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FORTY-THIRD
JAMES ARTHUR LECTURE ON
THE EVOLUTION OF THE HUMAN BRAIN
1973

THE ROLE OF HUMAN SOCIAL BEHAVIOR
IN THE EVOLUTION OF THE BRAIN,

RALPH L. HOLLOWAY

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†Published version: *The Brain in Hominid Evolution*, New York: Columbia University Press, 1971.

THE ROLE OF HUMAN SOCIAL BEHAVIOR IN THE EVOLUTION OF THE BRAIN

INTRODUCTION

The presentation of this lecture has particular significance for me because only slightly more than 11 or 12 years ago as a graduate student of human evolution I discovered with great excitement the existence of the James Arthur lectures; these surely decided my fate, at least in part.

I wish to discuss some of the brain endocasts of our earliest fossil hominid ancestors and to show that the human brain has been around for quite a long time, perhaps three million years — or longer. This is somewhat of an about-face for me, for when I wrote my dissertation about 10 years ago, I regarded endocasts as so much rock or plaster, with little, if any, potential of offering evidence on the evolution of the hominid brain. I believe I have mellowed. Today endocasts are the subject of my major research effort.

My questions about the human brain are: What lines of evidence can we use to learn about it; how did it evolve to its present state; can we find something in its evolution relevant for today's societal existence?

Before I discuss these questions in detail, I wish to briefly consider my basic conclusions:

1. The usual orthodox version of hominid evolution places the evolution of the brain as a terminal phase, one that occurs after all other parts of the body, such as the hands, the trunk, the teeth, and the locomotory anatomy for bipedalism have evolved. This view is very oversimplified, if not downright incorrect, and approximates truth only if we are willing to equate brain evolution with brain enlargement. Indeed, the evidence shows that brain modification to a human pattern occurred early in human evolution, at least three million years ago.

2. Both brain endocasts and bodily skeletal parts suggest that brain:body relationships remained fairly constant during most of human evolution, indicating an important set of selection pressures for body-size increase. This evidence also suggests that brain encephalization, as measured by Stephan's (1972) "progression indices" (related to a "basal insectivore" line), was already within the human range in the early fossil hominids. The mediating factor for increase must have been an endocrine-target tissue adjustment resulting in selection for increased delays of maturation, or prolonged growth and dependency times, important factors in any consideration of social behavior.
3. The humanly organized brain and resultant human cultural behavior have been interacting in a positive feedback manner during most of human evolution (Holloway, 1967). This feedback interaction is probably over, and unless some new radical genetic change occurs to interrupt man's present growth pattern, or a new social order that practices some form of genetic surgery comes into existence, I do not believe the human brain will show any further significant evolution in terms of size increase.
4. Brain endocasts have enormous value in the study of human evolution that extends far beyond brain-behavior correlations. They can give us information about variation, population statistics, and brain:body ratios, and therefore have importance in relating early hominid populations to ecological parameters such as biomass and growth and development.
5. Finally, we must realize that human behavior is not a recent achievement — our social behavior, our sociality has long evolutionary roots that cannot be abridged simply by cultural fiat.

Abbreviations used in the text and figures are:

ER, East Lake Rudolf
HE, Indonesian *Homo erectus*
MLD, Makapansgat, S. Africa
OH, Olduvai Gorge
OMO, Omo Valley, Ethiopia
SK, Swartkrans
STS, Sterkfontein

LINES OF EVIDENCE

DIRECT

It has long been appreciated that the only direct evidence for the study of brain evolution comes from the endocasts of our fossil ancestors (Edinger, 1929, 1949, 1964; Holloway, 1964, 1966a; Radinsky, 1967, 1970). Whether they are natural endocasts of the South African australopithecines (e.g., Taung, STS 60, Type 3, and SK 1585) or prepared in the laboratory from latex, plaster of Paris, and plasticine, they give only the most limited information about neural structure and no direct information about behavior. An endocast is simply a mold of the inside bony table of the cranium. Between the bone and the underlying brain there are three meningeal tissues of varying thickness, as well as a variably distributed amount of cerebrospinal fluid. The thick dura mater, the arachnoid space, the investing thin layer of pia mater, and the cerebrospinal fluid all "conspire" to eradicate the sulcal and gyral configurations imprinted by the surface of the cerebral cortex into the bony layer of the cranium. This "conspiracy" varies in different orders of animals; it is most severe, unfortunately, in the living and fossil species of apes and man. The reasons for this and the reasons for variation with age are not totally understood, but they are probably linked to differential growth rates of the brain and the overlying cranial bones in different regions (e.g., Hirschler, 1942; Keith, 1931).

