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Tool Culture, the Baldwin Effect and the Evolution of the Human Hand

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Abstract: Human tool culture seems to have influenced the evolution of human hand anatomy. Difficulties in establishing a causal connection centre on the fact that early hominin hand anatomies supportive of tool culture precede the earliest tools in the archaeological record. Various considerations suggest that the archaeological record may be misleading. Earlier tools would not be visible if they were manufactured from wood or plant material, or if they were natural objects subject to only slight modification. Moreover, the first appearance of stone tools in the record may reflect a switch in the location of home bases or butchering sites, and not the commencement of stone tool usage. Acquisition of modern human tool skills is generally via imitation. There is no strong reason to suppose that a small-brained hominin such as *Australopithecus* was incapable of imitation, or that members of this genus could not have been manufacturers of stone tools. It therefore seems likely that anatomical support for strong grasping and pinch grips, even as early as *Australopithecus*, is a specific adaptation to the cultural practice of tool usage, or perhaps to manipulative practices generally. The Baldwin Effect is a useful explanatory model. By substituting culture for individual learning, and thus reducing the costs of learning, we can use the model to predict the observed outcome, namely the genetic incorporation of bodily structures associated with tool usage, while tool usage itself continues to be cultural.

Keywords: Human evolution, tool, hand, Baldwin Effect, culture

INTRODUCTION

The modern human hand appears remarkably well-adapted to tool use and tool making. Compared with our fellow primates, we have for example a long thumb, the muscles of which are well differentiated. We also possess a specific muscle, the *flexor pollicis longus*, which is frequently absent in other primates. This muscle attaches to the forearm, and allows the thumb to flex at its mid-point (Susman 1988). A powerful, flexible, and relatively long thumb is very useful when grasping objects firmly in order to deploy them as tools.

Notice that we are asserting a link between an evolutionary outcome (hand anatomy) and a cultural practice (tool usage). At least two causal relationships can be recognized: that certain hand anatomies provided a base for culture and, conversely, that culture provided an environment that favoured certain hand anatomies. This paper assumes that evidence can be found to support both causal relationships, but focusses on the second. The influence of culture on bodily structure and function may be one of the distinguishing features of human evolution.

Let us start with some definitions. The term *tool* can be used inclusively to mean any detached object which is employed for a useful end. Following Wynn (1994), I will use the term more narrowly to mean 'a detached object that is controlled by the user to perform work (in the mechanical sense of transferring energy), usually as an extension of the user's anatomy'. Thus, a carpenter's hammer is a tool, but a bird's nest is not. I shall use the term *culture* to refer to: *shared patterns of behaviour which are acquired, within lifetime, from other members of the same species, usually in the context of social relationships between mutually recognized individuals.*

TOOL CULTURE

Modern human tool usage is predominantly cultural, as shown by the social learning needed to acquire even a moderate level of skill. In some species, however, tool usage shows little variation among individuals and populations (Panger 2002), and therefore may be predominantly genetic in origin. In order to assert a causal role for culture, it is necessary to establish that tool usage among early hominins was also cultural. There is no direct evidence for or against this view, but it gains support from the cultural nature of tool usage among our nearest living relatives, common chimpanzees (chimps). A review of the literature reports that all chimp populations subject to long-term study turn out to be tool makers and users, and that each population has its own customary tool kit (McGrew 1998). Work with the directors of the seven most long-term field studies of chimp behaviour identified a number of behaviours which were significantly present in one population, but absent in others, with no apparent ecological or genetic explanation. Most of these cultural behaviours involved tool usage (Whiten et. al. 1999).

It is not clear whether tool culture first developed in the common ancestor of chimps and humans, or developed independently in both lineages after branching speciation. The question is not fundamental because, on the reasonable assumption that both hominin and chimp tool behaviour has always been predominantly cultural, it is likely that tool usage was invented, lost and then re-invented many times over in all three lineages.

EVOLUTIONARY CAUSES

As a classic paper argued (Gould and Lewontin 1979), present utility does not establish evolutionary origin. The role played by hand anatomy in supporting modern human tool usage does not by itself establish that hand anatomy evolved as an adaptation to tool usage. In particular, hand anatomy may be an adaptation to ancestral practices in ancestral environments, providing a fortuitous pre-adaptation which humans then exploited via tool usage.

