip as refined as that in other hominids such as *Homo habilis* and perhaps even modern humans... They indicate that the South African ‘robust’ australopithecines engaged in tool behavior...at around 1.8 Myr BP”. Appropriately, Susman points out that the robust australopithecines probably did not use tools for cutting meat from bones, since they seem to have been

adapted for a very different sort of diet, one consisting of plant foods.

In a follow-up article, Susman (1994) repeated his views of robust australopithecine tool use, this time analyzing the metacarpal of the thumb to the exclusion of the phalanges on which he focused in his earlier report. The following year, several authors wrote brief comments disagreeing with Susman’s methods and conclusions. McGrew (1995) noted that modern apes use tools, even though their hands are anatomically quite different from those of humans. Hamrick and Inouye (1995) wrote that gorillas have thumb metacarpals which overlap with those of humans in the feature that Susman said was unique to tool-users. They suggested that no single anatomical feature could predict tool use in fossil hominids. Finally, Ohman *et al.* (1995) interpreted the robustness of the carpo-metacarpal joint in humans as a result of using the “power grip” rather than the “precision grip”. Susman’s response (1995) noted flaws in some of his detractors’ work and reiterated his conviction that tool behavior eventually leaves traces on the hand, and that we cannot know which hominid species made the earliest stone tools unless we see evidence of it in their anatomy. Subsequent work by Susman (1998) and others

(e.g., Marzke 1997, Smith 2000, Tocheri *et al.* 2003), focusing on the search for a few anatomical features of the hand which might be good indicators of tool use, has continued for the past two decades and is mentioned in a number of popular textbooks on physical anthropology (Aiello, Dean 1990, Conroy 2005, Klein 1999, Leakey, Lewin 1992, Lewin 2005, Park 1998, Poirier, McKee 1999, Relethford 2005, Staski, Marks 1992, Stein, Rowe 1995, Stein, Rowe 2000, Tattersall 1993, Wolpoff 1999).

All of these efforts rely on the supposition that details of hand anatomy can differentiate stone tool users from non-users. Gould and Lewontin (1979: 147) criticized this approach as part of the “adaptationist program” which they said, “proceeds by breaking an organism into unitary ‘traits’ and proposing an adaptive story for each considered separately”. Indeed, the difficulty in applying this approach to the question of tool use in hominids is apparent in at least three areas. Firstly, there are often disputes regarding each claim that a particular feature is able to distinguish tool users from non-users. Smith (2000), for example, noted that certain anatomical features which Susman claimed as indicative of tool use were not found in all modern humans. Secondly, an entire suite of characters, each of which individually overlaps with other living hominoids, restricts our ability to identify tool users among fossil remains. For example, Shrewsbury *et al.* (2003) wrote: “Dissections of specimens from six nonhuman primate genera indicate that these human features are shared variably with individuals in other species, although the full pattern of features appears to be distinctively human. Humans share variably with these other species all metric relationships examined here”. This statement suggests that no single trait can be used to determine whether or not an extinct hominid made stone tools, and we may need a rather large list of features, many of which will not be found among fragmentary, disarticulated fossil remains. Thirdly, the search for those few traits which enable a primate hand to form the grips required for tool use may be hopeless, since it may be impossible to determine which grips are really necessary. For example, the simplistic dichotomy between “precision” and “power” grips, as described by Napier (1993, 1962), has been questioned and modified by Marzke and Shackley (1986). These authors define thirteen distinct grips that were used in stone tool manufacture by modern human subjects (ib., 444, Table 2).

Problems such as those above indicate that the entire anatomical approach to tool use may be very limited. Alternatives were provided by Gould and Lewontin (1979 [13]) who “fault the adaptationist program...for its failure to consider adequately such competing themes as...production of non-adaptive structures by developmental correlation with selected features...” In other words, at least some aspects of hand anatomy in hominids may be adaptive, not in and of themselves and not for tool use, but as epiphenomena of other adaptations in the course of human evolution. Indeed, Smith (2000) suggested that, “as early hominids developed bipedal locomotion, changes in the toes led to changes in the fingers and thumbs through a correlated

developmental response” (ib., 343). Hence, reliance on morphological details to determine which hominids used stone tools and which did not, may be misguided.