Endocasts can be obtained from fossil cranial fragments in two ways. Natural endocasts occur when the skull is filled by fine sediments drifting through the cranial foramina, particularly the foramen magnum. The sediments may be compacted and solidified by percolating mineral solutions, resulting, in time, in a solid mass of sedimentary rock inside the skull. The skull bones may eventually erode away leaving the endocast intact. Usually the skull is preserved around the endocast, as is sometimes the case with the South African australopithecines, such as the Taung specimen, STS 60, Type 3, and the more

recent SK 1585 (figs. 1-8). In SK 1585 I deliberately removed the already eroded bones to disclose the fine-grained natural endocast (see Holloway, 1972a for details).

Endocasts may also be made by applying liquid rubber latex to the inner cranial surface of a skull. This method has been used for most of the endocasts, including all the rest of the hominids from East Africa, Asia, and Europe. Successive layers are built up until a reasonable thickness, perhaps an eighth of an inch, is reached. The latex is cured by heat and then collapsed from the skull, either before or after stabilizing the dimensions with plaster. The external details of the cerebral cortex, as transmitted through the dura mater, will be reproduced on the surface of the latex. If the inner bony table is eroded before the endocasts are made, the details will obviously be missing.



FIG. 1. Lateral view of Taung infant endocast and face positioned together. Arrow points to lambdoid suture, which is probably the most anterior extent of lunatic sulcus. Scale equals 3 cm.



FIG. 2. Lateral view of Taung infant endocranial cast. Arrow points to third inferior frontal convolution. Small portion of frontal lobe remains embedded in facial fragment. Scale equals 3 cm.

INDIRECT

Brains influence behavior, and occasionally the results of behavior become, so to speak, fossilized. Fortunately, the paleoanthropologist has lines of evidence for the evolution of the brain other than brains or endocranial casts. There are two sources of indirect evidence: (1) cultural products of brain and social behavioral activity, e.g., stone tools, shelters, animal remains at ancient butchering sites; and (2) skeletal components of the masticatory and locomotor systems. No indirect evidence can yet be used to demonstrate any specific changes in the brain observable at the surface. It is, however, indicative of different behavioral capabilities, which require, after all, neural com-



FIG. 3. Occipital view of Taung infant endocranium. Lambdoid suture is distinct. Notice gyral curvature (shown by dotted line and arrow) immediately superior and anterior to lambdoid suture, indicating that more forward placement of lunate sulcus would not be possible. Scale equals 3 cm.

plexes to effect them. In other words, it supports the idea of brain reorganization.

The first line of indirect evidence applies, as far as we know, only to hominids. There is no evidence from the fossil record of the cultural behavioral effects in other lines of primates. The second line of indirect evidence, that is, musculoskeletal, is far more general and applies to all lines of animals, most particularly to the mammals. But what we see in the hominid fossils is rather specific, at least when compared with other fossil primates, or extant ones, for that matter. The earliest hominids show definite changes in masticatory apparatus — in the teeth, jaws, and areas of muscle attachment for the temporalis and



FIG. 4. Lateral view of plaster replica of SK 1585, endocranial from Swartkrans, South Africa. A small portion of frontal lobe is missing. Lambdoid suture obscures posterior limit of lunatic sulcus. (See Holloway, 1972a.) Scale equals 3 cm.

masseter in particular. We find changes in the molars as far back as 10 to 14 million years ago in *Ramapithecus* (Pilbeam, 1969; Simons, 1961, 1964, 1969). Among the early hominids of East and South Africa there are changes in nuchal musculature related in part to advanced degrees of bipedal locomotion, which itself is corroborated by the remains of the locomotor skeleton (pelvis, lower vertebral column, limb bones such as the femur, tibia and fibula, and various bones of the foot). Even the hand bones, at least of the East African hominids, show changes in musculoskeletal structure suggestive of manipulative abilities greater than those of any fossil or living ape or monkey.

