

SIXTY-SECOND
JAMES ARTHUR LECTURE ON
THE EVOLUTION OF THE HUMAN BRAIN
1992

EVOLUTION OF THE BRAIN AND
COGNITION IN HOMINIDS

DEAN FALK

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- *Dean Falk, *The Evolution of the Human Brain and Cognition in Hominids*; April 14, 1992

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JAMES ARTHUR
1842-1930

Born in Ireland and brought up in Glasgow, Scotland, James Arthur came to New York in 1871. Trained in mechanics and gear-cutting, he pursued a career in the manufacture and repair of machinery, during the course of which he founded a number of successful businesses and received patents on a variety of mechanical devices. His mechanical interests evolved early into a lifelong passion for horology, the science of measuring time, and he both made some remarkable clocks and assembled an important collection of old and rare timepieces.

Early in this century James Arthur became associated with the American Museum of Natural History, and began to expand his interest in time to evolutionary time, and his interest in mechanisms to that most precise and delicate mechanism of them all, the human brain. The ultimate expression of his fascination with evolution and the brain was James Arthur's bequest to the American Museum permitting the establishment of the James Arthur Lectures on the Evolution of the Human Brain. The first James Arthur Lecture was delivered on March 15, 1932, two years after Mr. Arthur's death, and the series has since continued annually, without interruption.



James Anthony

EVOLUTION OF THE BRAIN AND COGNITION IN HOMINIDS

Comparative genetic analyses indicate that chimpanzees and people are descended from a common ancestor (CA) that lived in Africa approximately 5 million years ago (fig. 1). The CA was probably small, with long arms and large canines like those of living apes. Early on, certain descendants of the CA began walking habitually on two legs. At that point, these individuals ceased to be apelike protohominids and became the first true hominids, known today as australopithecines. As can be seen in figure 1, by 2 million years ago, australopithecines had given rise to the genus *Homo*, which eventually led to modern people.

In the late 1970s, a remarkable discovery of fossilized hominid footprints occurred at a site known as Laetoli, in Tanzania, East Africa (Leakey and Hay, 1979). Ironically, these 3.5 million year old footprints profoundly changed the then accepted view that hominid brain evolution was intimately linked to the evolution of bipedalism and its consequent freeing of forelimbs, production of tools, etc. Although the makers of the Laetoli footprints were bipedal, brain size in australopithecines that lived over 3 million years ago was in the apelike range, i.e., around 400 cm³ (Falk, 1987b). Indeed brain size, which remained conservative throughout australopithecine evolution, did not begin to increase dramatically until well over a million years *after* the Laetoli hominids took their walk, and then it did so only in the genus *Homo* (fig. 2). Thus the origin and initial evolution of bipedalism *preceded* the dramatic increase in brain size that characterized *Homo*.

Three and a half million years after the Laetoli footprints were made, another famous set of footprints appeared—this time left on the moon by the astronaut Neil Armstrong (Falk, 1991). The feet that made the impressions at Laetoli and those that left footprints on the moon were, for all practical purposes, the same (Tuttle, 1985). The part of the anatomy that differed between the earlier Laetoli hominids and the later astronaut was not the feet but the brain. What happened to the brain during hominid evolution that permitted Armstrong's species to place him on the moon? Referring to

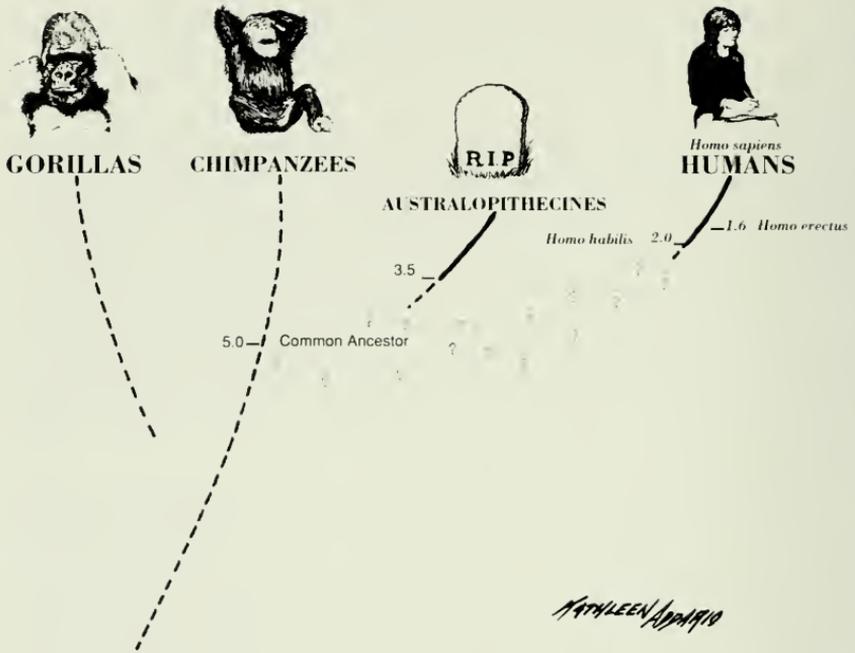


Fig. 1. Molecular evidence suggests that people and chimpanzees are descended from a common ancestor that lived approximately 5 million years ago. The fossil record for australopithecines and for *Homo* is indicated by solid lines. (Reprinted from Falk, 1991)

figure 2, this question may be divided into three parts: (1) What modifications occurred in the direct ancestors of *Homo* that facilitated or permitted the initial take-off in brain size? (2) Once brain size began to increase, how was the continued increase in brain size sustained, i.e., what behavior(s) were “targeted” by natural selection? (3) How did the external and internal organization of the human brain change as it enlarged and what were the cognitive correlates of these neurological changes?

