Thumbs Up for Our Early Ancestors

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Palaeontologists are often the subject of ridicule for constructing a whole animal or inferring specific behaviors from a single bone or tooth. However, such reconstructions can be more than wishful thinking. It is possible to make accurate inferences from small and unprepossessing bits of fossil, but only if these bits have a form that is unambiguously related to a particular function. This is precisely what Susman has demonstrated in the simple, but elegant, analysis presented on page 1570 of this issue (*1*). By pointing out that one of the bones of the human thumb, the first metacarpal, has a broad head in relation to bone length, Susman has given us an apparently foolproof way of determining which of our early ancestors would have had hands that functioned in a way similar to our own.

Modern human hands are specifically adapted to enable us to make and use tools, and one of the most important features of our hands is our strong and powerfully muscled thumb. As many other primates, we can oppose our thumbs to the rest of our fingers, but we are unique in our ability to apply significant force to objects that we grasp. Consider the force that we apply through our thumbs in everyday tasks such as opening a jar lid or grasping the handle of a hammer.

We are capable of generating this force because we have very well developed thumb muscles, including three extra muscles that are lacking in the African apes, our closest living relatives. One of these muscles, flexor pollicis longus, has a tendon that runs down the palmar surface of the thumb and inserts into the base of the terminal phalanx (the last segment of the thumb) just opposite the base of the thumb nail. The sole function of this muscle is to powerfully flex our thumbs. The second muscle, the deep head of flexor pollicis brevis, inserts into the base of the first segment (the proximal phalanx) of the thumb. This muscle provides force as the thumb moves toward the other fingers in opposition. The third unique muscle is the first palmar interosseous muscle of Henle, which helps stabilize the thumb across its knuckle. These last two muscles can also help flex the thumb.

Because our thumbs are much stronger than those of other primates, the thumb bones, as well as some wrist bones, must also be stronger to resist the increased force. Susman has demonstrated that the first (thumb) metacarpal has a broad head in relation to its length in humans but not in chimpanzees. He reasons that if a fossil first metacarpal has a head as broad in relation to metacarpal length as found in humans, the thumb must have been as heavily muscled. By inference, it would have come from a hand capable of generating the force essential for human tool use and manufacture. Our early human ancestors certainly did not have modern hammer handles to grasp or jar lids to open, but the same strong thumb would have been important for the effective manufacture and use of simpler stone or wooden tools.

Stout of thumb. The evolution of powerfully muscled thumbs may have benefited early human tool users, as it does this latter-day ax maker from the village of Langda in New Guinea. [Courtesy N. Toth, Ligabue Research Center, University of Indiana]

The really surprising aspect of Susman's work is not its simplicity or anatomical elegance, but the fact that only one out of the four fossil first metacarpals used in his analysis is nonhuman in form. This is the oldest first metacarpal and belongs to the species *Australopithecus afarensis*, which went to extinction at least 500,000 years before the first evidence of stone tools in the fossil record (*2*). It is logical that this species did not have a tool-making and tool-using thumb, but what may not seem logical to most palaeoanthropologists is that another species, *Paranthropus robustus*, apparently did have such a thumb.

Stone tools appear in the archaeological record about 2.5 million years ago, around the same time as the appearance of early members of our own genus, *Homo* (*3*, *4*). It has generally been assumed that these relatively big-brained early humans made the stone tools. There are no thumb metacarpals known for these first members of our genus, but one thumb metacarpal belonging to a slightly later hominid, *Homo erectus*, is consistent with tool use. The problem is that a second, contemporaneous metacarpal, thought to have belonged to the relatively small-brained but big-toothed *P. robustus*, is also stout. It seems that there were two very different types of toolmaker living about 1.8 million years ago, each making the same type of stone tools, the big-brained *H. erectus* and the much smaller brained *P. robustus*. Susman concludes that this, as well as limited additional evidence recovered over the past decade (*5*), suggests that all hominids subsequent to 2.5 million years ago may have used tools and occupied "cultural" niches.

Before we devise elaborate scenarios to explain the fact that there may have been at least two contemporaneous toolmakers with very different brain sizes and inferred intellectual capabilities among our early ancestors, there is one thing that needs to be kept in mind. There is no universal agreement that the metacarpal that Susman assigns to *P. robustus* actually belongs to this species and not to the contemporary species, *Homo erectus*. The *P. robustus* metacarpal comes from the same level of the same southern Africa site as does the *Homo* metacarpal (*6*) and cannot be convincingly distinguished from it on the basis of morphology (*7*). A distinction between the two bones might be size. But Trinkaus of the University of New Mexico has convincingly demonstrated that the two bones are similar enough in size not to rule out the possibility that they belong to the same species (*7*).

One of the banes in the lives of palaeoanthropologists is surely the lack of sufficient fossil evidence. Susman's elegant analysis gives us a sound technique for study of the evolution of the anatomical correlates of tool use and manufacture, but two ambiguous bones are insufficient evidence upon which to determine whether more than one contemporaneous species of our early ancestors made and used tools.

Susman's analysis could imply that only stout-thumbed hominids use tools. This is clearly not the case. There is a long and growing literature documenting tool use and manufacture among nonhuman animals, particularly among primates (*8*), and there is also tantalizing evidence that there are cultural differences within primate species in this behavior (*9*). What separates stout-thumbed hominids from other primates is not tool-using per se, but the specific type of manual dexterity that is

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thought to be essential for the manufacture and use of stone tools.

