

Human paleontological evidence relevant to language behavior

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Summary. The paleoneurological evidence for human language origins and other cognitive activities is tantalizing, but uncertain given the often incomplete, fragmented, and eroded cranial portions of our fossil ancestors. Nevertheless, both the Taung and A.L. 162-28 endocranial portions, attributed to the earliest-known hominids (i.e. *Australopithecus afarensis* and *affricanus*) evidence some cerebral organization beyond a typical pongid pattern, in that there appears to be a reduction in primary visual striate cortex, and thereby a relative increase in posterior and inferior parietal cortex. At 1.8–2.0 million years, there is clear fossil evidence for a *Homo* lineage showing a more modern and enlarged third inferior frontal convolution, expanded brain size (e.g., 750 ml), and strong cerebral asymmetries identical to those known for modern *Homo sapiens*. Additional evidence of sexual dimorphism in the modern human corpus callosum, in which the posterior splenial portion is larger in females, taken in conjunction with known clinical and psychological evidence relating to cognitive task specialization, suggests that this dimorphism represents a biological heritage from past selection pressures for a dichotomous but complementary social behavioral set of adaptations to favor a division of sexual labors compatible with nurturing offspring with delayed maturation, prolonged growth, and a longer period of postnatal neural plasticity.

Key words: Paleoneurology – Hominids – Cerebral asymmetries – Brain evolution.

It must be obvious that paleoneurology, or even the broader study of human origins, paleoanthropology, cannot prove when or how language behavior originated. It should also be apparent that it is pointless to discuss the “origin” of language; at most one can only offer reasonable speculations or hypotheses regarding “origins” and provide whatever corroborative evidence exists from the fossil record. None of the available scientific pursuits represented by paleoanthropology, paleoneurology, comparative primate behavior, or extant neurobiological science (e.g., comparative neuroanatomy), are developed enough to permit more than a few tentative, but tantalizing paradigms for our species’ speculations about its past.

It is the bias of this writer that the origins of human language behavior extend rather far back into the paleontological past, and were nascent, but growing, during Australopithecine times of roughly 2.5 to 3.5 million years ago. The form was undoubtedly primitive, but carried with it a limited set of sounds systematically used, and based on a well-known aspect of primate sociality, the ability, if indeed not penchant, for making vocal noise. Furthermore, it is my bias that language grew out of a social behavioral cognitive matrix which was basically cooperative rather than aggressive, and relied on a complementary social structural division of behavioral labors between the sexes. This was a necessary and adaptive evolutionary strategy to permit an extended period of infant dependency, extended times to reproductive maturity, a delayed maturation permitting greater brain growth and behavioral learning, all of which can be verified to varying degrees of empirical rigor through both primatology and the hominid fossil record. This bias has been published several times (Holloway 1966, 1967a, b, 1968, 1969a, b, 1970, 1973, 1975, 1976a, b, 1981a, 1983b, Holloway and de Lacoste-Lareymondie 1982), combining evidence from paleoneurology, the archaeological record of hominid behavior as seen in stone tools and their manufacture, and several gleanings from modern neurological sciences.

I have quite purposefully labeled the above thoughts as “biases”, for there does exist considerable controversy regarding the questions of (1) whether apes (chimpanzee) have the cognitive capacities for language behavior, and (2) whether human language is a recent invention, within the last 50,000 years. For a recent review of the history and experimentation with chimpanzees, the article by Rumbaugh et al. (1982) provides considerable evidence that apes do possess capacities for learning and using symbols, and as our evolutionary “cousins”, have developed such capacities rather close to our own. It nevertheless remains a fact that they do not “talk”, and there is very considerable reason to doubt that their repertoires of symbol-learning and stringing are anything more than a high level of associationism, as critically assessed by Terrace (1979), and Terrace et al. (1979). That they (chimps) do not naturalistically undergo the same neuro-ontogenetic maturation processes found in all small children of any human society, who “naturalistically” possess both the nuclei, fiber systems, and a unique genetic endowment for true language, seems self-evident. It is not that we have nothing to learn from trying to train apes to communicate

with symbol systems; it keeps many an ape, graduate student, and some professors very usefully occupied. Rather, it is the task of the paleoanthropologist to realize that *our* lineage developed both the capacities and competence to engage in vocal language, and its origins must be sought in human neuroanatomy and in whatever clues the total fossil record can provide regarding paleoneurology, cranial base anatomy, and the archaeological records of tools and their associations with fauna and activity sites.

Much attention has been drawn to the work of Lieberman et al. (1972) in which pharyngeal-laryngeal reconstructions have been attempted on the cranial basal structures of fossil hominids. The computer-simulation studies (Lieberman 1975) suggest that not even Neandertals could speak, as the spectrum of sounds possible was curtailed by their anatomy. (Who "told" the computer to "say" that?) No one doubts the importance of peripheral anatomical structures in producing a wide and complex range of sounds, but surely the central nervous system must have been a key element in the development of language capabilities. On the average, Neanderthal absolute brain sizes were larger than ours (e.g. Holloway 1981); Solecki (1971) has dramatically demonstrated that they buried some of their dead with flowers; their brain endocasts show modern human asymmetries (Holloway and de LaCoste-Lareymondie 1982; LeMay 1976), yet Lieberman (1975) can find no basis for their possessing language, and Marschack (1976) insists one must first have "art", i.e., drawn or inscribed representations before language is there (also Jaynes 1976). As I tried to point out in a previous article (Holloway 1976), paleoneurology will never decide the issue given the complexity of the cognitive phenomenon and the lack of cortical and subcortical details from endocasts. These latter objects, *residua* of once pulsating conscious brains can only offer corroborative evidence, not proof.

In this paper I will concentrate almost exclusively on the paleoneurological evidence as it is unfolding, and attempt to indicate some of the promises and pitfalls inherent in such studies. I would warn, however, that I do not see the paleoneurological evidence as anything but corroborative of the ideas suggested above; it certainly is not advanced enough to offer solid proofs of past evolutionary biological dynamics in human evolution. My argumentation will thus attempt to show that (1) absolute brain size, while undoubtedly important, cannot be used solely to decide issues of behavioral origins, including language; (2) there is growing evidence from paleoneurological studies that indicates some reorganizational changes as well as absolute size increase in hominids' brains; (3) patterns of cerebral asymmetry, and thereby cognitive functioning, did occur during hominid evolution; (4) the behavioral activities of hominids, i.e., toolmaking, and living, camp, and butchering sites, are crucial for understanding the evolution of human cognitive capacities; (5) studies of current, extant primate species (e.g., chimpanzee), while exceedingly worthwhile, interesting, and provocative, cannot offer evidence regarding human language behavior or its origins; (6) human brain sexual dimorphism should be more thoroughly studied to understand both biological heritage (not "fatalism" or "determinism"), and the complementary structure of cognition in nurturant behavior among females and males as a target for past evolutionary selection processes.