Paleoanthropologists use two methods to address these questions. The “direct method” relies on examination of fossil hominids for information about the external morphology of the convolutions and blood vessels of the brain (as reflected on casts of the interior of the braincase, or endocranial casts), and for estimates of brain size (which is approximated by cranial capacity). These features may then be interpreted in light of information determined from other parts of

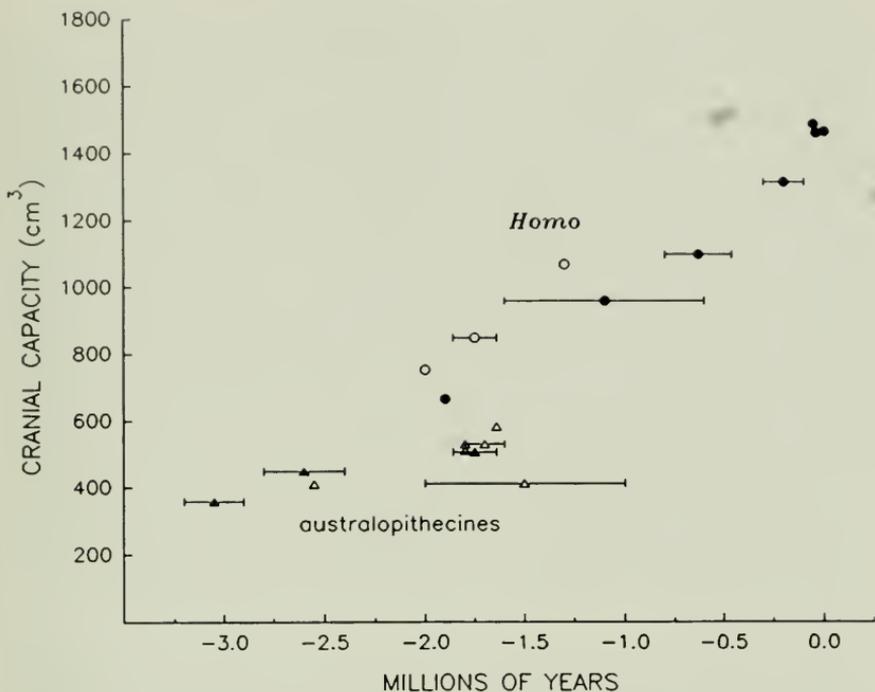


Fig. 2. Cranial capacities of hominids plotted against time. Triangles represent australopithecines, circles *Homo*. Filled symbols indicate more than one individual in the sample. Cranial capacity increased markedly in *Homo* but not in australopithecines. (Reprinted from Falk, 1991)

the skeleton (e.g., body size, dietary preferences), as well as the archaeological record that pertains to culture, climate, and habitat. The “comparative method,” on the other hand, is based on studies of the brains and cognition in monkeys, apes, and humans, along with the assumption that these primates approximate an evolutionary sequence. Because they share a fairly recent CA with humans, chimpanzees are especially important in comparative studies. Although the fossil record provides broad outlines that may be used to describe hominid brain evolution, the finer details must be filled in by synthesizing information from comparative psychology and comparative neuroanatomy/neurophysiology. Using these methods, each of the three questions outlined above will be discussed in this lecture (with particular attention to the third).

I. WHAT FACILITATED THE INITIAL TAKE-OFF IN BRAIN SIZE?

Discovery of the Laetoli footprints has caused paleoanthropologists to abandon the belief that bipedalism was intimately linked to an increase in brain size in early hominids. The feet went first. But why? As is frequently the case in evolutionary studies, a clue to this mystery may be found by examining the environment of the particular group of australopithecines that gave rise to *Homo*. These early hominids (known as gracile australopithecines) are believed to have spent their days roaming across open savanna grasslands in search of widely dispersed food, water, and trees. A number of workers have speculated that australopithecines were probably subject to intense solar radiation as they went about their business in the tropical savanna habitat (Wheeler, 1988). This is significant for hominid brain evolution because brains are exquisitely heat sensitive. In fact, according to one noted vascular physiologist:

A rise of only four or five degrees C above normal begins to disturb brain functions. For example, high fevers in children are sometimes accompanied by convulsions; these are manifestations of the abnormal functioning of the nerve cells of the overheated brain. Indeed, *it may be that the temperature of the brain is the single most important factor limiting the survival of man and other animals in hot environments* (Baker, 1979: 136, emphasis added).

For various reasons, I have hypothesized that selection for specific vascular features that controlled brain temperature released a physiological constraint on brain size, which then became a focus of natural selection in *Homo* (Falk, 1990).

The Radiator Theory

If a species evolves a new form of locomotion or habitual body posture, its circulatory system will be modified because of changed gravitational (or hydrostatic) forces associated with the new mode of life. Hydrostatic pressures may be envisioned by imagining a long tube half-filled with water. If the tube is horizontal, the water (and associated gravitational stress) is distributed along its entire length. However, if the tube is tilted to the vertical, all of the water is in its bottom half and that part of the vessel takes the stress from the

weight of the fluid. Natural selection favors vascular systems that are designed to cope with hydrostatic stresses. For example, arboreal snakes have evolved special mechanisms for pumping blood through vertically oriented vessels, as opposed to the situation in their horizontally inclined relatives (Lillywhite, 1987a, 1987b).

For physiological reasons, the circulatory systems of early hominids *had* to become modified during the evolution of bipedalism. Indeed, evidence of those modifications appears in modern humans. Because people sleep horizontally but move about in the world vertically, they have complex vascular systems that are designed to cope with hydrostatic pressures in a variety of postures by shifting the flow of blood with changing body position. Thus, if a person is lying down, blood flows out of the skull through the internal jugular veins. When the individual stands up, however, most of the exiting cranial blood shifts away from the jugulars and into a network of veins that surrounds the spinal cord. (Monkeys and apes have vascular systems that are tailored somewhat differently to their own forms of locomotion.)

Fortunately for paleoanthropology, certain details of the cranial vascular system appear in skulls of fossil hominids. These features include grooves that represent venous sinuses and meningeal vessels, as well as emissary foramina through which emissary veins penetrate the skull. Taken together, these features show that the cranial vascular systems of different groups of early hominids were adapted in one of two different ways as each group refined bipedalism in its own particular environment. On the one hand, the hominids from Ethiopia that are associated with the famous “Lucy” skeleton have an unusual venous sinus in the occipital region (the “occipital/marginal” sinus) that they share with later living australopithecines who were probably their descendants (Falk and Conroy, 1983). These australopithecines (known as robust australopithecines) ultimately became extinct without giving rise to more modern hominids. On the other hand, data regarding the emissary veins suggest that a different cranial vascular system developed in the gracile australopithecines who lived in thermally stressful habitats and eventually gave rise to *Homo*.