NEUROCENTRIC VIEW

There is an alternate perspective to the anatomical approach, one with an equally long history. In this view, neurological factors such as brain size, brain complexity and neural control of manual dexterity are the *sine qua non* of tool use. Aristotle (4th century BC) wrote: “We should expect the most intelligent [animal] to be able to employ the greatest number of organs or instruments to good purpose...” Hence, anatomically modern humans have evinced the greatest levels of technology (including stone tool technology) of all creatures on Earth. More recently, Jouffroy (1993) applied this notion to all primates, writing, “In this brief review it has been shown that all extant primate hands can grip small objects regardless of their shape... Reviewing the various types of primate hands therefore suggests that the capability to use tools is more directly related to brain development than to hand shape”. With regard to fossil hominids, Leakey *et al.* (1964) originally assumed that the Oldowan tools found at Olduvai Gorge, in Tanzania, were made by *Paranthropus*, but revised their hypothesis when *Homo habilis* was discovered there in the early 1960’s. These authors suggest that details of hand anatomy may be irrelevant to the question of early hominid tool use; rather, the origins and subsequent development of stone tool technology will be reflected more accurately in the skull than in the hands.

Thus we have two competing views of the minimum qualifications for tool use. What we will call the “Morphocentric View” relies on anatomical explanations for hominid tool use, whereas the “Neurocentric View” relies on mental explanations for hominid tool use. In the former instance, anatomical details such as those of the pollical metacarpal and phalanges studied by Susman (1988) or the capitate and trapezium studied by Marzke and her colleagues (Marzke 1983, Tocheri *et al.* 2003), can tell us if an earlier hominid used tools. In the latter case, brain size or organization, as estimated from fossil crania, will provide the best evidence of tool use or the absence thereof.

Hypothesis

Here, we focus on the Neurocentric View, to develop some specific hypotheses and predictions, and to test the validity of the Neurocentric View with respect to the genetic evolution of hand morphology. When adopting a Neurocentric perspective, it must be kept in mind that any attempt to explain the origins and development of tool use must account for the fact that early hominid hands, before the advent of stone tools, are more ape-like in their anatomy, while late hominid hands, including those of *Paranthropus robustus*, generally evince a morphology that approaches that of modern humans, even though their brains are not always much bigger than modern ape brains. This evidence

suggests a temporal correlation between hand anatomy and tool use, and is the major advantage of the Morphocentric View and the major challenge to the Neurocentric View.

To explain the similarities between robust australopithecine hands and those of other late hominids that have clear associations with stone tools, a hypothesis within the Neurocentric tradition is as follows:

Hominid tool use depends on neurological factors, rather than morphological ones. Therefore, late hominid hand morphology is not an adaptation for tool use. In fact, due to pleiotropy affecting both hands and feet, similarities in late hominid hand morphology are largely the result of selection for bipedalism. The anatomy of modern human hands, and the hands of any late hominid species, is largely the result of selection for foot anatomy that is adapted to terrestrial bipedalism. Thus, the hands of all recent hominids are adapted, not for tool use, but indirectly for bipedalism. (For example, shortening of the fingers is due to the pleiotropic effects of genes which cause shortening of the toes, especially the lateral toes.)

The foregoing hypothesis leads to a number of testable predictions, and they are part of a larger *Weltanschauung* with many other predictions and related hypotheses. The outline below enumerates many corollary ideas related to the Neurocentric View of the origins and development of hominid tool use. We offer these predictions here to place the current work in perspective, to solicit theoretical commentary and to encourage and perhaps guide future research. Letters in parentheses, at the end of each entry, indicate the kind(s) of study best suited to test the prediction in question. (C = Comparative studies of primates; F = Fossil studies, especially among hominids; G = Genetic studies; O = Ontogenetic studies, or studies involving only living humans).