Why belabor these points? Because they show, whether or not the precentral gyrus appears on the surface of the endocranial,



FIG. 5. Occipital view of plaster replica of SK 1585 endocrast. Scale equals 3 cm.

that natural selection has long been operating on behavior, favoring neural organizations capable of servicing the new musculoskeletal complexes.

This line of indirect evidence for brain reorganization need not be related only to motor or sensorimotor behavior, such as the various muscle contractions involved in bipedalism, but it must be taken to involve the whole adaptive complex (hunting, scavenging, carrying objects, and so on) in which these motor patterns are embedded and to include aspects of psychological restructuring as well. It is true that there is yet no way of comparing a gorilla endocrast to that of an australopithecine or a



FIG. 6. Basal view of plaster replica of SK 1585 endocrast. Scale equals 3 cm.

Homo sapiens to show correlated changes between brain surface features and motor behavior. Endocrasts may or may not reflect important adaptive changes in behavior and structure, but by themselves they cannot indicate whether the brain evolved before or after the sensorimotor changes.

THE EVIDENCE

Evidence from which I conclude that the brain has always been an important component of human evolution is as follows:

1. Gross Morphology: Hominid endocrasts show a human shape that is not found among a sample of 50 chimpanzee and gorilla endocrasts. Although there can be considerable variation in endocrasts of living pongids (figs. 9-16), none shows the combination of features seen on hominid endocrasts. The differences are as follows:

- a. The height of the brain above the cerebellar lobes is almost always greater in hominid brains. Occasionally the brain of

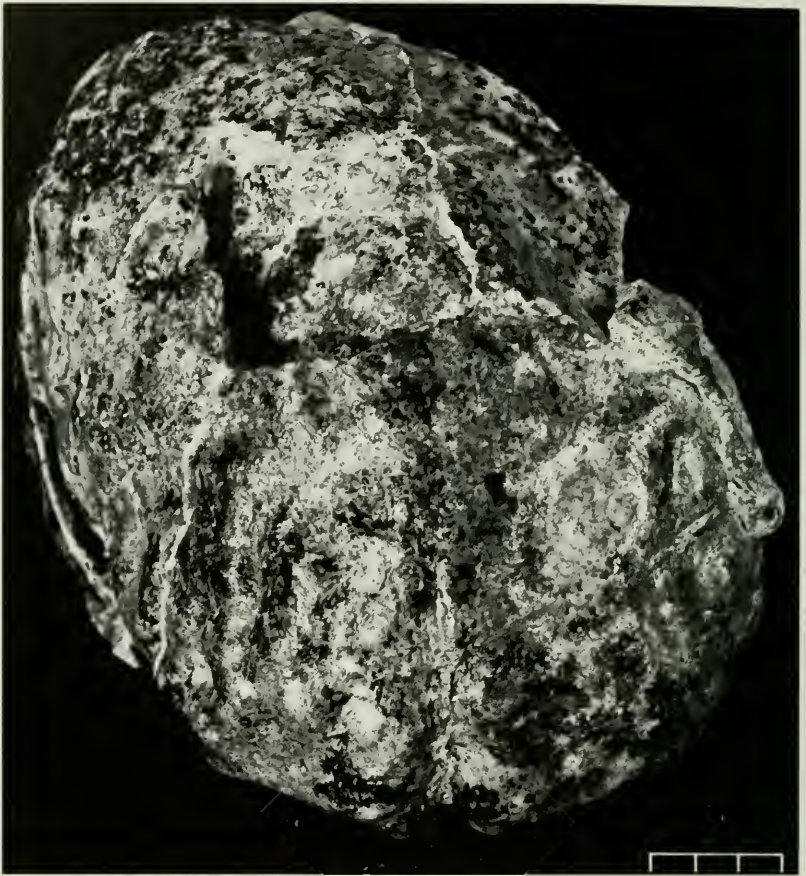


FIG. 7. Dorsal view of Type 3 endocast, a gracile australopithecine from Sterkfontein. Note double-valleyed fracture in parietal lobe, squared-off shape of frontal lobe, and suggestion of heavy gyral and sulcal relief. (See Schepers, 1946.) Scale equals 3 cm.