Innumerable tiny veins penetrate the outside of the human skull

and communicate with the diploic veins that are found within the bones of the skull itself. The diploic veins, in turn, penetrate the inside surface of the skull bones, where they communicate with meningeal veins that course on the surface of the dura mater that covers the brain. Thus, the human skull is covered on its outside and inside surfaces with a complex web of communicating veins that happen to lack valves. Significantly, several named emissary veins that are part of this network penetrate through specific foramina of the skull. Consequently, the presence of emissary veins can be surmised from fossil crania. Comparative data from skulls of living apes and humans (Boyd, 1930) and direct data determined from the hominid fossil record (Falk, 1986) reveal that frequencies of the mastoid and parietal emissary foramina increased dramatically in the lineage leading from gracile australopithecines to extant *Homo*, but not in the other early hominids (fig. 3). Moreover, the frequencies of these emissary veins seem to have increased in step with increasing cranial capacity (Falk, 1990). If emissary veins are viewed as a "window" into the wider network of cranial veins, these data suggest that cranial vasculature became increasingly complex as evolution progressed and brain size increased in *Homo*. What function could this network of veins have served?

The answer to this question is provided by physiological research that compared the direction of blood flow in emissary veins of human volunteers who were subjected to severe cold stress at one time, and heat stress at another (Cabanac and Brinnel, 1985). Cabanac and Brinnel found that under conditions of hyperthermia, cranial blood that had been cooled by the actions of sweating and evaporation at the scalp was brought from the outside surface of the skull *into* the brain case. (In cold subjects, on the other hand, blood flow was slow and flowed out from the cranium.) The researchers concluded that the entire network of cranial veins which the emissary veins represent functions to selectively cool the brain under conditions of severe heat stress. Thus, like the engine of a car, the human brain has a radiator that prevents overheating.

To summarize the radiator theory, evolution of a prototype network of cranial veins in gracile australopithecines released a thermal constraint that had previously kept brain size in check. This facil-

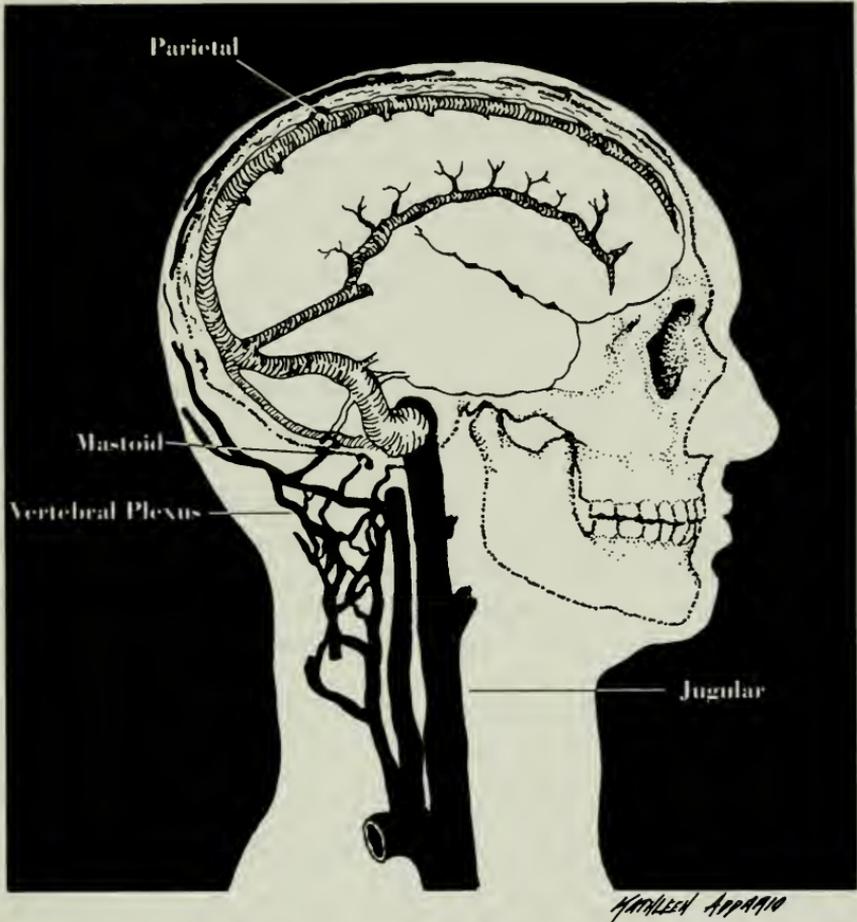


Fig. 3. The mastoid and parietal emissary foramina and the vertebral plexus of veins that receives cranial blood when people are upright. The emissary veins are part of a wider network of cranial veins that communicate between the outside and inside of the skull. This network helps cool the brain under conditions of hyperthermia, and also drains blood to the vertebral plexus. (Reprinted from Falk, 1992)

itated the take-off in brain size in *Homo*. Bipedalism in gracile australopithecines preceded the increase in brain size in *Homo* for two reasons. First, because of the constraints of gravity, bipedalism necessitated a rearrangement in cranial blood vessels. (Since this was also true for robust australopithecines, it was a necessary but not sufficient condition for the subsequent evolution in brain size.) Second, bipedalism allowed gracile australopithecines to minimize the

amount of body surface exposed to the sun, thereby reducing their heat loads and making it easier to adapt to thermally stressful savanna habitats (Wheeler, 1988). Thus, the vasculature of gracile australopithecines became modified in response to gravitational *and* thermal pressures that were associated with refinement of bipedalism on the savanna. One result was the beginning of a cranial radiator network of veins that could help cool the brain under conditions of intense exercise. More important, once in place, this system was itself modifiable and could therefore keep up with the increasing thermolytic needs of an enlarging brain.

The radiator theory is mechanistic. The dramatic increase in brain size in *Homo* is viewed as having simply been *facilitated* by the release of thermal constraints that previously kept brain size in check. Thus, the radiator network of veins is seen as a prime releaser, not a prime mover of brain evolution. One must turn to other theories for speculation about the behaviors that were selected for once the brain had acquired an adjustable radiator and *could* get bigger.

II. WHAT BEHAVIORS WERE TARGETED BY NATURAL SELECTION?

Brain size doubled during the past 2 million years in the genus *Homo*, increasing from an average of approximately 700 cm³ to a modern mean of about 1400 cm³ (fig. 2). Although body size (or stature) also enlarged during this time, it did not keep up with the increase in brain size. Consequently, the brain of humans is three times as large as is mathematically expected for an ape of equivalent body size (Passingham, 1975; Falk, 1980b). What factors were responsible for the sustained increase in brain size? Since at least Darwin's time, scientists have attempted to answer this question by identifying specific behaviors that were the primary target of natural selection. Some workers have gone so far as to suggest that a single behavior was responsible for human brain evolution. Classic "prime mover" candidates include warfare, language, tool production, and hunting. These are discussed elsewhere (Falk, 1980b). Two new candidates may now be added to this list—throwing (Calvin, 1982) and social (or Machiavellian) intelligence (Byrne and Whiten, 1987).