I. Feet

- A. Later hominids will all have feet well-adapted for bipedalism (F)
- B. If “ontogeny recapitulates phylogeny”, then the specialized features of human feet (and hands) will develop during the course of individual ontogeny (O)
- C. Our feet will start out with relatively long toes which will shorten during the life of the individual (O)
- D. Anatomical changes in the feet (and hands) that are not anatomically or developmentally dependent on one another will occur in random order (F)
- E. Because of continuing selection for bipedalism, descendant species will have all the adaptations their ancestors had, and will perhaps have additional adaptations; i.e., foot adaptations to bipedalism are unlikely to be lost (F)

- F. Different hominid species in different lineages can have different foot (and hand) features, so long as their last common ancestor did not have one of the features in question (F)
- G. Contemporaneous hominid species can differ from one another by being more advanced in some features but more primitive in others (F)
- H. To the extent that later hominids relied on tools for their survival, changes to the feet which severely debilitate the hands will not occur (be preserved); i.e., hand morphology will constrain foot morphology, to a slight degree, but only in later, tool-using hominids (C, F)
- I. Human feet will be unique among primates, since no other primates are habitual, terrestrial bipeds (C)
- J. Non-genetic changes, those caused by use, will occur immediately, perhaps much earlier than genetic changes (C, F, O)
- K. Non-genetic changes in the feet will not affect the hands (F, O)

II. Hands

- A. After a few million years of bipedalism, all hominids will have similar hands, regardless of tool use (F)
- B. Since bipedalism occurred before tool use, even early hominids' toes and fingers should show progressive shortening (F)
- C. Due to pleiotropy, the hands and feet will change simultaneously in any given lineage (F)
- D. Human hands will be unique among primates, since no other primates are habitual, terrestrial bipeds (C, F)
- E. Those (non-hominid) primates with the most terrestrially adapted feet will have some changes to the hands that will make their hands somewhat similar to human hands (C, O)

III. Tools

- A. Details of hand morphology in primates will not correlate closely with stone tool technology (C, F)
- B. Brain size (or EQ) and brain architecture in primates will correlate fairly closely with tool technology and tool use (C, F)
- C. Where archaeological evidence of stone tools is found, paleontological evidence of relatively large-brained hominids will also be found (F)

IV. Genes

- A. There will be many genes which affect both feet and hands (G, C)
- B. The vast majority of genes affecting toe length will be the same ones that affect finger length (G, C)
- C. The vast majority of genes affecting toe/foot form will be the same ones that affect finger/hand form (G, C)

- D. Human and chimpanzee genome projects will show that some genes which distinguish humans from chimpanzees shorten and straighten both toes and fingers (G, C)

V. Neurology

- A. Increased neurological control of hands will be associated with humans (and other hominids that used stone tools), to a much greater extent than with those living primates which do not make sophisticated tools (C)
- B. Hominid fossils with larger, more complex brains will produce more sophisticated tools (F)
- C. Humans, with their large and powerful brains, will be able to make and use tools, even if they are unable to use their hands (O)

In this work, we were particularly interested in testing the Neurocentric View in regard to genes (Part IV, Sections A-C, in the outline above). Bipedalism first evolved in the human lineage about six million years ago, and by the time *P. robustus* and *H. habilis* arrived on the scene, two and a half million years ago, it is likely that all hominids would have evolved bipedally adapted feet. Known adaptations of modern human feet include shortened toes (especially the lateral toes), a hallux adducted so that it is in line with the other toes, as well as large tarsal bones and a longitudinal arch. We know from Susman's work (Susman *et al.* 1984, Stern, Susman 1983) and the work of others (McHenry 1975, Clarke, Tobias 1995, Duncan *et al.* 1994, Latimer, Lovejoy 1990, Tuttle 1981, Tuttle *et al.* 1991) that earlier hominids had already begun some of these adaptations, particularly the changes in the toes, even before the advent of *P. robustus* and the genus *Homo*. But, if hominids were under selective pressure to develop feet that were well-adapted to bipedalism, and if the genes which control foot anatomy are the same ones that control hand anatomy, then the hands would most likely have changed, too. Since all hominid lineages would have similar feet, they would also have similar hands and we needn't look for any other reasons for the purported resemblances in hand anatomy of *P. robustus* and *Homo*. It remains only to determine whether in fact pleiotropy exists in this case, such that the genes which affect the toes also affect the fingers.