Pre-adaptation is clearly an important component of the story, as can be seen by considering chimp tool usage. Unlike monkeys, which move around in trees by traversing the tops of branches or by hanging from their tails, apes (including chimps) lack tails, and move around by climbing, or by hand over hand movement (*brachiation*) while hanging from a branch. The hands of apes are adapted to this style of movement by providing a powerful grip, using four fingers pressed firmly against the palm. Chimps are also ground-dwellers as well as tree-dwellers. It seems to be happenstance that, when using or making tools, chimps have been able to exploit this arboreal ape grip for a different function. If this explanation works for chimps, then it presumably works at least to some degree for the earliest hominins. We too must have been ground-dwelling opportunists who took advantage of an anatomy originally adapted to a tree-dwelling environment.

A second point in favour of pre-adaptation is that it seems to be consistent with the archaeological record of early hominins. The earliest known tools date from 2 to 2.5 million years ago (mya). However, remains of *Australopithecus afarensis* dated to 3.2 mya show anatomical features which provide greater support for tool culture than those of modern chimps, for example a longer thumb relative to the fingers than in chimps. In general, Marzke (1997) identifies eight distinctively human features of the hand (see below), of which *Australopithecus afarensis* exhibited three. Perhaps anatomy did precede tool culture, at least amongst early hominins.

Pre-adaptation, however, cannot be the whole story, for there are just too many distinctive features of the modern human hand which too neatly support tool culture. The important question is not whether a particular hand anatomy is capable of supporting stone tool culture, but the degree to which hand anatomy provides 'economical and effective' support (Marzke 1997).

Stone tools can be made by striking or throwing a softer stone against a harder surface. They may also be made by placing a softer stone against a substrate, and then striking with a harder stone. Efficient production, however, is generally by striking a hard hammer stone held in one hand against a softer core held in the other hand, thereby producing flakes from the core (hard-hammer percussion). Efficient use of flakes as cutting instruments is generally by grasping the flake between the thumb and the forefinger, with or without the support of other fingers. In general, use of prehistoric stone tools places similar demands on anatomy as manufacture of the tools (Marzke and Marzke 2000).

Certain grips are favoured by modern humans who have taught themselves hard-hammer percussion, and these grips are in turn supported by the following anatomical features (Marzke 1997).

1. As noted above, humans have a longer thumb relative to the second finger. The thumb is able to control objects of varying sizes and shapes by moving against all four fingers. If the core is held using an ape-like power grip, i.e., without recruiting the thumb, 'the core must be repositioned for each strike either by dropping it and retrieving it in a new orientation or by shifting its position with the hand holding the hammer stone.'

2. Humans have well-developed intrinsic muscles of the thumb (i.e., muscles attached at both ends to bones within the hand). In humans, thumb intrinsic musculature is 39% of total intrinsic hand musculature, compared with 24% in chimps.

3. As noted above, humans have a proportionately large *flexor pollicis longus* muscle. This muscle attaches to the forearm, and is frequently absent in other primates. It controls the joint at the mid-point of the thumb, allowing the thumb pad to be oriented towards the fingers, and the thumb to be braced against pressure by the fingers.

4. Humans have relatively large pads on the tips of the fingers and thumb. These pads are supported by broader tufts on the distal phalanges (the bones forming the top segment of the fingers and thumb). The larger surface area of these pads 'distribute pressure during forceful grasping', for example when grasping a hammer stone.

5. In humans, the third metacarpal head is oriented towards the thumb. The metacarpus is five bones which are joined to each of the four fingers and thumb, and together provide the skeletal substructure for the palm. The head of the third metacarpal bone is attached to the longest finger, and its orientation towards the thumb assists in grasping large objects such as stones for hammering or throwing.

6. In humans, there is marked asymmetry of the second and fifth metacarpal heads, so that the index finger and little finger are oriented towards each other when grasping a large object, once again maximizing the contact between the inner surface of the fingers and the surface of the object.

7. In humans, the joints between the second metacarpal and three bones in the wrist (the trapezium, trapezoid and capitate) are oriented so that the metacarpal can pronate (rotate palm-downwards) during strong pinch grips between the thumb and the side of the index finger.