According to Calvin's (1982) throwing hypothesis, one of the earliest lateralizations that occurred in the hominid brain was for rapid motor sequencing of the right hand and arm (represented in the left frontal lobe). Calvin believes that the cause of this lateralization was natural selection for right-handed throwing of stones at prey. He further suggests that neural machinery for throwing may also have been used for the oral-facial musculature (which is represented near the hand in the brain) and that, if so, this sequencing machinery provided the scaffolding for the subsequent development of another left hemisphere product, human language. Although the throwing hypothesis is consistent with some research concerning neurophysiology of the motor cortex (Ojemann, 1983), the assertion that skilled throwing *preceded* the evolution of language remains interesting but speculative.

Because nonhuman primates are extremely complex in their social relationships, primatologists have recently focused attention on social intelligence as a possible prime mover of brain evolution. For example, Byrne and Whiten (1987) hypothesize that selection occurred for "Machiavellian intelligence" in which individuals relentlessly selected for still more cleverness (including deceptive behavior) in their companions. Other workers extend this concept by suggesting that humans evolved as a result of a process of "runaway social competition" between competing groups (Alexander, 1989). This latter form of "intelligence" shades into another prime mover candidate, namely warfare. A problem with social intelligence as a prime mover of hominid brain evolution is the fact that many species of nonhuman primates are extremely clever in their social interactions, yet without benefit of the extremely encephalized brain that characterizes humans.

As discussed elsewhere (Falk, 1980b), although entertaining, the search for prime movers of human brain evolution is highly speculative and does not lend itself well to hypothesis testing. Furthermore, whether or not it is reasonable to attribute all of hominid brain evolution to selection for only one behavior is debatable. As described below, the human brain underwent a remarkable reorganization as it enlarged. One would suppose that if selection of one behavior was primarily responsible for brain evolution in *Homo*,

that behavior would be tied functionally to the neurological reorganization that occurred. It should also clearly distinguish all people from other primates. These issues will be returned to later.

III. NEUROLOGICAL REORGANIZATION AND ITS COGNITIVE CORRELATES

Under some circumstances, details of the cerebral cortex, blood vessels, venous sinuses, and sutures are reproduced on casts of the interior of the braincase (endocranial casts or endocasts). Endocasts may occur naturally when fine sediment consolidates inside a skull or can be prepared artificially with latex. One limitation of endocasts is that the relatively largest-brained species within various groups of mammals, including primates, fail to reproduce clear details of the pattern of convolutions on endocasts (Radinsky, 1972). Thus, endocasts from skulls of *Homo sapiens* reveal little information about the surface of the brain, whereas small-brained australopithecines are associated with a fossil record of nicely detailed natural endocasts.

A second limitation of endocasts is that they fail to reproduce all areas of the cerebral cortex equally well. For example, early hominid endocasts usually do not reveal many details from the occipital region of the brain, while the frontal lobe is reproduced in much better detail. Interpretation of the external morphology of australopithecine occipital cortices has been subject to a good deal of controversy, partly because of this limitation. Ralph Holloway believes that the outside surface of australopithecine occipital lobes appears humanlike in certain respects, whereas my comparison of chimpanzee, gorilla, and human brains led me to conclude that australopithecine sulcal patterns are apelike in the occipital and all other regions of the brain (Falk, 1980a; Radinsky, 1979). During the past decade, a good deal has been published on this controversy, and details are available elsewhere (Falk, 1992).

One is on firmer ground with the frontal lobe, not only because it happens to show up better on endocasts, but because it is the one area of the brain in which sulcal patterns clearly distinguish human brains from ape brains (Connolly, 1950). In the frontal lobes of great

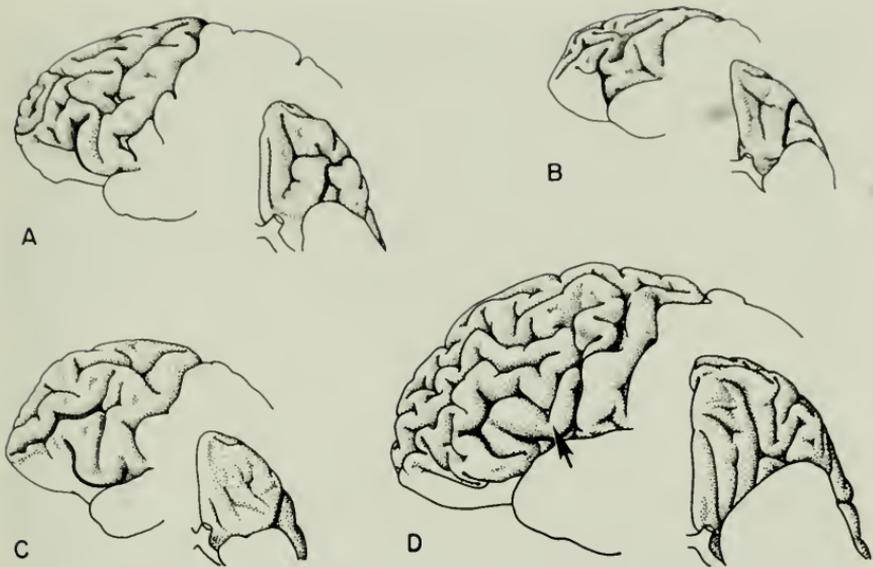


Fig. 4. Left frontal lobes (lateral view above, rotated to basal view below): (A) chimpanzee, (B) orangutan, (C) gorilla, and (D) human. Orbitofrontal sulci are darkened in the ape brains. Sulci darkened in the human brain include the inferior frontal and those limiting the pars triangularis (arrow) associated with Broca's speech area. (Reprinted from Falk, 1983)

apes (fig. 4A–C), an orbitofrontal sulcus (darkened in the illustration) incises the lateral border and continues to course back toward the temporal lobes on the underneath surface. This sulcus is not visible on human brains, however, because it has been displaced deep within the Sylvian fissure by the expanded convolutions of the frontal lobe. Instead, human frontal lobes are usually characterized by two small sulci that delimit a triangular patch of gray matter (arrow in fig. 4D) that forms part of Broca's speech area in the left hemisphere. (As discussed below, although this pattern is generally similar on the right and left sides, the functions of the two hemispheres differ—i.e., the human brain is lateralized.) In keeping with its expanded size and reorganized sulcal pattern, the human brain also has frontal lobes that appear squared in front (from a dorsal view) as compared to ape brains (Falk, 1983).