Material and methods

To test whether the genes affecting the hands and the feet are indeed the same ones, the authors used OMIM, the Online Mendelian Inheritance in Man website, sponsored by the National Center for Biotechnology Information and edited by Victor A. McKusick and his colleagues at Johns Hopkins University and elsewhere. Internet access to OMIM provides a searchable list of approximately 14,600 human genes which have been identified by medical and genetic research. Each entry in the list includes information on the expression, transmission, history of discovery, localization, biochemical action and bibliographic references for the gene in question. The entire list, including the descriptive

material, can be searched using keywords or Boolean combinations thereof. The search terms utilized in this study are as follows:

cheiridia	halluces	pollical
digit	hallux	pollices
digits	hand	thumb
feet	hands	thumbs
finger	phalangeal	toe
fingers	phalanges	toes
foot	phalanx	
hallucal	pollex	

The results of a search appear as a list of genes preceded by their six-digit catalog numbers (*Table 1*). Clicking on the catalog number takes the viewer to a description of that gene. The description of each gene was checked to determine what effect it has on the cheiridia. Specifically, each gene was scored according to the cheiridium affected (hand, foot, both) and the type of effect on the digits (form or length). For example, polydactyly is considered to affect the form of the cheiridia, since it involves an unusual number of digits. Brachydactyly, on the other hand, was scored as affecting the length of the digits. Note that, in scoring the type of effect, when a gene affects both form and length of fingers or toes, form takes precedence since it may be considered to include length.

TABLE 1. Sample OMIM search results.

189000	TOE, FIFTH, NUMBER OF PHALANGES IN
219070	CURVED NAIL OF FOURTH TOE
189100	TOE, MISSHAPEN
158100	MONOPHALANGY OF GREAT TOE
126500	DOUBLE NAIL FOR FIFTH TOE
113475	BRACHYMETATARSUS IV
189150	TOE, ROTATED FIFTH
189200	TOES, RELATIVE LENGTH OF FIRST AND SECOND
#107480	TOWNES-BROCKS SYNDROME; TBS
#116860	CEREBRAL CAVERNOUS MALFORMATIONS; CCM
189230	TOES, SPACE BETWEEN FIRST AND SECOND
*186350	SYNDACTYLY-POLYDACTYLY-EARLOBE SYNDROME
#254130	MIYOSHI MYOPATHY; MM
272150	SUGARMAN BRACHYDACTYLY

Once the data were scored for cheiridium and effect, the results were separated into several categories, according to their scores, and compared. As noted above (IV, A through C), our hypothesis predicts that "there will be many genes which affect both feet and hands; the vast majority of genes

affecting toe length will be the same ones that affect finger length; the vast majority of genes affecting toe/foot form will be the same ones that affect finger/hand form”. These predictions can be tested in the sense that, if a very high percentage of the genes which affect toe length also affect finger length, we can reject the null hypothesis (that they are independent) with a high level of certainty. This is based on the assumption that mutations are generally random and therefore no individual or species can choose which mutations it receives. In the absence of any evidence to the contrary, we can assume that one gene is as likely to be mutated in a beneficial way as any other. Therefore, the genes used by natural selection to cause adaptation of hominid feet are “chosen” at random. Those genes which provide a selective advantage in adapting a hominid to bipedalism are more likely to be retained within a population, probably increasing in frequency from generation to generation. Through natural selection, those mutations which are significantly harmful (relative to the average population fitness) will be eliminated.

Results

In total, 800 genes were found to affect the fingers and/or toes. Of these, about 65% affect the form of the digits, while 35% affect the length; about 70% affect the toes, and 94% affect the fingers. Their distribution in our scoring system is given in *Table 2*.

Results of this genetic survey indicate a high probability that selection for bipedally adapted feet also altered the hands. Specifically, of the genes found to affect the length of the toes (Toes + Both = 189), 94.2% also affect the fingers. Of the genes which affect the form of the toes (373), 90.1% also affect the fingers. Overall, among the genes which have any effect on the toes (562), 91.5% also affect the fingers. We take these results to show approximately a 92% chance that pleiotropy combined with selection on hominid feet had a significant effect on the anatomy of hominid hands.

TABLE 2. Genes which affect feet, hands or both.

Cheiridium	Form	Length	Form + Length
Feet	37 (7%)	11 (4%)	48 (6%)
Hands	145 (28%)	93 (33%)	238 (30%)
Both	336 (65%)	178 (63%)	514 (64%)
Total	518 (100%)	282 (100%)	800 (100%)

Conclusions

Since mutations are random and no species gets to choose which mutations it receives, the genes used by natural selection to cause adaptation of hominid feet are “chosen” at random. This suggests that the probability of a new mutation which can adapt the feet to bipedalism is equal to the frequency at which such genes occur. Furthermore, the probability of those same genes also affecting the hands is equal to the proportion which also affect the hands.