the pygmy chimpanzee, *Pan paniscus*, shows less flattening in height than that of either the gorilla or the chimpanzee (*Pan troglodytes* sp.) but it is not so high as that of the early australopithecines (table 1).

b. The anterior tips, or poles, of the temporal lobes are

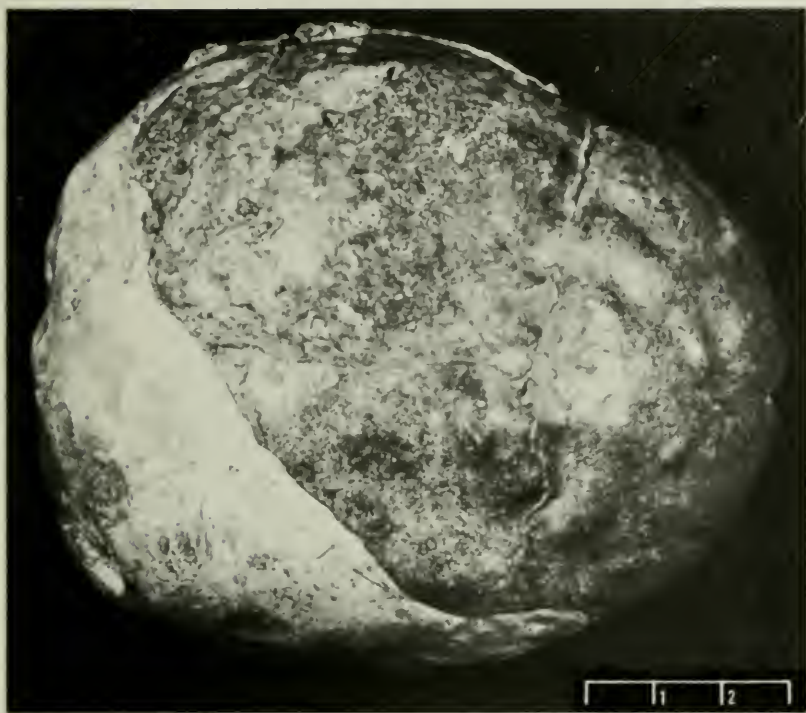


FIG. 8. Dorsal view of endocranial cast of STS 60 from Sterkfontein. Scale equals 3 cm.

distinctly more rounded and larger in hominids than in pongids (part of this is, of course, due to the different shape of the greater wing of the sphenoid and the dural sheath surrounding the tip of the lobe).

- c. The orbital surface of the frontal lobe is generally angled upward, with a more pointed and pronounced beak in pongid than in hominid brain casts.
- d. In pongid endocranial casts the position of the famous "lunate" or "simian" sulcus, which divides the primary visual cortex from the so-called parietal "association" cortex, is usually in a fairly anterior position (although less so than in cercopithecoids). Although only a few hominid endocranial casts [particularly the original Taung (1924) endocranial cast] show the sulcus

clearly, it is definitely in a posterior, human-like position (figs. 3, 5). It is probably this feature, more than any other, that so firmly suggests cortical reorganization to a human pattern. This observation was first noted by Dart (1925), later by Schepers (1946), and was more or less verified by Sir Wilfred LeGros Clark (1947); a close examination shows no alternative position.

- e. The inferior border of the temporal lobe also shows enlargement, reflected in a smaller, or more acute, angle of the petrosal cleft.

Taken together, these features form a Gestalt that is very difficult to demonstrate by linear measurements, as many physical anthropologists would wish. It is these 'Gestalten' that enable one to distinguish between pongid endocasts, such as between those of chimpanzees and gorillas, even though most measurements and indices tend to overlap.