The earliest indication of a humanlike frontal lobe in the known hominid fossil record occurs in KNM ER 1470, a *Homo habilis*



Fig. 5. Endocranium of left frontal lobe of KNM ER 1470, a *Homo habilis* specimen that is a little less than 2 million years old. Dots are reconstructed portion of frontal lobe, hatching represents damaged area. *fi*, inferior frontal sulcus; arrows indicate sulci that may delimit an area that is homologous with the pars triangularis of human brains. (Reprinted from Falk, 1983)

specimen from Kenya that is almost 2 million years old (fig. 5). Although brain size in this specimen was only about 750 cm³ (Holloway, 1978), its endocranium reproduces the sulcal pattern in the left frontal lobe that is associated with Broca's speech area in living people. This suggests that *Homo habilis* may have been capable of rudimentary speech (Tobias, 1981; Falk, 1983). Corroborative evidence that the frontal lobe was already lateralized in early *Homo* has been provided by an archaeological analysis of stone flakes, which indicates that knappers may already have been right-handed by 2 million years ago (Toth, 1985). (Recall that the speech organs and the right hand are represented by adjacent areas in the left frontal lobe.)

As noted above, the australopithecine endocraniums appear apelike in the sulcal patterns of their frontal lobes. They also lack the squared shape of the frontal lobe that can be seen in the earliest representatives of *Homo*, including ER 1470. Furthermore, these differences between australopithecines and *Homo* are not merely due to scaling (allometric) factors whereby enlarged brains have more sulci than smaller brains. (For discussion of allometry, see Jerison, 1991.) In



Fig. 6. Right hemispheres of a juvenile chimpanzee brain (top), the Taung endocast (left), and a human newborn (right). In all major respects, the Taung endocast appears apelike, not humanlike. (Reprinted from Falk et al., 1989)

order to control for allometry, sulci from the frontal and temporal lobes of the right hemisphere of the Taung australopithecine endocast were precisely measured and compared to corresponding sulci in the brains of a juvenile chimpanzee and a human newborn whose cranial capacity was close to the size of Taung's (Falk et al., 1989). (See fig. 6.) Once size differences had been taken into account, the ratio of the summed frontal lobe sulci of Taung relative to that for the human baby brain was markedly impoverished—even compared to the chimpanzee brain! Since this was not the case for the temporal lobe, it appears that *frontal lobe expansion was particularly dramatic during the subsequent evolution of Homo*.

Other evidence points to the frontal lobes (or the behaviors that depend upon them) as a particular focus for natural selection during the evolution of *Homo*. Using a new gyrification index (GI) that measures the degree of convolutedness in any given location of the brain, Armstrong and her colleagues compared the extent of folding in the various lobes of monkeys, apes, and humans (Armstrong et

al., 1991). They found that whereas the GIs of apes and humans completely overlap in the occipital region, the human brain is much more convoluted in the frontal lobes than are ape brains. The findings for the occipital region suggest that changes in sulcal pattern occurred only when brain size increased and that the occipital cortex in the Taung endocast was therefore probably apelike. Having studied the entire surface of the brain, the authors concluded (on p. 347): “that the proximal cause or mechanisms by which the hominid brain increased in size are more likely to have been either a response to changes in the frontal lobes or to events that influenced all regions of the brain.”

Besides language (which will be discussed below), what behaviors were elaborated with the continued expansion of the frontal lobes during the evolution of *Homo*? Although any answer to this question will necessarily be speculative, it is informative to consider frontal lobe functions that occur in monkeys (and presumably apes) and note their elaborations in humans. Because medical research has focused extensively on macaques, the circuitry in the prefrontal cortex and its regulation of behavior are fairly well understood for these monkeys. A major function of macaque prefrontal cortex is to assess memories (symbolic representations related to visuospatial information, emotions, etc.), keep them “on line,” and use them to guide motor behavior in the absence of external stimuli (Goldman-Rakic, 1987). According to Goldman-Rakic (p. 406), “many integrated higher-order functions including language, concept formation, and planning for the future may be built on this functional element.” In keeping with this, it is well known (from the old days of lobotomies) that damage to the human prefrontal cortex frequently causes disturbances of attention, an inability to use past experience to grasp the essence of a situation, and a loss of the ability to plan ahead. A “flattening” of personality and inappropriate social behaviors may also result from prefrontal damage.

The archaeological record provides glimpses that suggest frontal lobe abilities may have increased along with increasing brain size in the genus *Homo* (at least up to the relatively recent time of Neanderthals). Preparation of even simple stone tools (associated with early *Homo*) takes some ability to keep a task in mind and execute

a plan. Apparently, abilities pertaining to the manufacture of stone tools continued to evolve so that, by 300,000 years ago, *Homo erectus* was demonstrating relatively sophisticated notions of perspective, control of spatial quantity, and an understanding of composition (Wynn, 1989). Although the human propensity for worrying about the future is difficult to gauge from the archaeological record, most anthropologists would probably agree that the first deliberate burials (attributed to Neanderthals) indicate an upper boundary for the appearance of an acute consciousness of time.

Brain Lateralization

Turning our attention to brain lateralization, its evolution may be investigated by comparing shapes of lobes (petalia patterns) in the brains of nonhuman primates and people. Analyses of CAT scans and radiographs reveal that right-handed people tend to have right frontal lobes that project farther and are wider than the left frontal lobes (i.e., a right frontal petalia), whereas their left occipital lobes are usually wider and protrude more (LeMay, 1976; Galaburda et al., 1978). (The reverse condition of left frontal and right occipital petalias is more likely to be found in left-handers.) Petalias give both the brain and the overlying skull a characteristic lopsided appearance that can be detected on endocasts. These shape asymmetries occur in monkeys and apes, but not to the extent that they do in humans (LeMay et al., 1982). The human pattern of left-occipital-right-frontal petalias appears early in *Homo* and, in keeping with the comparative findings, may have been foreshadowed in australopithecines (Holloway and de Lacoste-Lareymondie, 1982).