Thus, since less than 10% of the genes which affect the form of the toes do not affect the fingers, we interpret the results to mean that the chances of changing the form of the toes, without also affecting the form of the fingers, are less than 10%. Furthermore, the chances of shortening the toes, without also shortening the fingers, are only about 6%. Overall, the chances that the same genes which have altered the toes of hominids have also altered the fingers, are 91.5%. Therefore, the chances of adapting the toes to bipedalism, without also affecting the fingers, are only 8.5%.

Thus, it is no longer necessary to postulate tool use in *Paranthropus robustus*, a hominid with a brain only slightly larger than that of a modern ape and, as Susman points out (Susman 1988, 1989), little or no interest in using stone tools to obtain meat. The data presented here eliminate the advantage of the Morphocentric View in that any similarity in late hominid hands can potentially be explained by pleiotropy among the genes that control hand and foot shape. Indeed, we find it quite likely that our initial hypothesis is largely true; the hands have most likely been affected by adaptations to bipedalism. Therefore, it is quite plausible that all late hominids, including *Paranthropus robustus*, will have similar hands in part because of selection for bipedally adapted feet. Fine anatomical details of hand morphology may not be due to adaptations for tool use, at all. Indeed, as suggested by the works of handicapped artists and the nests of weaver birds, even the thumb itself may not be necessary for fine manipulation (a fact made even more significant by the relative simplicity of early stone tool industries). Maybe, as Jouffroy (1993) wrote, any primate hand will do.

DISCUSSION

Playing the percentages

The fact, that about 92% of the genes which affect the toes also affect the fingers, is convincing evidence that foot adaptations for bipedalism have affected the hands of hominids. Hence, we have stated our conclusions quite strongly. However, we do not claim that hands could not have evolved without affecting the feet. In fact, the likelihood of this is about 30% (*Table 2*). Thus, it is not our position that the entire anatomy of the hands is precisely tied to (and caused by) the evolution of the feet. However, the minute details of hand anatomy are unlikely to shed much light on a hominid’s ability to make and use stone tools, especially when an unknown number of features of the hand are quite likely to be the indirect results of adaptations to bipedalism.

“Disease genes”

It is reasonable to ask if many of the genes used in this survey are “disease genes”, and one might question the validity of using “disease genes” in the context of a search for genes which have been adaptive for hominid bipedalism. In fact, nearly all the genes used in our results are identified by their harmful alleles. However, “disease genes” is a misnomer for deleterious alleles. Furthermore, this is the

nature of OMIM and probably any search for particular genes within a species. While there is the possibility of beneficial new alleles arising through mutation, it is much more likely that a mutation will produce a harmful allele. The disorders thus produced are our main means of identifying genes. Therefore, it is a feature of the human genome and our research technology that the vast majority of the genes listed here were discovered by recognition of one or more deleterious alleles. However, the discovery of a deleterious allele presupposes the existence of a normal allele, and what is currently the normal (wild type) allele may have other, unknown, non-harmful alleles. This is true not only of the current wild type allele, but of all preceding wild type alleles throughout hominid evolution. Therefore, the use of OMIM provides us with a list of the genes which have an effect on the cheiridia and which therefore might have been used to improve the anatomy associated with hominid bipedalism.

Historical relevance

Although there is still a great deal more work to be done, based on the results presented here, it appears that what makes a hominid a tool user may not be the details of hand anatomy, and may instead be its relatively sophisticated brain and the concomitant ability to conceive of stone tools and the process of making them. This idea was put forth many years ago when Leakey first discovered *Homo habilis* at Olduvai Gorge (Leakey *et al.* 1964). Initially, Leakey had assumed that *Paranthropus* was the maker of the Oldowan industry, since at first no remains of any other hominid species were known from the lower layers at Olduvai. However, after the discovery of *Homo habilis* in the early 1960's, he revised his earlier position and attributed the stone tools to the bigger-brained *H. habilis*. This contrasts with the Morphocentric view which suggests that it is merely coincidence that *H. habilis* had a cranial capacity about 20–30% larger than *Paranthropus* (Tobias 1964, McHenry 1988, Aiello, Dunbar 1993).