- f. Finally, it is possible that there is more sulcal and gyral development in hominid cortices, particularly on the frontal lobe, than in pongid cortices; however, this is not easily measured on endocasts and is at best an impressionistic judgment.

2. Gross Size: This parameter (or to follow Jerison, 1973, "statistic") is perhaps the crudest of all. The small absolute sizes of the australopithecine endocasts tended to deny them hominid status long after their discovery. Elsewhere I (Holloway, 1964, 1966a, 1968, 1970, 1972b) have detailed my observations on the significance of this measurement of the brain. Some chimpanzees and most gorillas have larger brains than the early hominids (see, for example, Tobias's 1971 compilations). The range of variation in normal present-day *Homo sapiens* is from about 1000 to 2200 cc., or about as much as the total evolutionary gain from *Australopithecus africanus*, at ca. 450 cc., to the average value of modern *Homo sapiens* of about 1400 cc. Yet there has never been any demonstration, among living populations, of a relationship between brain size (measured either by weight or volume) and behavior. Although some human microcephalics have brain



FIG. 9. Lateral views of rubber latex endocasts of (top) *Pan paniscus*, pygmy chimpanzee, (middle) *Pan troglodytes*, and (bottom) *Gorilla gorilla*. (Rubber latex endocasts made by author from specimens belonging to the American Museum of Natural History.) (See figs. 10 and 11 for occipital and dorsal views of same specimens.) Scale equals 3 cm.

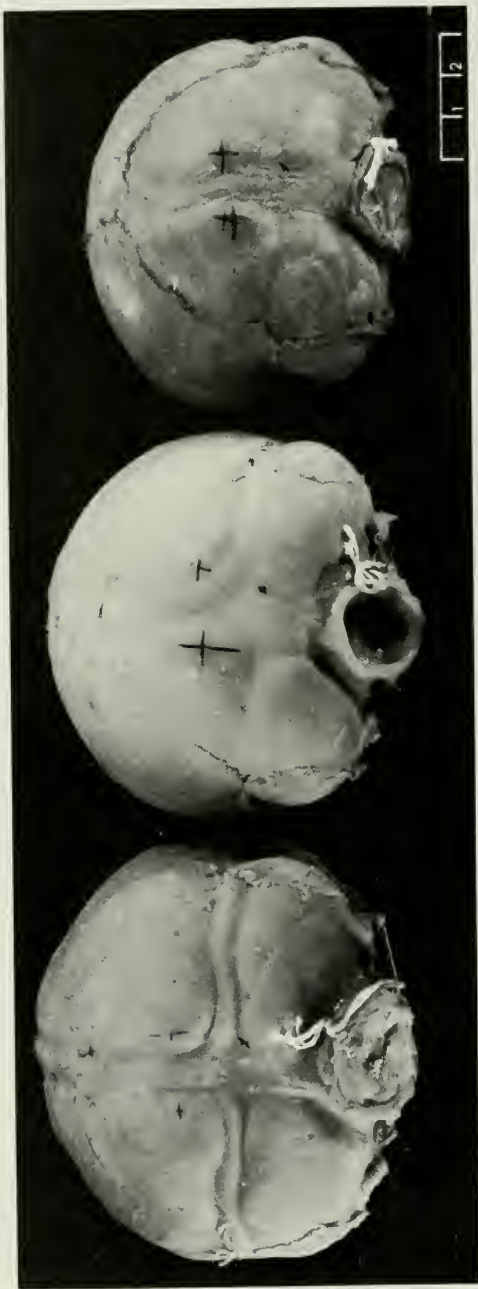


FIG. 10. Occipital views of rubber latex endocasts of (left) *Gorilla gorilla*, (middle) *Pan troglodytes*, and (right) *Pan paniscus*. (See figs. 9 and 11 for lateral and dorsal views of same specimens.) Scale equals 3 cm.



FIG. 11. Dorsal views of rubber latex endocasts of (left) *Gorilla gorilla*, (middle) *Pan troglodytes*, and (right) *Pan paniscus*. (See figs. 9 and 10 for lateral and occipital views of same specimens.) Scale equals 3 cm.