8. In humans, the pads on the tips of the fingers and thumb are less mobile than the pads on the remaining finger segments. This allows a firm pinch grip using the tips, while nevertheless allowing greater cushioning and a larger sensory area in the rest of the fingers and thumb.

On the basis of the evidence, it is reasonable to conclude that tool culture has been a key selective agent in the evolution of the human hand. This conclusion does not commit us to any of the fallacies identified by Gould and Lewontin (1979). The object of our interest is not a single trait considered in isolation from the rest of human anatomy, but a series of interconnected traits. The traits are almost certainly not byproducts of a different adaptation, and we have given due weight to the role of pre-adaptation.

EARLIEST HOMININ TOOL USAGE

Having reached this conclusion, we must address the difficulty mentioned above, namely that remains of *Australopithecus afarensis*, dated to 3.2 mya, show anatomical features supportive of tool culture, when the earliest known stone tools date only from 2 to 2.5 mya. Specifically, the following traits were identified (Marzke 1997).

§ A longer thumb relative to the fingers than in chimps.

§ Asymmetry of the second and fifth metacarpal heads, so that the index finger and little finger are oriented towards each other when grasping a large object.

§ The joints between the second metacarpal and bones in the wrist support strong pinch grips between the thumb and the side of the index finger.

In making the reasonable assumption that these traits evolved sometime after hominin separation from the chimp lineage, i.e., that they were not inherited from the last common ancestor, some explanation is required.

Let us review the evidence for early tool usage. This usage probably would have involved wooden and bone implements, in addition to stone, but the earliest available evidence is almost exclusively of stone tools. This evidence takes two forms. First, direct evidence comes from the form of the tools themselves, and associated remains such as the cores from which they were flaked. Secondly, indirect evidence is provided by microwear analysis of cut marks on animal bones thought to form the remains of hominin meals. Both point to 2 to 2.5 mya as the earliest known date for stone tools (Panger 2002).

Several possible explanations can be suggested for the absence of earlier evidence. If tools were made of other materials such as wood or plant fibre, they would leave little evidence, either directly in the form of tool remains, or indirectly in the form of cut marks. In addition, 'found tools' may have been employed, only slightly modified for the purpose, in the manner of modern chimps. In that case, tool remains may be present but unrecognizable in the archaeological record. It has been suggested that *Australopithecus* discovered the food content of the underground storage organs of plants, such as tubers and rhizomes (Wrangham 2001). Amongst tool-using populations, we can imagine that pieces of wood may have been abraded against a hard substrate, and then used as digging-sticks grasped firmly with the assistance of a relatively long thumb. Such practices would leave little or no evidence in the archaeological record.

Another possibility is that hominins did manufacture stone tools prior to 2.5 mya. It has been argued that the earliest known tools are too sophisticated to be the first examples of their type, as they exhibit evidence of multiple flakes from a single core, some flakes have been re-touched, and the raw material for their manufacture has been transported throughout the landscape (Panger 2002).

It has also been argued that the earliest stone tool usage may be hidden in the archeological record for ecological reasons. Most evidence of stone tools has been gathered from sites containing hundreds or even thousands of stone artifacts. Whether interpreted as home bases, butchering sites, or workshops for making tools, these sites represent a geographic concentration over a relatively short time period. Factors influencing the location of such sites would have included protection from bad weather and the availability of shade. One population living in a savanna environment might have located them under shade trees, while a second population living in a more arid environment might have located them under rock outcrops. Because rock outcrops have a much longer potential lifespan than trees, they will support a greater concentration of stone tools and meal remains over time. Perhaps the emergence of manufactured stone tools in the archaeological record merely marks the first time such tools became archaeologically visible (Brooks and Laden, cited in Panger 2002). This suggestion gains plausibility from the fact that Africa's environment was becoming more arid in the relevant time period, driven by a new ice age.