In historical context then, some authors have returned to an idea about *Paranthropus robustus* that was posited in 1959 by Leakey, but which was subsequently abandoned by him when new evidence of *Homo habilis* was discovered. Once again, newer evidence (i.e., the genetic data provided hereabove) suggests that the genus *Homo* may in fact be the first and only stone tool maker, and the association between stone tools and details of hand anatomy is spurious. Therefore, arguments about which hominid left the metacarpal at Swartkrans (Klein 1999) are probably superfluous.

Australopithecus garhi

The Bouri site, in Ethiopia, appears to be mirroring Olduvai Gorge in its historical development. Asfaw *et al.* (1999) claimed that the newly named species, *Australopithecus garhi*, was a tool user, citing mammalian bones with cut marks and percussion marks made by stone tools and “rare, isolated, widely scattered cores and flakes” in the same beds as the hominid fossils (de Heinzelin *et al.* 1999). They also point out that *A. garhi* has a relatively small brain (450 cc). Is

this then evidence against the Neurocentric Model? We think not. Despite the authors' repeated statements to the contrary, the reported features and measurements show a number of masticatory similarities with *Paranthropus*, including large molars, molariform premolars, non-projecting canines, narrow incisors, sagittal crest and large premolar surface area (Asfaw *et al.* 1999). Furthermore, like the “Black Skull” (KNM-WT 17000), the only other specimen of *Paranthropus* dated to 2.5 Ma BP, the Bouri specimen (BOU-VP-12/130) shows mild clinorhynch in that there is some antero-posterior curvature of the palate (Walker *et al.* 1986, Asfaw *et al.* 1999). All these features and its date suggest that *A. garhi* is an early member of the robust lineage.

Early analyses of microwear patterns suggested that *Paranthropus* ate small, hard objects (Grine 1981), such as seeds and nuts, and further research has reinforced the idea that they ate hard foods, rather than soft, tough foods such as meat (Teaford, Ungar 2000). Subsequently, palaeoisotopic analyses suggested a significant amount of meat in their diets (Sillen 1992). However, further studies of palaeoisotopes in teeth and bones and other types of analysis indicate a complex (eurytopic) diet (Wood, Strait 2004) which may have included insects (Lee-Thorp, Sponheimer 2006), sedges (Sponheimer *et al.* 2005) and papyrus (van der Merwe *et al.* 2008). The consensus appears to be that *Paranthropus* had a more varied diet than originally thought, but that it is unlikely to have eaten much mammalian meat. Why, then, would *A. garhi* have used stone tools to make “bone modifications [which] indicate that large mammals were disarticulated and defleshed and that their long bones were broken open, presumably to extract marrow” (de Heinzelin *et al.* 1999)?

Furthermore, the mammal bones with cut marks on them come from a layer “within 1 m above the MOVIT [Maoleem Vitric Tuff]” (de Heinzelin *et al.* 1999) while the fossil hominid on which *A. garhi* was named comes from “within 2 m of the top of the Maoleem vitric tuff” (Asfaw *et al.* 1999). While it is hard to tell from the authors' descriptions, it appears that *garhi* was found about 1 m above the bovid bones with cut marks. From de Heinzelin *et al.* (1999: 626) who estimate a deposition rate of 10.9 cm per 1000 years, this represents approximately 9000 years of separation – clearly not a very close association between *A. garhi* and the evidence of stone tool use.

The brain size of *A. garhi* is also a clue to its association with *Paranthropus* and may indicate an inability to make stone tools of Oldowan style. At 450 cc, the cranial capacity of BOU-VP-12/130 lies well within the range for the australopithecines but also well below that of *Homo habilis* (McHenry 1988). It compares favorably with the cranial capacity of 410 cc for WT 17000. Therefore, in accordance with the predictions listed above (III. C), we predict that new discoveries at the Bouri site will include a larger-brained hominid referable to *Homo habilis*, as happened at Olduvai Gorge in the 1960s. After all, if early *Homo* and *Paranthropus* can co-exist at Olduvai Gorge, why not also at Bouri? Unfortunately, this prediction is not falsifiable, since our inability to find such a hominid does not prove that it was never there.