Paleoneurological evidence

The fossil evidence for human evolution deserves some introductory comments, since most of the readers of this article are not paleoanthropologists, but rather neurobiologists. Needless to say, the topic bristles with controversy, and the evidence is spotty, there being many hiatuses, incomplete specimens, very low sample sizes, unreliable absolute dating (particularly for the S. African specimens), taxonomic quandaries, and very much speculation.

Basically, two genera are recognized as representing the lineages most importantly linked with human evolution: *Australopithecus*, and *Homo*. Of the latter genus, we recognize but two or three species as an evolutionary sequence, beginning roughly 2 million years ago. These are: *Homo habilis*, *Homo erectus*, and *Homo sapiens*. These fossils are regarded as a lineage by most although the status of *Homo habilis* is controversial, being a more or less convenient link between the earlier (and earliest) genus of hominids known as *Australopithecus* and later, *Homo erectus*. *Australopithecus*, as a genus, appeared in Africa at least 3 or 4 million years ago, and at present, three species (or varieties) are recognized from the fossil record: *afarensis*, *africanus*, and *robustus*. The latter group of robust australopithecines is regarded by almost all anthropologists as an evolutionary dead-end, terminating at about 1.5 million years ago, and without being a part of the true *Homo* lineage. The fossil evidence for a robust group (perhaps subspecifically divided) would appear to be greater than 2 million years, and there are some paleontologists who regard the *A. afarensis* species as an ancestral candidate for both the robust and gracile groups of *Australopithecus*. Others regard the *A. afarensis* assemblage from both Hadar, Ethiopia and Laetoli, Tanzania (ca. 3–4 million years ago) as not one species, but two: one leading to further *Australopithecus* evolutionary differentiation, and one leading to the earliest and most primitive genus of *Homo*. Certainly, by 1.5 million years ago, there is clear evidence for *Homo erectus* which extends through time to roughly 300,000 to 500,000 years ago in Africa, Asia, and Europe, and from which more primitive forms of *Homo sapiens* (including Neandertals) later evolved.

A conservative consensual view is that from some late Miocene pongid (ape) precursor, about 8 to 12 million years ago, one group became bipedal, retaining small, ape-sized brains (ca. 400 ml), and evolved into *Australopithecus*. This genus probably underwent a "mini" adaptive radiation from which *A. afarensis* became a basal hominid species from which the gracile *A. africanus* form would evolve (ca. 3–4 million years ago), one group of them evolving into *Homo habilis* at roughly 2 million years ago, and another into *A. robustus*, *Zinjanthropus boisei*, "*Paranthropus*", etc. *Homo habilis*, known only from Olduvai Gorge, Tanzania, and possibly E. Lake Turkana, Kenya, is reckoned as being about 1.8 to 2.0 million years old, bipedal, but with an expanded brain size (i.e. about 700 ml), and fashioning crude, but definitely standardized forms of stone tools, and engaging in some form of hunting (as well as gathering) behavior. The KNM-ER 1470 specimen, demoted from a 2.9 to a 1.8 million-year age; is perhaps the leading candidate for this taxon. The problems of identification of species, and lineage relationships is compounded by the fact that the

earliest discoveries of *Australopithecus* occurred in S. Africa, where there are no volcanic tuff strata available for absolute dating techniques (e.g., K/A), whereas the more recently discovered fossils in E. Africa come from sediments yielding relatively accurate dates. (For differing accounts of these fossils, their discoveries, controversies, etc., the following references might be useful: Eldredge and Tattersall 1982; Johanson and Edey 1981; Leakey 1981; Wolpoff 1980.)

Until a few months ago, the hominid remains from the Hadar region of Ethiopia, assigned to a new species of *Australopithecus* (*afarensis*) (see Johanson et al. 1982 for the history of these discoveries), were dated at approximately 3.6 million years ago (m.y.). Newer dating, both by chemical (Brown et al. 1982) and faunal comparisons (Boaz et al. 1982), have reduced the probable age of these bipedal, small-brained hominids to a range of 2.9 to 3.2 m.y. This dating, if correct, places the *A. afarensis* taxon at a time roughly contemporaneous with the previously discovered species of *A. africanus*. Whether or not the two groups are truly separate at the species level is a topic of considerable debate (Tobias 1981; Olson 1981; White et al. 1981; Kimbel et al. 1982), and both newer discoveries and further morphometric analysis will be necessary to bring further light to the controversy. The re-dating and controversies aside, there are three specimens from the Hadar sites which, while fragmentary, do provide the possibility of learning something about their paleoneurological organization, although rather imperfectly. The celebrated "Lucy" find (Johanson et al. 1982), A.L. 288-1 is unfortunately so incomplete in its cranial aspect that not even a brain size can be calculated with any accuracy. Nor do the small fragments contain any visible neuroanatomical information which relates to matters of cerebral organization.

Three other specimens, however, are useful to various degrees, and will be discussed below.

The infant A.L. 333-305 endocast, prepared by this author (see Holloway 1978 and 1983b, c), provides a distorted basal region, showing considerable convolution detail of the inferior frontal, temporal, and cerebellar lobes. In terms of size, this specimen, when reconstructed, approximates 320 ml. As it is clearly an infant, we can reasonably expect an additional 20 to 25% growth to an adult size, suggesting that its adult value would approximate 400 ml. This is speculative, of course, but a reasonable estimate, nevertheless. Unfortunately, the entire dorsal surface is missing, thus convolutional patterns for occipital, parietal, superior and middle temporal, and dorsal frontal cortex are unavailable. Thus it is impossible to examine the parieto-occipital cortical area to discern any deviation from a common pongid pattern, shared by *Pan*, *Gorilla*, *Pongo*, and *Hylobates*, with regard to the position of a lunate sulcus (LS), interparietal sulcus (IP), and lateral calcarine sulcus (LC) (see Holloway 1983c). There is a strong indication, however, of a marginal accessory sinus, skirting the foramen magnum, which is found in robust (but not gracile) australopithecines (Tobias 1967; Holloway 1972, 1983b, c).