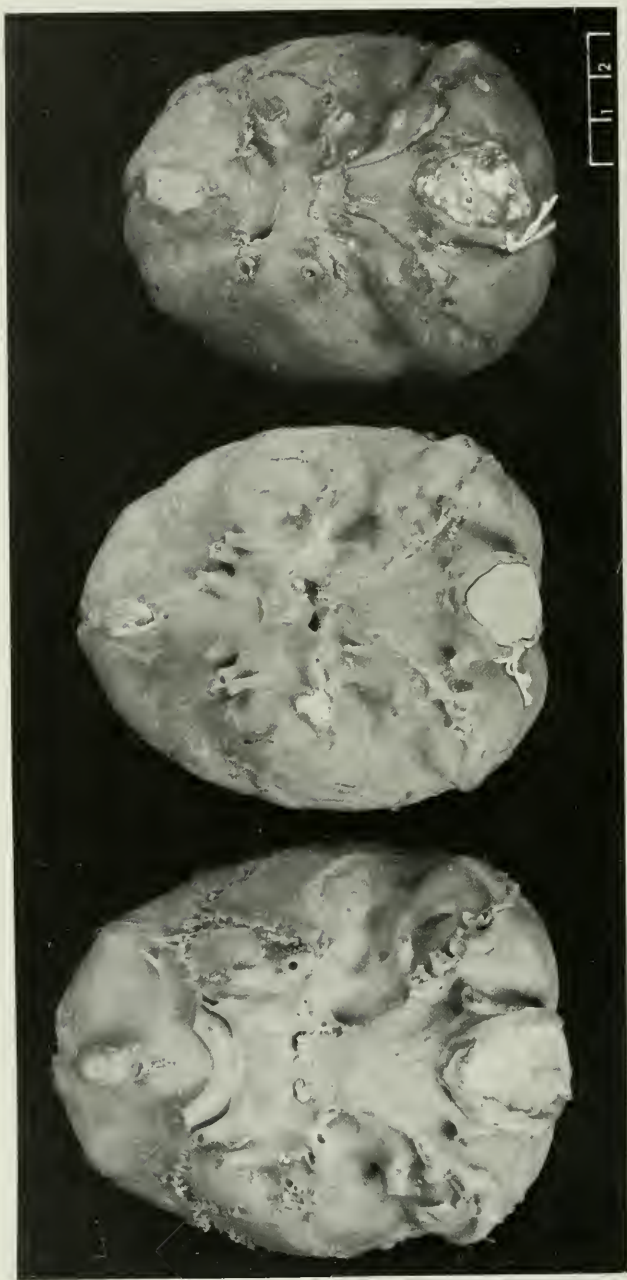


FIG. 12. Basal views of rubber latex endocasts of (left) *Gorilla gorilla*, (middle) *Pan troglodytes*, and (right) *Pan paniscus*. Scale equals 3 cm.



FIG. 13. Dorsal view of endocast of different, or another *Pan troglodytes* showing excellent gyral and sulcal markings. Arrows indicate anterior limit of lunate sulcus. (Rubber latex endocast made by author from a specimen at the American Museum of Natural History.) Scale equals 3 cm.

volumes that gorillas, and perhaps a few large chimpanzees, might disdain, they do not exhibit simian behavior, but rather show the species-specific ability for symbolic language, albeit disadvantaged.

The usefulness of this crude measure of the brain lies in its statistical utilization as a parameter from which other neural measures, such as neuron size, glial/neuron ratio, neural density, and dendritic branching may be calculated. All of these variables are closely tied in with behavioral variation, although it remains for future scientists to demonstrate this unambiguously (see Holloway, 1964, 1966a, 1966b, 1968; Jerison, 1973).



FIG. 14. Endocast of modern *Homo sapiens*, lateral view. Note great height of cortex above cerebellum, expansion of temporal lobe in anterior and posterolateral margins, and slight slope of orbital surface on frontal lobe. (Rubber latex endocast made by author from specimen belonging to Columbia University.) Scale equals 3 cm.