The manual dexterity involved in the manufacture and use of stone tools not only involves a powerful thumb, but also other nuances of hand morphology that allow power in grasping and efficient positioning of the tool in the hand. Marzke of Arizona State University has outlined a number of important features (*10, 11*). Among these are a relatively long thumb in relation to the other fingers as well as the ability to spread and oppose the thumb and fingers as, for example, when grasping a small ball or using a hammer stone. This type of grip requires the palm to assume a cupped shape, which helps position the thumb and fingers around a spherical object. It is relevant that although *A. afarensis* lacks the stout thumb, it has both a relatively long thumb in relation to its other fingers and the necessary modifications on the index and middle finger side of the hand to allow partial cupping of the palm. Marzke concludes that although *A. afarensis* could not have grasped a hammer stone with all five fingers as modern humans can, it could have grasped it between its palm and its thumb, index, and middle fingers. *Australopithecus afarensis*, therefore, had hands that were more capable of tool use than those of living apes and would have occupied a half-way position in tool use between the stout-thumbed hominids and their more slender-thumbed antecedents.

There is no doubt that stout-thumbed hominids were anatomically more effective toolmakers and users than primates without this adaptation, but how much more effective were they? The suggestion that all early hominids subsequent to 2.5 million years ago might have occupied "cultural" niches and the implication that living primates as well as those hominids that lived before this date did not, must be clearly understood to be an inference drawn solely from the manual dexterity implied by the possession of stout thumbs. What a "cultural" niche means in this context is unclear. We are treading on dangerous ground if we jump to the conclusion that it means any more than a difference in manual dexterity that can be associated with the production and use of stone tools. Care should be taken not to overinterpret the stout-thumbed feature to suggest that it implies a major watershed in the intellectual, linguistic, or symbolic ability of our early ancestors. We must keep clearly in mind the distinction between those inferences that are firmly rooted in the evidence and those that may fall into the category of wishful thinking.

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Attractive Axon Guidance Molecules

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Nerve cells are wired to other nerve cells over distances that are regularly more than a thousand times larger than their cell bodies. In many instances, these connections are unfailingly precise from the time they are formed during embryonic development. How do nerve cells find their partners? Santiago Ramòn y Cajal (*1*) was one of the first to ask this question and to suggest a cellular mechanism. In embryonic nervous tissue, he observed amoeboid thickenings at the tips of what he interpreted correctly as elongating nerve processes (axons or dendrites). He called these thickenings "growth cones" and intuitively attributed to them a role in pathfinding and target recognition. He further speculated that substances released by the target tissue could lay a trace for the advancing growth cones by a mechanism similar to chemotaxis of whole organisms. In order to be able to navigate to the target, the growth cones would sniff out gradients of these chemotropic molecules and orient their migration accordingly.

Although Cajal's notion of the growth cone as the essential player in the development of neuronal connections has found its way to textbooks, his further speculation, the chemoattraction hypothesis, has only recently been put on more solid ground. Evidence for the existence of chemoattraction has come from in vitro studies pioneered by Lumsden and Davies (*2*). In this type of assay, two pieces of tissue, one containing the target cells and the other giving rise to axons, are placed beside each other in a drop of collagen. The collagen matrix provides a suitable environment for axonal outgrowth and at the same time stabilizes the diffusion gradient of target-released factors by abolishing convection. If one of these factors is chemotropic, outgrowing axons turn toward the source of this factor, providing a straightforward assay of axon guidance. Such an assay then can be the starting point for biochemical purification and molecular cloning of guidance molecules.

This route has now been successfully followed by Marc Tessier-Lavigne and his co-workers at the University of California in San Francisco and at Columbia University (*3, 4*). The two molecules cloned, which they call netrins (after the Sanskrit "netr" meaning "guiding"), are the first chemotropic factors identified by their function. Other factors, like nerve growth factor, have been implicated in axon guidance in vitro (*5*), but a related function in vivo has remained obscure [see (*2*), for example].

In the new work (*3, 4*), the guidance of a population of axons in the spinal cord of chick and rat was examined. These axons originate from the so-called commissural neurons in the dorsal spinal cord and grow ventrally to the floor plate as an intermediate target. Here, their growth cones cross the midline and make a turn toward the brain. The initial phase of axon guidance to the floor plate can be reproduced in vitro by placing pieces of dorsal and ventral spinal cord into collagen. The ventral piece attracts commissural axons from the dorsal piece at the appropriate embryonic stages over a distance of a few hundred micrometers (*6*). This chemotropism is perfectly correlated with an outgrowth-promoting (trophic) effect on commissural axons in a much simpler assay: When a piece of dorsal spinal cord is exposed to floor plate–conditioned medium, there is a dramatic increase in the number and lengths of axons (*6*). The outgrowth assay was used to biochemically purify the activity, with the hope that tropic and trophic effects were caused by the same factor. It is now clear that taking this risk paid off.

Netrin-1 and netrin-2 are two novel secreted proteins of molecular weight 75,000 and 78,000 that are 72% identical to each other (*3*). They are for the most part membrane-associated, but also exist in soluble form. Netrin-1 is expressed solely by floor-plate cells, whereas netrin-2 transcripts are detected more widely and at lower levels in

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