A.L. 333-45 adult

This is by far the most complete specimen, described by Kimbel et al. (1982). The posterior portion does provide an endocast which is relatively undistorted. Reconstruction,

by the addition of plasticene to simulate the frontal portion, provides an estimate of roughly 500 ml, a value close to a 485 ml volume based on a regression equation using bi-asterionic breadth (Holloway, unpublished). Unfortunately, the preservation of convolutional details is very poor, and one cannot define with any assurance either LS, IP, or LC landmarks. There is, however, a very slight *left* occipital petalia, but it would be frankly speculative to argue that this demonstrates any significant cortical asymmetry, as reported by Holloway and de Lacoste-Lareymondie (1982), for many of the hominid endocasts in contrast to pongid patterns of asymmetry. In addition, this specimen also shows a marginal accessory sinus system found in robust australopithecines.

A.L. 162-28 adult.

A preliminary report on this interesting posterior cranial fragment (Kimbel et al. 1982) is in press (Holloway 1983b, c). Here, despite a small adult size of approximately 400 ml, there are some remnants of cortical convolutional detail which is very intriguing, as it suggests a pattern more in accord with a human condition than that of a typical pongid (Fig. 1). If the groove "A" is correctly labeled as IP rather

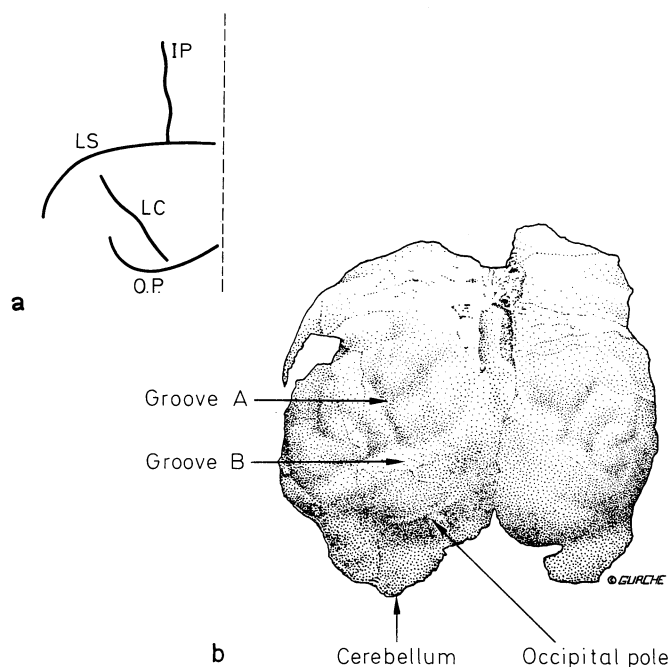


Fig. 1a and b. Schematic drawing of the usual pongid configuration of posterior and dorsal cerebral surface, showing the invariant relationships between the occipital pole (OP), lateral calcarine (LC), the lunate sulcus (LS) and the interparietal sulcus (IP). **b** Line-stipple drawing of the same view of the Hadar A.L. 162-28 endocast by John Gurche. Groove "A" could be either the LC or IP. Groove "B" is not a cerebral sulcus, but a depression caused by the inferior lip of the posterior portion of the parietal bone at the lambdoid suture, of which a remnant still exists on this endocast. If "A" were LC, there should be a strong curved sulcus just anterior to it, which would be the lunate (LS). There is no continuation of Groove "A" toward the occipital pole. Thus, Groove "A" is more probably interpreted as IP rather than LC, and thus the endocast suggests a non-pongid orientation, different from the typical pattern seen in 1 "a" (see Holloway 1983c for further details)

than LC, its posterior placement would corroborate a posterior location for the lunate sulcus, a clear demonstration of cortical organization in so far as the lateral extent of primary visual cortex (area 17) is concerned. A similar finding has been suggested for the Taung endocast (Dart 1925, 1956; LeGros Clark 1947; Schepers 1946; Holloway 1981d), but Falk (1980, 1983) is not in agreement with such a posterior placement of the LS. Thus, the controversy continues regarding cerebral organization in the earliest-known australopithecine hominids of roughly 3 m.y.

There is a very slight indication for a left occipital petalia, but the caution mentioned above for the A.L. 333-145 specimen applies to this specimen also. There is no trace of a lateral sinus leading to the sigmoid, but as the basal portion is missing, one cannot be certain that there was a marginal accessory system.

These endocranial values are similar to those described elsewhere for *Australopithecus africanus* (e.g., Holloway 1972, 1973, 1975, 1976b, 1983b), but less than the 530 ml average for known *Australopithecus robustus* specimens from both East and South Africa, which date from about 1.6 to 1.9 m.y.

Relative brain sizes cannot be accurately calculated for these hominids despite McHenry's (1982) contentions, and thus E.Q.'s, or "encephalization coefficients" cannot be reasonably ascertained, although Holloway and Post (1982) have made such efforts, believing E.Q.'s for these hominids to be advanced over *Pan* values, but certainly not as advanced as early *Homo*, whether *habilis* or *erectus*. "Lucy" was clearly smallish, but body-weight estimates for the whole Hadar sample range from roughly 75 to 150 pounds.¹

There are no stone tool sites associated with these finds, nor is there clear evidence for a dietary predilection based on animal protein, whether through scavenging or hunting. Primitive dental patterns (White et al. 1982) suggest a possible tongue-larynx-pharynx pattern more pongid than hominid.

In sum, these earliest specimens do not provide very strong support for tool-making, early language based on a human-like mode of symbol manipulation, particularly although both the Taung and A.L. 162-28 specimens suggest a cortical reorganization where posterior parietal cortex (both inferior and superior) were relatively large, associated with a diminution of lateral primary visual striate cortex. In so far as such a parietal expansion suggests an incipient enlargement of parietal "association" cortex, one can speculate that perhaps a modification of the so-called Wernicke's area had occurred by 3 m.y. This is totally speculative, of course, and a bias of this author (Holloway 1972, 1975, 1981a, b, 1981d, 1983b, c), but only that (cf. Falk 1980, 1983).