Not too long ago, it was thought that humans were unique among primates in manifesting asymmetries in lengths and configurations of certain cortical features, e.g., having a longer left Sylvian fissure and larger left planum temporale. Largely because of recent advances in medical imaging, the alternative idea that cortical asymmetries of humans are end products of a long evolutionary history is now supported by comparative evidence regarding sulcal lengths and areas of cortex delimited by sulci. Thus, rhesus monkeys exhibit numerous asymmetries in their frontal lobes including right frontal

petalias (Falk et al., 1990). These asymmetries, which may involve short-term memory for visual information, correlate with functional lateralization for certain vocal and visual processing in macaques. Analysis of a large sample of macaque endocasts revealed that both gross and detailed morphology of the brain are heritable (Cheverud et al., 1990), a finding that is consistent with a hypothetical genetic component for cortical lateralization.

A greater number of cortical asymmetries have been discovered in humans (Falk et al., 1991) than in monkeys or apes, not just in frontal lobes, but throughout the brain. Taken together, the evidence from endocasts of fossil hominids and the comparative data regarding the external morphology of the cerebral cortex suggest that *brain lateralization became more elaborate as brain size increased in Homo*. What were the cognitive correlates of an increasingly lateralized brain during the evolution of *Homo*? One way to approach this question, is first to observe the functional aspects of brain lateralization in people, and then to compare the cognitive abilities of humans with those of their closest nonhuman cousin, the chimpanzee.

The literature on functional brain lateralization in humans is multifaceted and sometimes difficult to interpret because differences between hemispheres are often subtle but statistically significant (Falk, 1987a, 1992). Upon close inspection, however, contradictory data obtained by separate studies may frequently be attributed to slightly different methodologies or to differences in the populations that were tested. For example, the musically sophisticated and left-handers do not test like the general population on certain measures of brain lateralization. Nevertheless, as a result of various kinds of tests (e.g., dichotic listening, tachistoscopic viewing, etc.) performed on enormous numbers of normal and clinical populations, certain generalizations may be made about the specializations of right and left hemispheres (fig. 7).

As illustrated in figure 7, the left hemisphere is associated with language functions, skilled movements (e.g., like those engaged in by over 90% of right hands), and analytical, time-sequencing processes. This hemisphere is also involved in processing positive emotions. The right hemisphere, on the other hand, engages in holistic,

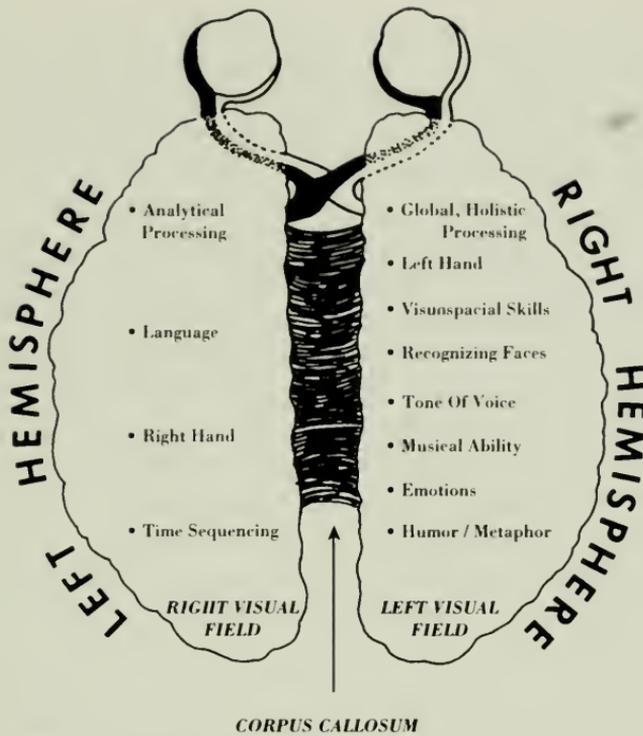


Fig. 7. General specializations of left and right hemispheres. Dorsal view of the brain, which is shown connected by the corpus callosum. (Reprinted from Falk, 1992)

global pursuits. Mental imaging, visuospatial skills, and musical abilities are also associated with the right hemisphere. The right hemisphere processes negative emotions and has a noticeably greater role than the left hemisphere in generally expressing emotions, as well as reading them in other people. In fact, although the left hemisphere processes language, it is the right hemisphere that provides tone of voice, an important and sometimes decisive aspect of verbal communication. The right hemisphere also seems to have an edge over the left in recognizing faces, in the ability to understand metaphor, and in certain aspects of humor. It is important to note, however, that the right and left hemispheres are, of course, connected in normal individuals. (Figure 7 is therefore an oversimplification, i.e., most tasks will have some input from both sides of the brain.)

There is an incredible amount of variation and complexity in the

patterns of asymmetries for various skills expressed by different individuals. Furthermore, males and females seem to be organized somewhat differently with respect to both functional and anatomical brain lateralization. Lateralized behaviors in humans have been hypothesized to be the result of asymmetrical distributions of neurochemicals, as has been shown for certain rodents and birds. Interestingly, it has also been suggested that different patterns of brain lateralization in humans may be the result of developmental events (such as prenatal exposure to testosterone) that differentially influence males and females (Geschwind and Galaburda, 1987). (For further discussion see Falk, 1992.)

One way to assess which behaviors “drove” hominid brain evolution is to compare the frontal lobe and asymmetrically mediated behaviors in chimpanzees and humans (including where the two categories overlap). What do the human and chimpanzee have in common? Beginning with the frontal lobe, both species can bring visuospatial memories on line and carry out related tasks. In fact, chimpanzees are every bit as good as humans at remembering the location of cached food and retrieving it at some later time. Unlike most animals, chimpanzees and humans both recognize themselves in mirrors, a feat that my colleague Gordon Gallup attributes to a frontal-lobe sense of “me” (Maser and Gallup, 1990). Furthermore, both species have fairly good motor skills, e.g., they can work puzzles that require manipulation of parts, and each expresses emotions through gestures that are controlled by frontal lobe motor cortex.

But the similarities stop here. According to Savage-Rumbaugh (Falk, 1992), chimpanzees cannot keep very many tasks in mind at once, the way that humans can. In terms of frontal lobe planning, chimpanzees do not have a humanlike awareness of death or a religion (Maser and Gallup, 1990). With respect to regulating behavior through accessing symbolic representations, chimpanzees are not very good at controlling emotional outbursts—a frontal lobe mediated activity in which almost all human children eventually become proficient. Although they can manipulate objects, chimpanzees as a population are not lateralized for handedness, unlike humans. Finally, the most dramatic (lateralized) frontal lobe differ-

ence between chimpanzees and humans is, of course, that chimpanzees lack the human capacity for speech.