OTHER EVIDENCE AND THE NEUROCENTRIC MODEL

There are already a number of lines of evidence which are relevant to the Neurocentric Model. Of particular interest to those studying the genetic changes which affect the cheiridia, is evidence of simultaneous changes in early hominid hands and feet (predictions II. B and C, above). A mounting body of data indicates the changes in the feet of early hominids as they adapted to bipedalism, evincing a variety of intermediate forms in the hominid fossil record. For example, Stern and Susman (1983) noted several features of the AL 333-115 foot (*A. afarensis*) which were quite similar to the feet of modern great apes, but also pointed out that the proximal articulation of the proximal phalanges is incipiently human as are the lengths of the middle phalanges relative to the proximal phalanges; metatarsal I is more ape-like, but the heads of metatarsals II-V are more human, and the shaft of metatarsal V (AL 333-78) is human-like proximally and ape-like distally. The cuneiforms and naviculars from the same site are also intermediate in form. Later, Susman *et al.* (1984) pointed out the relatively long proximal pedal phalanges of *A. afarensis* and the fact that phalanx III is apparently longer than II, an ape-like trait. Recently, Harcourt-Smith (2005) has even questioned whether *A. afarensis* had a longitudinal arch sufficiently well-developed to have made the Laetoli footprints. In short, *A. afarensis* evinces “a foot skeleton that trends in the hominid direction but which also shows a number of features that preserve a conservative hominoid...character” (Stern, Susman 1983).

Clarke and Tobias (1995) studied a nearly complete South African australopithecine skeleton from Sterkfontein (StW 573), dated at about 3.3 Ma BP and considered to be “an early member of *Australopithecus africanus* or another early hominid species”. They found that the hindfoot (particularly the talus) was very much like that of modern *Homo sapiens*, while the forefoot was “strikingly ape-like”. Specifically, they conclude that the anatomy of the medial cuneiform and metatarsal I strongly indicate a divergent and relatively mobile hallux, and they place StW 573 between modern apes and OH-8 (*Homo habilis*) in some features, while OH-8 is placed between early hominids and modern humans.

Day and Napier (1964) first described the OH-8 foot, shortly before it was assigned to *Homo habilis* (Leakey *et al.* 1964). They concluded that it was remarkably human, though it still had not achieved exactly the same features as a modern human. Specifically, the estimated forefoot and hindfoot proportions were intermediate between humans’ and gorillas’, though much closer to humans’. They also point out that the horizontal angle and the angle of inclination of the neck, while similar to *Paranthropus* from Kromdraai, are not quite human. Further work by Day and Wood (1968) suggested that the tali from Kromdraai and from the OH-8 partial foot are quite similar to each other and intermediate between humans and living African apes, but distinct from all other forms in some features.

At the same time as these evolutionary developments in the feet were taking place, changes in the hands also

occurred. Bush (1982: 384–385) initially described elements of the hand bones of *A. afarensis* as showing “some similarities to *H. sapiens*; other elements show similarities to the African apes”. Marzke (1983), too, noted that the ratio of the length of the first digit to the third digit in *A. afarensis* is intermediate between humans and chimpanzees. Bush (1982) also found the thumb anatomy of *A. afarensis* to be intermediate between those of modern humans and modern apes. Clarke (1999) described the nearly complete, 3.3 Ma BP skeleton, StW 573 (*Australopithecus africanus* or *afarensis*), from Sterkfontein, South Africa. His preliminary analysis showed a unique shape to the trapezium, rather human-like metacarpals, and phalanges with approximately the same amount of curvature as the *A. afarensis* phalanges from Hadar. Alemseged *et al.* (2006) also point out the somewhat curved manual phalanges of a juvenile *A. afarensis* from Dikika, Ethiopia. Unfortunately, though the skeleton of this juvenile specimen is fairly complete, including the left foot, it is still partially encased in matrix and no precise description of the foot is available at this time. However, it is clear that changes in the hands of early hominids were occurring at the same time as changes in the feet (prediction II. C, above).