¹ The estimates of 75 to 150 lbs were originally provided by Dr. Lovejoy and Mr. Bill Kimbel. More recently, the estimates have been revised to 50 to 90 lb, which if correct, at least as "ball-park" figures, would raise the encephalization quotient's (EQ) to a level somewhat higher than the chimpanzee, thus suggesting an early but australopithecine hominid phase. Thus, with a body weight of 22.7 kg (50 lb) and a brain weight of 400 g, the EQ would be 4.49, or 65% of the modern human average. With a body weight of 40.8 kg (90 lb), and a brain weight of 500 g, the EQ would be 54.5% of the human value. The modern chimpanzee's EQ is about 40% of modern *Homo*. (See Holloway and Post 1982 for equations and calculations, and discussion on p. 72-73.)

The third inferior frontal convolution, containing in particular the *pars triangularis*, *pars orbitalis*, and *pars opercularis* regions, are not well enough defined on these early australopithecine endocasts to firmly corroborate a "Broca's area." Indeed, Falk (1980, 1983) believes quite the opposite, claiming they retain a primitive pongid pattern with regard to the fronto-orbital sulcus.

The quality of these endocasts simply precludes such definitive suggestions. To this author (Holloway 1981d, etc.), a true Broca's area does seem possible, but I fail to see how the issue can be objectively, empirically demonstrated.

The genus Homo

Pinpointing exactly when the genus *Homo* emerges is impossible. The famous KNM-ER 1470 cranium from East Lake Turkana, Kenya, was originally believed to have been 2.6 to 2.9 m.y., based on a K/A date for the KBS tuff, with the cranium coming from sediments lower in time. Through re-dating (Drake et al. 1980; White and Harris 1977), this specimen is regarded as being about 1.8 to 2.0 m.y. maximally.

Clear-cut evidence for true *Homo erectus* also can be found in Lake Turkana sites, i.e. KNM-ER 3733 and 3883, and these are dated to about 1.6 m.y. More problematic are smaller crania, KNM-ER 1813 and 1805, which appear to occur almost contemporaneously with the KNM-ER 1470 and the hyperrobust australopithecine, as represented by KNM-ER 406, 407, and 732. A quite fragmented, but thick-boned, large calotte exists, known as KNM-ER 1590, which is regarded as roughly contemporaneous with 1470.

From Olduvai Gorge, Tanzania, hominids attributable to both australopithecines, *Homo habilis*, and *Homo erectus* have been found, which date from about 1.4 to 1.85 m.y. Stone tools, including standardized shapes, exist from about 2.2 million years.

It must be emphasized that this melange of fossil specimens is the focus of much controversy regarding their taxonomic affinities. *Homo habilis* as a taxon is not universally accepted, and both Lake Turkana (Kenya) and Olduvai Gorge (Tanzania) specimens are sometimes considered as more advanced australopithecines (e.g., OH 24, OH 7, OH 16; KNM-ER 1805 and 1813). In addition, there are some fragments from both Sterkfontein and Swartkrans in South Africa that have been labeled as *Homo habilis*. These will be ignored in this paper, as there are no fragments large enough to provide reliable brain size estimates or neuroanatomical details of interest.

Almost without exception, the entire fossil hominid assemblage mentioned above from both Lake Turkana and Olduvai Gorge are fragmentary, and the internal table of cranial bone poorly preserved. Consequently, almost no convolutional detail is present, and this is particularly the case for posterior parietal and anterior occipital regions. Almost the only morphometric detail provided are the cranial capacities, as given in Table 1. In particular, OH 7, supposedly the *type* specimen for the *Homo habilis* taxon, is devoid of any convolutional relief, and controversy regarding its brain size is still current (Holloway 1980, 1983a cf. Wolpoff 1981). Thus, in what follows below, only certain highlights will be mentioned which are suggestive of morpho-

Table 1. Endocranial volumes of reconstructed hominid specimens

Specimen	Taxon	Region	Endocranial volume (ml)	Method ^a	Evaluation ^b
Taung	<i>A. africanus</i>	South Africa	440 ^c	A	1
STS 60	<i>A. africanus</i>	South Africa	428	A	1
STS 71	<i>A. africanus</i>	South Africa	428	C	2-3
STS 19/58	<i>A. africanus</i>	South Africa	436	B	2
STS 5	<i>A. africanus</i>	South Africa	485	A	1
MLD 37/38	<i>A. africanus</i>	South Africa	435	D	1
MLD 1	?	South Africa	500 + 20	B	3
SK 1585	<i>A. robustus</i>	South Africa	530	A	1
OH 5	<i>A. robustus</i>	East Africa	530	A	1
OH 7	<i>H. habilis</i>	East Africa	687	B	2
OH 13	<i>H. habilis</i>	East Africa	650	C	2
OH 24	<i>H. habilis</i>	East Africa	590 ^d	A	2-3
OH 9	<i>H. erectus</i>	East Africa	1067	A	1
OH 12	<i>H. erectus</i> (?)	East Africa	727	C	2-3
ER 406	<i>A. robustus</i>	East Africa	510 + 10	D	2
ER 407	<i>A. robustus</i>	East Africa	510 ^e	B	2-3
ER 732	<i>A. robustus</i>	East Africa	500	A	1
ER 1470	<i>H. sp. ?</i>	East Africa	752	A	1
ER 1805	<i>A. sp. ?</i>	East Africa	582	A	1
ER 1813	<i>A. sp. ?</i>	East Africa	510	A	1
ER 3733	<i>H. erectus</i>	East Africa	848 ^f	A	1
ER 3883	<i>H. erectus</i>	East Africa	84 ^f	A	1
OMO 338	<i>A. sp. ?</i>	East Africa	427	C	1-2
HE 1	<i>H. erectus</i>	Indonesia	953 ^f	A	1
HE 2	<i>H. erectus</i>	Indonesia	815 ^f	A	1
HE 4	<i>H. erectus</i>	Indonesia	900 ^f	C	2-3
HE 6 (1963)	<i>H. erectus</i>	Indonesia	855 ^f	A	2
HE 7 (1965)	<i>H. erectus</i>	Indonesia	1059 ^f	C	1-2
HE 8 (1969)	<i>H. erectus</i>	Indonesia	1004 ^f	A	1
Salé	<i>H. erectus</i>	Morocco	880	A	1
Solo I	<i>H. erectus</i> (Soloensis)	Indonesia	1172	A	1
Solo V	<i>H. erectus</i> (Soloensis)	Indonesia	1250	A	1
Solo VI	<i>H. erectus</i> (Soloensis)	Indonesia	1013	A	1
Solo X	<i>H. erectus</i> (Soloensis)	Indonesia	1231	A	1
Solo XI	<i>H. erectus</i> (Soloensis)	Indonesia	1090	A	1
Spy I	<i>H. sapiens</i> (Nean)	Europe	1553	A	1
Spy II	<i>H. sapiens</i> (Nean)	Europe	1305	A	1
Djebel Ihroud I	<i>H. sapiens</i> (Nean)	Morocco	1305	A	1
A.L. 333-45	<i>A. afarensis</i>	Ethiopia	485-500 ^f	C	2
A.L. 162-28	<i>A. afarensis</i>	Ethiopia	ca. 400 ^f	est.	2
A.L. 333-105	<i>A. afarensis</i> (infant)	Ethiopia	310-320 ^{f*}	C	2