There are other important cognitive attributes of humans (compared to chimpanzees) that depend on an overall lateralized brain (fig. 7). As noted elsewhere:

No chimpanzee ever wrote a book, composed a symphony, painted a realistic portrait, performed a *Singing in the Rain*-quality tap dance, calculated the day of the week upon which a certain date will fall next year, developed a math proof, took apart and reassembled a watch, programmed a computer, designed a bridge, or theorized about the origin of the universe (Falk, 1992: 58).

In short, these human arts and sciences spring from an enlarged lateralized brain that has numerous circuits subserving specialized functions. These circuits are sometimes referred to as modules (Fodor, 1983).

Can these modules be understood in terms of the specific *internal* reorganization that took place in the brain during the course of brain evolution in *Homo*? Since one cannot turn to endocasts for the answer to this question, investigation of brain growth during human development may be informative. Although humans are born with their full complement of neurons, profound changes occur in the nervous system postnatally (Gibson, 1991; Konner, 1991). As the human brain enlarges after birth, there is a proliferation of synapse formation, dendritic branching, and division of glial support cells that form the myelin sheaths around axons (thus giving the white matter its characteristic appearance). Myelination, which increases the speed and specificity of nerve transmission, occurs in specific sequences that appear to correlate with the development of motor, social, and intellectual skills (Gibson, 1991). For example, the appearance of social smiling and fear of strangers in infants is correlated with myelination of specific neurological structures during the first year of life, whereas cortical association areas subserving "higher" intellectual functions continue to myelinate up to the age of 30 years (Konner, 1991).

Comparative studies provide another important source of information regarding hominid brain evolution. Since larger mammalian brains have larger, more widely spaced neurons than do smaller

brains, this trend and other related scaling (allometric) factors probably occurred during brain enlargement in *Homo*. Thus, although the absolute number of neurons would have increased with brain size, their density would have decreased. There also should have been an increase in the overall fraction of the cortex devoted to axonal interconnections (i.e., cortical white matter), along with an increase in dendritic branching. Significantly (see below), the fraction of cells with which any one cell communicates directly (“percent connectedness”) would have decreased as brain size increased in *Homo* (Ringo, 1991).

Based on these comparative data, Ringo (1991) has developed an eloquent model that accounts for a general trend toward cortical specialization within larger-brained mammals. As brain size (and therefore neuron number) increases in the various species, each neuron must be connected to a decreased *fraction* of the total number of neurons. Otherwise large brains would be “swamped” by geometrically increasing numbers of connections relative to their absolute number of neurons. (To use Ringo’s example, a 100% connected two-neuron system would have two connections whereas a 100% connected four-neuron system would have 12 connections, etc.) Because absolute connectivity nevertheless increases with enlarged brain size, the “interconnection problem” is resolved by decreased neuronal density, i.e., more volume is available per neuron in larger brains. Since long axons take more space than short axons in such a system, they are minimized, and specializations result. In Ringo’s words:

One interesting possibility is that this increasing load from interconnectedness is avoided by utilizing specialization so that only within major groupings of neurons need there be full interconnection, while between major groupings only ‘results’ need to be passed. This then suggests the argument that big brains need hemispheric specialization, because of interconnections getting out of hand, and further suggests that large hemispheres will be more specialized than small ones. This simply means that cortical areas will be more specialized. This tendency appears to follow across the best investigated species. . . . (Ringo, 1991: 5)

Comparative data from prosimians (*Galago*) and monkeys (*Macaca*) suggest that; in keeping with Ringo’s hypothesis, new areas were added to the cerebral cortex as brain size increased early in anthro-

roid evolution (Preuss and Goldman-Rakic, 1991). Interestingly, the addition of new areas occurred specifically in prefrontal cortex.

LANGUAGE: THE PRIME MOVER?

What behaviors were targeted by natural selection during the extraordinary neurological evolution of *Homo*? Converging evidence suggests that, during the past 2 million years, changes were especially dramatic in the prefrontal cortex and that, at the same time, overall brain lateralization increased. The prime mover candidate that clearly spans both of these themes is language, which is also the one candidate that clearly separates *all* people from apes. Ringo's (1991) hypothesis, on the other hand, suggests that various concomitant specializations (modules) that are associated with lateralized brains may have been the focus of natural selection. Ringo, however, notes that his theory is general and that it does not preclude specific adaptations for individual species. Thus, any one of numerous specializations that occurred in the enlarging hemispheres could have been selected for during the course of hominid evolution. If selection were strong enough, the end result would have been to fix the target cortical specialization (and its related behaviors) in all members of the population, while retaining a variety of other specializations that are distributed across the cerebral cortex and manifested in varying degrees in different individuals. Since all people talk (but not everyone is musical or mechanically inclined), the frontal lobe's role in accessing symbolic representations, holding them on line, and using them to guide motor output in the absence of external stimuli may have been elaborated during hominid evolution by selection for language-related behaviors. Indeed, the notion of language as a focus for natural selection together with the mechanism outlined by Ringo forms a compelling model that is consistent with much of the evidence outlined in this lecture.

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REFERENCES

- Alexander, R. D.
1989. Evolution of the human psyche. In P. Mellars, and C. Stringer (eds.), *The human revolution*, pp. 455-513. Princeton: Princeton Univ. Press.
- Armstrong, E., K. Zilles, M. Curtis, and A. Schleicher
1991. Cortical folding, the lunate sulcus and the evolution of the human brain. *J. Human Evol.* 20: 341-348.
- Baker, M. A.
1979. A brain-cooling system in mammals. *Sci. Am.* 240: 130-139.
- Boyd, G. I.
1930. The emissary foramina in the cranium of man and the anthropoids. *J. Anat.* 65: 108-121.
- Byrne, R. W., and A. Whiten
1987. *Machiavellian intelligence*. Oxford: Oxford Univ. Press.
- Cabanac, M., and H. Brinell
1985. Blood flow in the emissary veins of the human head during hyperthermia. *European J. Appl. Physiol.* 54: 172-176.
- Calvin, W. H.
1982. Did throwing stones shape hominid brain evolution? *Ethol. Sociobiol.* 3: 115-124.
- Cheverud, J. M., D. Falk, M. Vannier, L. Konigsberg, R. C. Helmkamp, and C. Hildebolt
1990. Heritability of brain size and surface features in rhesus macaques (*Macaca mulatta*). *J. Hered.* 81: 51-57.
- Connolly, C. J.
1950. *External morphology of the primate brain*. Springfield, Ill: C. C. Thomas.
- Falk, D.
1980a. A reanalysis of the South African natural endocasts. *Am. J. Phys. Anthropol.* 53: 525-539.
1980b. Hominid brain evolution: the approach from paleoneurology. *Yearb. Phys. Anthropol.* 23: 93-107.
1983. Cerebral cortices of East African early hominids. *Science* 221: 1072-1074.
1986. Evolution of cranial blood drainage in hominids: enlarged occipital/marginal sinuses and emissary foramina. *Am. J. Phys. Anthropol.* 70: 311-324.
1987a. Brain lateralization in primates and its evolution in hominids. *Yearb. Phys. Anthropol.* 30: 107-125.
1987b. Hominid paleoneurology. *Ann. Rev. Anthropol.* 16: 13-30.
1990. Brain evolution in *Homo*: the "radiator" theory. *Behav. Brain Sci.* 13: 333-381.
1991. 3.5 Million years of hominid brain evolution. *Semin. Neurosci.* 3: 409-416.
1992. *Braindance: new discoveries about human origins and brain evolution*. New York: Henry Holt.