More recent fossil hominid hands still showed some ape-like features. For example, the original description of the OH-7 hand bones, by Napier (1962), suggested that although it could have made stone tools and was largely human, it was more robust with somewhat more curved phalanges than a modern human hand, and was somewhat ape-like in the trapezium and relative length of the thumb. At that time, Napier was unsure of the taxonomic affinities of the Olduvai hand, and left open the question of whether it was properly associated with the robust australopithecine skull described earlier. Subsequent studies confirmed the intermediate nature of the OH-7 hand. Susman and his colleagues (Susman, Stern 1982, Susman, Creel 1979), after the specimen was assigned to *Homo habilis*, found that the trapezium and distal phalanges “suggest that changes in the human direction are well advanced in...*Homo habilis*” (Susman, Stern 1982), but that some aspects of its trapezium, scaphoid and proximal and middle phalanges remained primitive (Susman, Creel 1979).

Thus, early hominids from about 4 to 3 Ma BP seemed to have had somewhat ape-like hands and feet, while later hominids’ hands and feet (from about 2 Ma BP on) are more human-like, though not precisely human. With slight modification, perhaps Susman and Brain said it best (1988): “The foot [and hand] of *Australopithecus afarensis* could best be described as only incipiently bipedal. By 1.8 m.y. BP the feet [and hands] of both the ‘robust’ australopithecines and early *Homo* were essentially human-like. It is perhaps not surprising that one finds similar adaptation to plantigrade bipedality in two separate lineages at a point where both had enjoyed a 1.5 million year terrestrial apprenticeship” (Susman, Brain 1988: 14; words in brackets are added by us).

For the most part, the foregoing description of hominid cheiridial evolution provides only a rough correlation

between the hands and feet, rather than a feature-by-feature comparison. Only in the features of phalangeal length and curvature do the feet and hands show a clear parallel. Nevertheless, the discussion above shows clearly that hands were evolving towards the modern human condition at the same time that feet were. This is particularly important, since some of these hand changes occurred after bipedalism began but well before the first known stone tools. Therefore, they were probably not adaptations to stone tool use, though they may have been indirect adaptations to bipedalism.

EVIDENCE FROM THE CHIMPANZEE AND HUMAN GENOME PROJECTS

Recently, Prabhakar *et al.* (2008) discovered evidence of rapid evolution in a non-coding region of human DNA. Specifically, they found an 81-base pair module on human chromosome 2 that is quite conservative and highly constrained in terrestrial vertebrates, but which has undergone extremely rapid evolution since the separation of humans from chimpanzees. They termed the region *HACNS1*, for human-accelerated conserved non-coding sequence 1, and showed that it acts as a transcription enhancer affecting expression of genes in the distal developing forelimb, including the first digit, and in corresponding structures in the hindlimb. Prabhakar *et al.* (2008) note that the rate of evolution of this DNA segment is four times the local neutral mutation rate, a clear indication that natural selection acted quite strongly on the *HACNS1* region. The authors point to differences in the human hand compared with other primates, and “human-specific changes in hindlimb morphology, such as the characteristic inflexibility and shortened digits of the human foot, [that] facilitated habitual bipedalism. The gain of function in *HACNS1* may have influenced the evolution of these or other human limb features...” Their work suggests that differences between humans and other hominoids will be found not only in the genes which control foot and hand morphology directly (prediction IV, above), but also in the regulatory sequences that have indirect control of foot and hand development.

SUMMARY

In summary, the Neurocentric Model provides an alternative explanation to Morphocentric hypotheses for certain aspects of hominid hand anatomy, and it is supported by genetic evidence. We do not question other authors’ knowledge of hominoid cheiridial anatomy. We feel, however, that the answer to the question, “Which hominids made stone tools?”, does not lie in the morphology of the hands. Therefore, the oft-cited interpretation of the similarities in *Paranthropus* and *Homo* hands as adaptations for tool use is probably incorrect. Furthermore, those who argue against it on morphological grounds may be wasting their efforts,

since hand morphology is unlikely to be the key to tool use. Our interpretation, based on the genetic hypothesis presented hereabove, accounts equally well for those similarities and is a better hypothesis, because it accounts for and is more consistent with other kinds of evidence (e.g., simultaneous changes in hands and feet, and the fact of larger brains in *Homo*). In the context of late hominid tool behavior, it is unfortunate that hands and feet can be fossilized, but brains and spinal cords cannot.

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