^a A, direct water displacement of either a full or hemiendocast with minimal distortion and plasticine reconstruction; B, partial endocast determination, as described by Tobias (1971); C, extensive plasticine reconstruction, amounting to half the total endocast; D, determination based on the formula $V = f^{1/2} (LWB + LWH)$, (Holloway, 1976), where L = maximum length, W = width, B = length, bregma to posterior limit of cerebellum, H = vertex to deepest part of temporal lobe and f appears to be a taxon specific coefficient; ^b an evaluation of 1 indicates the highest reliability, 3, the lowest; ^c postulated for adult - the value of the actual specimen is 404 ml; ^d possible overestimate; ^e provisional estimate; ^f these values, while published, have not been described and should be regarded as provisional. This is particularly the case with regard to the last three values for the purported *Australopithecus afarensis* taxonomic group. Assuming that the infant A.L. 333-105 infant had realised but 75% of its adult volume, the adult value would be approximately 400 ml

logical changes in the brain. (A fuller, more detailed description of these endocasts is being prepared.)

KNM-ER 1470

Two reconstructions of the basal portion of this distorted, but relatively complete cranium have provided brain volumes of 752 and 753 ml, respectively. The endocast shows the following provocative features: (1) the left Broca cap is relatively well developed, although the three major convolutional *pars* cannot be discerned; (2) the frontal lobe is definitely squarer, less pointed, than in known australopithecines; (3) there is a pronounced left-occipital-right-frontal petalial pattern; (4) the dorsal portion is relatively

high, domed, and parietal regions fuller than in australopithecines. There is no evidence for a marginal accessory sinus drainage pattern. Figure 2 shows a line drawing of the specimen.

KNM-ER 3732

This endocast portion, while too incomplete to even hazard a guess as to its size, nevertheless shows a distinct, well-defined, and largish left Broca cap region, with a possible delineation between the *pars triangularis* and *pars opercularis* portions. There is certainly no pongid-like fronto-orbital fissure posterior to the Broca cap region. This specimen, incidentally, is regarded as most probably a *Homo habilis*,

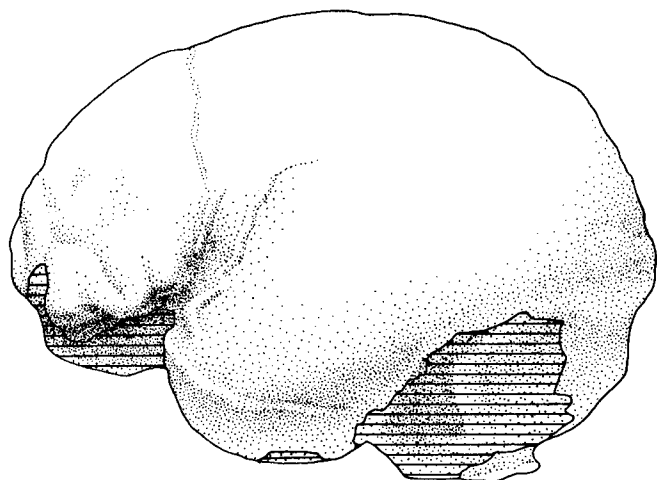


Fig. 2. Left lateral view of the East Lake Turkana KNM-ER 1470 endocast, as drawn by John Gurche. The anterior portion clearly shows a *Homo* delineation of "Broca's" area, but the remaining dorsal and lateral endocast surface lacks any convolutional detail. The apparent large size of the temporal lobe is an artifact due to post-mortem distortion of its inferior portion. The cranial capacity is 752 ml

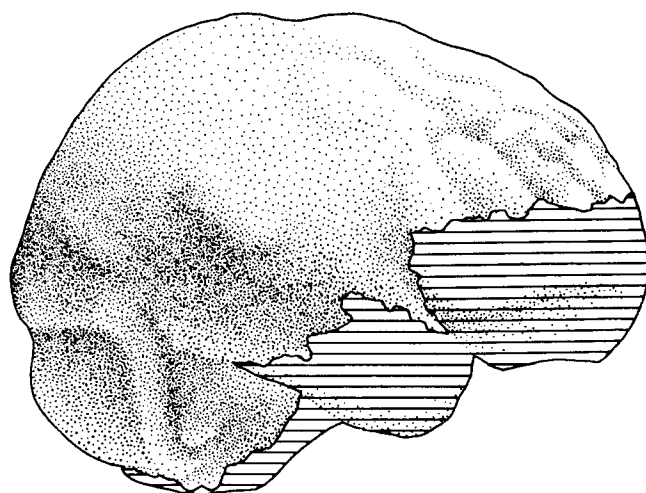


Fig. 3. A right lateral drawing of the KNM-ER 1813 endocast drawn by John Gurche. This endocast is roughly 510 ml in volume when reconstructed (shaded portions). Note complete lack of any convolutional relief in the posterior portion of the endocast, but a relatively high and bossed parietal surface

given its geological context and overall size. In my own estimation, the fragmentary right parietal portion shows an IP sulcus or groove, but it cannot be followed posteriorly toward the lambdoidal sutural region. The parietal zones appear bossed, and *Homo*-like to this author, but this is frankly a subjective, *gestalten*-like impression. Nothing can be said of asymmetry, drainage pattern, or the degree of roundedness or bluntness of the anterior frontal lobe.