- Falk, D., and G. Conroy
 1983. The cranial venous sinus system in *Australopithecus afarensis*. *Nature* 306: 779-781.
- Falk, D., C. Hildebolt, J. Cheverud, L. A. P. Kohn, G. Figiel, and M. Vannier
 1991. Human cortical asymmetries determined with 3D MR technology. *J. Neurosci. Methods* 39: 185-191.
- Falk, D., C. Hildebolt, J. Cheverud, M. Vannier, R. C. Helmkamp, and L. Konigsberg
 1990. Cortical asymmetries in frontal lobes of rhesus monkeys (*Macaca mulatta*). *Brain Res.* 512: 40-45.
- Falk, D., C. Hildebolt, and M. W. Vannier
 1989. Reassessment of the Taung early hominid from a neurological perspective. *J. Human Evol.* 18: 485-492.
- Fodor, J. A.
 1983. The modularity of mind. Cambridge, MA: MIT Press.
- Galaburda, A. M., M. LeMay, T. L. Kemper, and N. Geschwind
 1978. Right-left asymmetries in the brain. *Science* 199: 852-856.
- Geschwind, N., and A. M. Galaburda
 1987. Cerebral lateralization: biological mechanisms, associations, and pathology. Cambridge, MA: MIT Press.
- Gibson, K. R.
 1991. Myelination and behavioral development: a comparative perspective on questions of neoteny, altriciality and intelligence. In K. R. Gibson and A. C. Petersen (eds.), *Brain maturation and cognitive development*, pp. 29-63. New York: Aldine de Gruyter.
- Goldman-Rakic, P. S.
 1987. Circuitry of primate prefrontal cortex and regulation of behavior by representational memory. In V. B. Mountcastle, F. Plum, and S. R. Geiger (eds.), *Handbook of physiology, the nervous system V*, pp. 373-417. Bethesda: American Physiological Society.
- Holloway, R. L.
 1978. Problems of brain endocast interpretation and African hominid evolution. In C. Jolly (ed.), *Early hominids in Africa*, pp. 379-401. New York: St. Martins Press.
- Holloway, R. L., and M. C. de LaCoste-Lareymondie
 1982. Brain endocast asymmetry in pongids and hominids: some preliminary findings on the paleontology of cerebral dominance. *Am. J. Phys. Anthropol.* 58: 108-110.
- Jerison, H. J.
 1991. Brain size and the evolution of mind. The James Arthur Lecture. New York: American Museum of Natural History.
- Konner, M.
 1991. Universals of behavioral development in relation to brain myelination. In K. R. Gibson and A. C. Petersen (eds.), *Brain maturation and cognitive development*, pp. 181-223. New York: Aldine de Gruyter.
- Leakey, M. D., and R. L. Hay
 1979. Pliocene footprints in the Laetoli beds at Laetoli, northern Tanzania. *Nature* 278: 317-323.

- LeMay, M.
1976. Morphological cerebral asymmetries of modern man, fossil man, and non-human primates. *Ann. New York Acad. Sci.* 280: 349-360.
- LeMay, M., M. S. Billig, and N. Geschwind
1982. Asymmetries of the brains and skulls of nonhuman primates. *In* E. Armstrong and D. Falk (eds.), *Primate brain evolution: methods and concepts*, pp. 263-278. New York: Plenum Press.
- Lillywhite, H. B.
1987a. Circulatory adaptations of snakes to gravity. *Am. Zool.* 27: 81-95.
1987b. Snakes and pressure. *Nat. Hist., Nov.*, pp. 59-67.
- Maser, J. D., and G. Gallup
1990. Theism as a by-product of natural selection. *J. Religion* 70: 515-532.
- Ojemann, G. A.
1983. Brain organization for language from the perspective of electrical stimulation mapping. *Behav. Brain Sci.* 6: 189-230.
- Passingham, R. E.
1975. Changes in the size and organization of the brain in man and his ancestors. *Brain Behav. Evol.* 11: 73-90.
- Preuss, T. M., and P. S. Goldman-Rakic
1991. Myelo- and cytoarchitecture of the granular frontal cortex and surrounding regions in the strepsirrhine primate *Galago* and the anthropoid primate *Macaca*. *J. Comp. Neurol.* 310: 429-474.
- Radinsky, L. B.
1972. Endocasts and studies of primate brain evolution. *In* R. Tuttle (ed.), *The functional and evolutionary biology of primates*, pp. 175-184. Chicago: Aldine.
1979. The fossil record of primate brain evolution. *The James Arthur Lecture*. New York: American Museum of Natural History.
- Ringo, J. L.
1991. Neuronal interconnection as a function of brain size. *Brain, Behav. Evol.* 38: 1-6.
- Tobias, P. V.
1981. The emergence of man in Africa and beyond. *Philos. Trans. R. Soc. London B*, 292: 43-56.
- Toth, N.
1985. Archeological evidence for preferential right-handedness in the lower and middle Pleistocene, and its possible implications. *J. Hum. Evol.* 14: 607-614.
- Tuttle, R. H.
1985. Ape footprints and Laetoli impressions: a response to the SUNY claims. *In* P. V. Tobias (ed.), *Hominid evolution: past, present and future*, pp. 129-133. New York: Alan R. Liss.
- Wheeler, P.
1988. Stand tall and stay cool. *New Scientist* 12 (May): 62-65.
- Wynn, T.
1989. The evolution of spatial competence. Champaign-Urbana: Univ. Illinois Press.





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