It may be argued that *Australopithecus* had a relatively small brain, and was therefore not smart enough to have been a manufacturer and user of stone tools. This makes some assumptions about the cognitive capacities required, which can be tested against modern evidence. Studies of tool use in the modern era indicate that two styles of cognition dominate. The first style dominates in the acquisition of skills, the second in the application of those skills to solving problems. Overwhelmingly, tool skills are learned by repetitive showing and doing, rather than desk-based learning, with apprenticeship as the classical form of relationship between teacher and novice. Although the apprentice may later be able to place tasks in a hierarchy of routines and sub-routines, the tasks are initially learned in sequential fashion (first job 1, then job 2, then job 3 . . . then finish). The task sequences are committed to motor memory by repetition, using temporal or spatial contiguity to cue the next action in the sequence. It is a cognitive style 'commonly encountered in any human behaviour requiring precise motor coordination. Instrumental musicians, for example, use much the same technique in learning complex passages of music. It is also the essence of most sport' (Wynn 1994). In addition, it is close to the cognitive style which characterizes chimp tool behaviour, although for chimps the phrase 'observing and doing' is more appropriate than 'showing and doing'. Subject to this qualification, the difference between humans and chimps is quantitative rather than qualitative.

If the cognitive processes required to learn tool skills are simple, this is not necessarily true of the cognitive processes involved in actually using the tools, i.e., in adjusting tool behaviour to the specific challenges presented by individual circumstances. Wynn (1994) argues that in this respect modern human tool usage can be an altogether more complex process, involving a sort of 'dialogue' between known sequences (sitting in motor memory) and plans for the task at hand. This will usually involve contingency planning i.e. imagining possible problems, and conceiving possible solutions, before attempting the task. It should be contrasted with the mainly trial-and-error method employed by chimps, and almost certainly early hominins.

The problem-solving skills of modern humans do not appear to be specifically related to tool culture, but represent the application of a generalized intelligence which appears to have evolved for other reasons, possibly connected with group social complexity (Dunbar 1994). If repetitive showing and doing (or observing and doing) is the essential element in tool culture, it seems reasonable to conclude that a small-brained animal could have developed some form of stone tool manufacture and use. Recent discoveries in Flores indicate as much, regardless of whether we regard *Homo floresiensis* as an offshoot from the *Homo erectus* lineage, or as more directly linked to *Australopithecus*.

In conclusion, a range of explanations is possible. At one extreme is the possibility that tool usage among the earliest hominins was no more sophisticated than the tool usage which is plausibly ascribed to our chimp-like ancestor (because we observe it among modern chimps, whose ecology appears to be largely unchanged). At the other extreme, it is possible that tool usage was at a level of complexity somewhere between chimps and the earliest hominin tool culture for which there is archaeological evidence. At the latter extreme, it is not difficult to understand why the hands of *Australopithecus* show some anatomical features supportive of tool culture. At the former extreme, if *Australopithecus* tool culture and modern chimp tool culture are very similar, we must ask ourselves why *Australopithecus* hand anatomies provide some support for tool culture, but those of modern chimps do not.

Let us be clear that chimp hand evolution is not entirely unaffected by chimp manipulative behaviour. In typically thorough fashion, Marzke (1997) has identified features which provide some support for precision grips, but it remains true that the chimp hand is not as well adapted for manipulation. The most likely reason is that the hands of chimps are required to perform multiple functions, and are therefore subject to strongly conflicting selection pressures. Chimp hands are used to support three functions, arboreal climbing and swinging, manipulative activities such as food handling and tool usage, and terrestrial knuckle-walking (chimps use the backs of their fingers to support themselves while travelling on the ground). Hominins, by contrast, had already adopted a bipedal posture by the time of *Australopithecus*. There is a venerable argument that walking on two legs 'frees the hands' for manual activities. This argument has in the past been used to support what we can now see is a mistaken notion, that bipedal locomotion is necessarily associated with tool usage. If re-phrased, however, it does seem to have an element of truth. Perhaps the semi-arboreal existence of *Australopithecus* resulted in a hand more fully open to the selective pressures of manipulation and tool usage, by removing knuckle-walking as a competing pressure, and reducing the pressure in favour of arboreal climbing. If this semi-arboreal existence was sufficient to produce an evolutionary novelty, namely bipedal locomotion, then why not a shift in hand anatomy?

It is also possible that tool culture was insignificant prior to 2–2.5 mya. *Australopithecus* hand anatomy may be an adaptation to manipulative practices generally, and may therefore provide a pre-adaptation to tool usage exploited by subsequent species in the hominin lineage. For example, practices such as breaking nuts or smashing bones for marrow may account for the anatomical features in question (Marzke 1998). However such practices are likely to have been as cultural as tool usage. Perhaps our subject should be manipulative culture more broadly rather than tool culture specifically, but this would not alter the central thesis of this paper, namely that culture has been a selective agent in human evolution.