KNM-ER 3733 and 3883

The crania are unmistakably *Homo erectus*. Endocranial casts have been made, yielding brain volumes of 804 and 848 ml, respectively. The internal table of bone was badly damaged by erosional processes on both of these crania, thus convolutional details are lacking. However, both show rounded frontal lobe regions, left-occipital-right-frontal petalias, and true Broca caps, all characteristics common in *Homo erectus* endocasts from Asia (see Holloway 1981c, Holloway and de Lacoste-Lareymondie 1982).

KNM-ER 1813 and 1805

Figures 3 and 4 show line drawings of these two smallish (513 and 582 ml, respectively) endocasts. They remain taxonomically problematic, given their *Homo*-like dentition, but small brain sizes. We do not know, truly, if these were advanced australopithecines, most closely related to *A. africanus*, or smallish habilines. The assignment of these to the *Homo habilis* taxon purely on the basis of "expected" statistical fit of cranial capacities by Jerison (1979) and Passingham (1982) is premature.

Aside from their volumes, and the presence of slight degrees of left-occipital-right-frontal petalial patterns, they are nearly devoid of convolutional details, although Falk (personal communication) believes that KNM-ER 1805 retains a pongid-like fronto-orbitalis groove, a finding this author does not share.

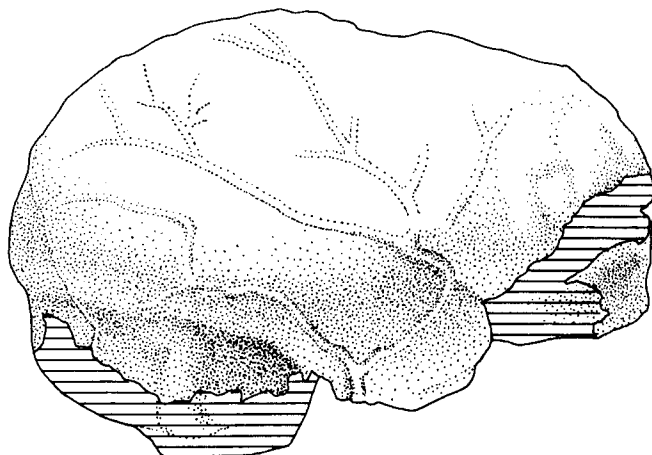


Fig. 4. A right lateral view of the KNM-ER 1805 endocast drawn by John Gurche, based on the author's reconstruction, yielding a volume of 582 ml. Convolutional details are totally absent on this endocast, and aside from a more modern temporal lobe configuration, this endocast is similar to those for *Gorilla* in overall shape. There is no paleoanthropological consensus on the taxonomic placement of either KNM-ER 1813 (Fig. 3) or KNM-ER 1805. Dentally, they appear to be either primitive *Homo* or advanced *Australopithecus*

Parietal bossing is somewhat more present than in South African *A. africanus* endocasts, but no details exist for delineating LS IP, or LC sulci.

Discussion

I would suggest that four brain traits, or character-sets, are relevant toward paleoneurological investigations bearing on language origins: (1) brain size; (2) evidence for reorganization or neural enlargement of cortical zones related to motor control (or participation) of sound production, i.e., "Broca's cap"; (3) reorganizational evidence for the posterior receptive and associative functioning of superior and posterior

temporal cortex, parietal lobule enlargement, and a concomitant reduction in lateral extent of primary visual striate cortex; (4) evidence of petalial asymmetries suggestive of handedness and differentiation of symbolic and visuospatial integration cognitive tasks between hemispheres. Size is problematic and always has been. "Rubicon" models die hard, as evidenced by the recent Eldredge and Tattersall (1982) book. Obviously some minimal mass is required for complex cognitive functioning, and I do not wish to belabor previous publications on this matter (Holloway 1966, 1968, 1975, 1981a, 1983b) but there are microcephalics who *can* talk with brain size less than a large gorilla's, or many of the later fossil hominids. My point is not that microcephaly was a phylogenetic stage in human evolution, but merely that these natural "experiments" also suggest that some minimal re-wiring of the brain from a pongid-like condition is necessary for language behavior. Rubicon models have an interesting logic: once a threshold (e.g., 750 ml) is passed, the logic ends! The addition of units, mass, so necessary to the inception of a function, language, become meaningless as a parameter relatable to cognitive functioning. There is, as common knowledge, the fact that modern *Homo sapiens* have brains which vary in size between 1000 and 2000 ml, with no known relationship to cognitive functioning, information processing, efficiency, complexity of behavior, etc., etc.

This is a problem of considerable merit in paleoanthropology. Almost all of the hominid specimens described above cannot be assigned reliable body weights. Relative brain size is thus unknown, and encephalization quotients are very dependent on the reference equation chosen (see Holloway and Post 1982). When we try to compare *Australopithecus* (i.e. *afarensis*, *africanus*, *robustus*, *boisei*), with early *Homo* (i.e., *habilis*), there is clearly some small possibility of brain size overlap, but we do not know about their relative brain weights, or true encephalization quotients. Figure 5 provides some models suggesting some of the difficulties in assessing evolutionary events with regard to the hominid brain. Certain kinds of reorganizational changes could have had a tremendous impact on early human evolution without being ascertainable by size criteria alone.

The point of this is that the paleoneurological picture, as we presently understand it, can prove nothing. Its value is corroborative and/or correlative. Thus paleoneurological evidence suggesting a posteriorly displaced lunate sulcus in one *A. afarensis* specimen (A.L. 162-28) and in the Taung child, is interesting, but hardly conclusive, given controversial perceptions of its most likely position. Asymmetries add corroboration, but again, no proofs. Broca's caps are corroborative, but *beware*, as largish ones can be found on chimpanzee endocasts!

Bipedality, taken by itself, cannot add to our knowledge of early hominid cognitive functioning, except to provide speculative thoughts regarding how the hands were used, and what bipedalism "meant" as a locomotor adaptation in the sense of securing subsistence.

The only true "evidence" for early human cognitive behavior somehow "resides" in the products of cognition, which are the stone tools the hominids once manufactured, their purported usage, and the kinds of sites (tool-making, camping, butchering, living, shelter, etc.) that can be uncovered and analyzed by the archaeologists. These, too, are

"mute," given any lack of consensus as to what these artifacts portray regarding cognitive functioning (e.g., Holloway, 1969, 1976a, 1981a, 1983b).

Experimentation with other primates, such as chimpanzees, orangutans, gorillas, etc., in which Ph.D.'s or doctoral candidates laboriously teach them to fashion and or use crude tools, or use symbol-strings for gaining attention, food, pleasure, affection, or objects, are very interesting, but

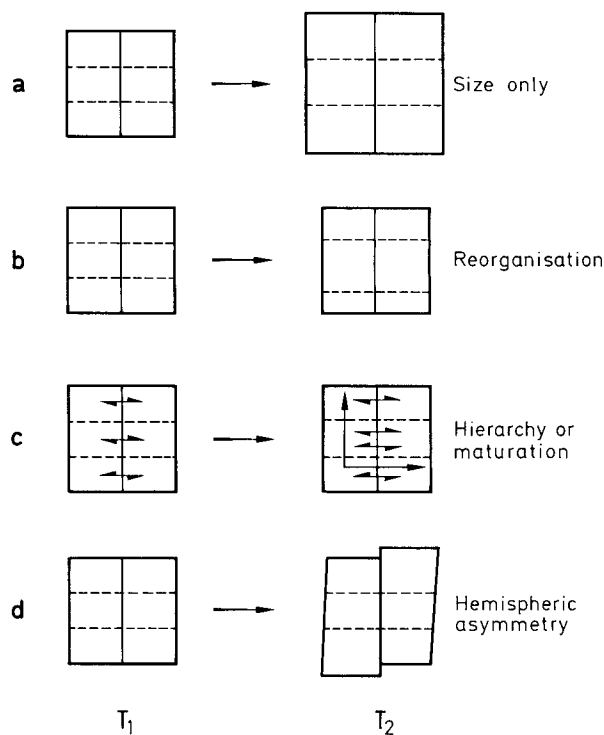


Fig. 5a–d. This figure shows four different possibilities of brain changes through time (T₁ to T₂). a The brain is shown with two hemispheres (left and right), and two transverse dotted lines which represent the central and lunate sulci, respectively. The change from T₁ to T₂ is simply an increase in size (absolute) without any change between the size of components or connections between them. This change could occur isometrically or allometrically. b The change from T₁ to T₂ does not involve any change in absolute brain size, but rather a change in components, such that the lunate sulcus is placed more posteriorly, thus expanding the posterior portion of parietal association cortex. This is a *reorganizational* model. c Depicts changes in *hierarchical* development without any change in absolute brain size from T₁ to T₂. The arrows represent fiber systems maturing at different rates and/or increasing in number between different cortical regions through the corpus callosum, although other brain structures and fiber systems could be involved. d Absolute brain size remains the same from T₁ to T₂, but a more human-type of hemispheric asymmetrical petalial pattern has emerged (i.e., left-occipital, right-frontal). It is important to note that these four models do not exhaust the possibilities of brain changes through time when size, reorganization, or hierarchy are considered in different combinations. It is most probable that all four of these possibilities have been realized in human brain evolution at different times. Empirical paleoneurological evidence *does* exist for models a, b and d but model c can only be inferred from comparative neuroanatomy, although it must have lawful relationships with b and d. It is hopefully obvious that any plot of brain size vs. time ignores possibilities b, c, and d, each of which could have had very profound effects on cognition, social behavior, and adaptation. Indeed, the shift from T₁ to T₂ in model b could represent a true case of "punctuated equilibria," as could c or d. Model a could be interpreted as a "P.E.," but in fact might simply be due to a slight increase in body size, e.g., allometry

hardly proof of past hominid evolutionary paths. They expand our consciousness of our nearest relatives' potentialities, but not of our fossil ancestral capabilities.

There remain a considerable number of problems in attempting to find correlative or corroborative evidence for human language origins. First, the paleoneurological base is weak, not only because there are so few complete endocasts, but also because there is no methodology existent which is truly objective, quantitative, and replicable. The controversy between myself and Falk regarding the position of the lunate sulcus on the original Taung australopithecine endocast is a case in point. Without a single empirically-demonstrated, quantitative technique, Falk (1980) proclaims, through visual inspection and palpation, that the superior end of the lunate is in a typical pongid position. Using a stereoplotting technique, Holloway (1981d) showed that her placement was almost a full centimeter anterior to any typical pongid (e.g., chimpanzee) position of the lunate. Using stereoplotting coordinates (see Holloway 1981b for details), a typical pongid placement violates all of the remaining convolutional morphology on the Taung specimen. Falk's (1983) rebuttal is based on a technique using measurements from photographs, and some totally unspecified, undefined "shape" factor. Even direct tape measurements on the actual chimpanzee brain casts (Holloway, in press) shows that a pongid position placed on the Taung specimen is still posterior, by 2.5 standard deviations, from Falk's placement. The point is, we need a better methodology for assessing the positions of what few endocranial details we have.

Secondly, comparative neuroanatomical studies have yet to delineate organizational brain differences among living primates. In recent years, most quantitative analyses (e.g., see Passingham 1982 for review; Armstrong and Falk 1982; Holloway 1979, 1983b) have been almost exclusively allometric in orientation. Whatever one considers a truly species-specific behavioral repertoire is not reducible to allometric equations between brain and body weights, or brain structures plotted against brain size. We are very little closer to knowing anything about neural variability and its relationship to behavioral variability, across species (Holloway 1969b, 1970, 1976a, 1979, 1981a, 1983b).

Thirdly, within-species variability, i.e., between brain structure and function, is very poorly understood, although much progress has been made during the past decade with regard to questions of cerebral asymmetry in different species, sexual dimorphism of parts of the hypothalamus (see Bleier et al. 1982 for a review), or sexual dimorphism in both brain and cognition among humans (e.g., McGlone 1980, Kimura 1980, 1983, de Lacoste-Utamsing and Holloway 1982). These matters are nevertheless of particular importance to paleoneurological investigations, less from the viewpoint of biological "fatalism" or "determinism," but more from the viewpoint of biological "heritage." For example, it is doubtful how far reported differences between the splenial portion of the corpora callosa between human females and males can be accepted as evidence for a cognitive dichotomy, given the variabilities of cultural milieus and educational opportunities provided to growing brains. There are simply too many variables to consider. But when such a difference is reported as present by age 26 weeks prenatal (Baack et al. 1982), it suggests that

structural differences do exist, existed in the past, and were probably under natural selection. They may thus be evolutionary residua. Cognitive task specialization among primate females and males may have been an important component of a complemental social behavioral adaptation in the evolutionary past of the human animal, particularly during times when parental investment and complex nurturant behavior toward offspring manifesting delayed maturation, prolonged growth, and prolonged periods of brain plasticity during growth and development were occurring. But to date, these morphological differences only appear in extant species' brains, and are not visible on the cerebral surface, let alone on the very imperfect endocasts of what were once living, pulsating brains.