AN EVOLUTIONARY MECHANISM

If tool culture has been a key selective agent in the evolution of the human hand, by what mechanism did natural selection occur? A useful model is the Baldwin Effect, which may be explained as follows. Imagine a species whose members must individually learn a certain task in order to survive in their environment. Individual learning has costs. It may be dangerous not to perform the task to a high standard immediately (e.g., flight for birds), learning may be distracting and so make predation more likely, and it consumes time and energy which would otherwise be available for other essential tasks such as looking for food. Over generations, individuals with some genetic predisposition for the task are likely to enjoy greater reproductive success. Eventually, genetic predisposition becomes full genetic assimilation, so that what originally had to be individually learned from scratch becomes part of the genetic endowment of the species. This may apply both to behaviour, i.e., the task performance itself, and any bodily processes and structures associated with the behaviour.

Now imagine that the task is cultural in origin, for example being learned by imitating others, rather than individually from scratch. Imitation consumes less time and effort, and reduces the costs of learning. It is in this respect a form of free-loading. The Baldwin Effect can still be expected to operate, but it is now more likely to work on the bodily processes and structures associated with the behaviour, rather than the behaviour itself. Over evolutionary time, humans have become more efficient absorbers and practitioners of tool culture, because our hands (and no doubt other parts of our bodies, including our brains) have evolved to provide more efficient support for the behaviour involved. The behaviour itself, however, has remained cultural.

The Baldwin Effect presupposes that individual organisms must learn a task in order to survive, i.e., it assumes a significant degree of compulsion. Before flight became instinctive, immature birds had to learn to fly because adult member of their species had adopted flight as a 'way of life'. Applying the Baldwin Effect to tool culture also assumes a significant degree of compulsion. There is no direct evidence that tool culture was a compulsory 'way of life' for early hominins, but we can reason backwards from contemporary human culture.

Cultures define the methods to be used in subsistence tasks, but social relationships enforce the use of those methods. Enforcement can work in different ways, sometimes by the explicit use of force, but more often by implicit assumption. Let us imagine a band of scavengers of the genus *Homo*, which happens upon a recent kill. The band might quickly organize itself to ward off competing scavengers, and to remove as much flesh as possible from the carcass before the return of the predator responsible for the kill. These tasks might have been at least partly accomplished with the help of stone cutting tools to remove flesh, as well as weapons, which for this purpose can be considered tools because they are used forcefully to transfer energy (e.g., wooden clubs or spears to ward off other scavengers).

In our imaginary scenario, the enforcement of technique is largely implicit. The group habitually has tools and weapons with it, in the expectation of using them. It is passing through this location at least in part in expectation of finding a fresh kill. Its adaptation to its environment requires group members to be proficient with tools, alternative approaches being effectively ruled out. Some individuals may be more proficient at consuming flesh rapidly at the site of the kill, like the competing scavengers, but we can imagine that explicit group prohibition prevents them. Our imaginary scenario of enforced tool usage specifically mentions the *Homo* genus. While some have contrasted *Homo* as an 'obligate' tool user with *Australopithecus* as merely a 'facultative' tool user (Tobias 1994), it is difficult to assess the validity of such distinctions. It may be that hominin tool culture developed very gradually and unevenly, out of step with the relatively sudden branching speciations which seem to have occurred in the hominin lineage.

CONCLUSION

Pre-adaptation plays a major role in any evolutionary explanation of human hand anatomy. We have inherited five digits from our vertebrate ancestry. The basic configuration of the five digits, and the fact that they terminate in nails rather than claws, derives from a more immediate arboreal ape ancestor. Anatomical support for strong grasping and pinch-grips, however, seems to have occurred in the hominin lineage alone, and to be a specific adaptation to the cultural practice of tool usage. The Baldwin Effect is a useful explanatory model. By substituting culture for individual learning, and thus reducing the costs of learning, we can use the model to predict the observed outcome, namely the genetic incorporation of bodily structures associated with tool usage, while tool usage itself continues to be cultural.

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