Our findings from paleoneurology (Holloway and de Lacoste-Lareymondie 1982) for cerebral asymmetries on early hominid endocasts suggests that the human pattern of left-occipital-right-frontal petalias was certainly established by early *Homo* times (i.e., 1.5–1.8 m.y.), and may have been nascent in australopithecines. Asymmetries do occur in extant primates (LeMay et al. 1982, and their references), but not as strongly or in a patterned way as found in modern *Homo*. The paleoneurological findings corroborate (but do not prove) an early cerebral asymmetry and thus possibly cognitive task specializations between left and right hemispheres. The growing recent literature (e.g., McGlone 1980; Kimura 1980) indicates that the *degree* of task distribution may be sexually dimorphic, not only between left and right sides, but also between anterior and posterior cerebral locations (e.g. Kimura 1983).

The fossil hominid endocasts are simply too few in number, incomplete, and poorly preserved to determine sex with any confidence, and we do not have an objective, quantitative methodology for delimiting regional cerebral differences between evolutionary taxa, let alone sexes: nevertheless, some speculation seems worthy, if for no other reason than to frame ideas which can become better stated in the future.

This author believes that one of the most important evolutionary events in human phylogeny was the trend to extending the time of infant dependency (and vulnerability), and immaturity, and prolonging the duration of growth. Mann's (1972, 1975) meticulous studies of hominid dental eruption patterns is of great importance in establishing these trends empirically. These events could not take place without evolutionary changes in hormonal-target-tissue interactions, and a socially complex nurturant system with both socio-emotive and cognitive elements which placed a premium on a sexually-dimorphic but complemental set of social and subsistence-behavioral divisions of labor. Parental investment and extended kin nurturance were important evolutionary strategies, presaged in earlier and more primitive primate groupings. A more precocial female neuro-ontological developmental pattern with attendant competence in communication skills (meaning language and its imbeddedness in social structural perceptivity) appears wholly concordant to this author with both modern neurobiological findings and the evolutionary past. Complemental to this important social structural advance would be the increased competence in visuospatial integration and manual dexterity associated with hunting behavior, and in particular, complex throwing behavior and tool making. This is not a totally dichotomized view, but a complemental one in which "nurturant"

behavior is a complex amalgam of social intercourse, subsistence skills (gathering, scavenging, and hunting), and involves increasing sophistication in both understanding the "spatial terrain" and communicating about objects and relationships in both time and space. Both sexual division of labor along complementary lines and cerebral hemispheric specializations within the species could have been an enormously potent evolutionary advance, necessary to sustain a very difficult evolutionary "decision" to delay growth and maturation, and extend postnatal dependency times. The "payoff" was not only larger and more complexly wired brains capable of more complex learning, but also a complementary social structural adaptation in which language behavior was essential. This, I believe, is our biological heritage, but does not account for our necessary individual fates.

In sum, there is much room for speculating about human origins, and the role of language in human evolution, and its relationship to the brain. But there is even greater room for more detailed, quantitative, replicable studies which provide the connections between brain and behavioral variation. Paleoneurology is not self-reliant on such issues.

Conclusion

The paleoneurological evidence for the origins of human language and other cognitive activities is tantalizing, but uncertain, hampered not only through a scarcity of early brain endocasts which are complete, but also through the lack of any consistent methodology which can unambiguously delineate key features of cerebral convolutional detail relevant to either motor or receptive elements which are involved in language behavior. There are a few indications from early australopithecine brain endocasts (i.e., Taung, Hadar A.L. 162-28) that some reorganization of the posterior parietal and anterior occipital regions toward a more human pattern had occurred prior to brain size enlargement beyond current pongid values. By roughly 1.8–2.0 million years ago, there is clear fossil evidence for a *Homo* lineage showing brain endocast patterns suggestive of a more modern and enlarged third inferior frontal convolutional complex, expanded brain size (e.g., 750+ ml), and cerebral asymmetries which are strong and seemingly identical to those known for modern *Homo sapiens* (i.e. left-occipital-right-frontal petalias). In so far as these patterns correlate with right-handedness and a left-right asymmetry of cognitive functioning regarding symbolic language behavior (left) and visuo-spatial integration (right), it is possible to speculate that early *Homo* cognitive patterns were similar, albeit less advanced. More recent findings from both comparative neuroanatomy and clinical neurobiological sciences suggest that a sexual dimorphism in cognitive task specialization exists in many animals, but is perhaps best known from studies on modern humans. It is suggested that cerebral hemispheric asymmetry was an early evolutionary development, present in early *Homo* (and possibly earlier *Australopithecus*), and developed as a sexually complementary strategy related to nurturant behavior and parental investment in an animal where natural selection was favoring delayed maturation, prolonged growth, longer periods of postnatal dependency and neural plasticity in offspring. It is possible that gestation time increased slightly in early hominids, leaving the female gravid for a slightly longer period of time

than in pongids. It is speculated that current findings relating to sexual dimorphism of the corpus callosum, particularly the splenial portion which interconnects the more posterior parts of the cerebral hemispheres, have their origins in evolutionary biology, where natural selection favored an increased degree of cognitive task specialization relative to both social nurturance and parental investment of relatively immature offspring, and subsistence patterns in which males were relatively more skilled in visuospatial integrative tasks involving forceful and accurate throwing of weapons, and location of high-protein animal sources, and activity sites related to hunting, butchering, stonetool making, and sharing of food. In this schema, females retain a cerebrally-based advantage relative to symbolic communicative skills which must be skillfully imbedded within the realities of social structure, in which dominance and power relationships were keenly understood. In other words, I am speculating that females did have a socially-sophisticated edge over males in communicative skills and social structural knowledge. Furthermore, these are regarded as complementary rather than competitive, and probably involved earlier maturation of cortical tissues and interconnecting fibers (in females), and slightly more parietal cortex relative to frontal cortex in females (per de LaCoste and Woodward, 1982). These dimorphisms are regarded as biological *heritages* from past selection pressures, and *not* as biological "fates" for individuals with our own modern species.

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