Gross brain size is also related to body mass and time, and thus it can be used in combination with these other variables to give us clues about changes in growth rates during evolution in particular phyletic lines. The study of brain:body allometric relationships in different animal lines has had a long history and is a subject that is receiving considerable attention by modern scientists (see, for example, Jerison, 1973). So far, however, most of these studies have been concerned with comparisons between high-level taxa, such as between carnivores and herbivores, reptiles and birds, pongids and modern man. But if brain and body size can be measured with reasonable accuracy within a phyletic line, such as the Hominidae, the changes in allometric relationships with time can provide extremely im-



FIG. 15. Same specimen as figure 14, occipital view. Scale equals 3 cm.

portant clues to selection pressures operating on variables such as growth rates of different parts of the body, encephalization, postnatal growth, and so on, which obviously have important biological relationships with social behavior and adaptation. In other words, another significant use of gross brain size, beyond that of simply indicating overall size increase, is as a key to other relationships that may have been more concerned with selection pressures.

Unfortunately our samples for various hominid lineages are terribly small, and many specimens (e.g., the South African hominids) are not firmly dated; it is thus impossible to plot brain size against time in any accurate manner. If we could, the rates might give us some interesting clues to past selection



FIG. 16. Same specimen as figure 14, basal view. Scale equals 3 cm.

pressures and dynamics (see Holloway, 1972b). Table 2 gives a number of newly determined endocranial capacities for various hominids. The methods used to arrive at these figures are given in the footnotes to this table.

3. Relative Brain Size and Encephalization: There appears to be a lawful relationship between brain and body size in all vertebrate taxa (see Jerison, 1973, for a thorough review of this relationship). In general, following the principle of allometry, larger-bodied animals tend to have a proportionally smaller brain weight. It is possible to plot the size of the brain against the weight of the body on double-logarithmic graph paper and to discern some reasonably straight-line relationships. Regression lines are of the general form $E = kP^y$, where E = brain weight, P = body weight, y = an exponent probably reflecting the

relationship between volume and surface area, and k = a constant, often taken to reflect "encephalization," or the relationship between brain:body weight ratios in different animals. Plotting different orders of vertebrates on the same graph tends to give an exponent of 0.66; for closely related species the exponent usually falls between 0.20 and 0.30. Within the species, however, there seldom appears a relationship, but this is probably debatable.¹ The human brain is neither the smallest nor the largest in terms of relative size. Table 3 gives a few examples of animals with large and small relative brain weights. This table does not show, however, the range of variation within each category for brain:body weight ratios, for which few published data exist.

Using a large number of "basal" insectivores (representing the sort of primitive stock out of which the primates may have evolved), Stephan (1972) was able to construct a "basal" insectivore line, defined as $\log_{10} h = 1.632 + 0.63 \log_{10} k$. By substituting a primate's body weight in the equation (k), it is possible to solve for " h ," which gives the expected brain weight of a "basal" insectivore with such a body weight. If this weight is then divided into the actual brain weight of the particular primate, an "index of progression," or measure of encephalization, results (table 4 shows a number of "progression indices" for different primates, including some fossil hominids). This last step requires making a hazardous assumption about the body weight of the fossil hominid. Nevertheless, allowing for maximal and minimal body weight, the South African gracile australopithecines fit either within the range for modern man or just below it, but always above the pongid range. This is indirect evidence for reorganization of these early hominid brains to a

¹Very little secure data exist for large samples of healthy individuals, which requires study by more sophisticated statistical methods, such as partial correlations. To date no such study has been published, not even in the excellent article by Pakkenberg and Voigt (1964) on the Danes. I give this warning because a preliminary analysis of a partial correlational study between the variables of age, weight, body height, and brain weight suggests more of a relationship between brain and body weight than is usually recognized. I hope to publish these results in the near future, thanks to the courtesy of Dr. Pakkenberg, who has given me the original data.

human pattern, but it does not tell us whether there is a general allometric increase in overall size or whether there has been differential development of particular elements of the brain.

Still, these data are more relevant for understanding evolutionary change than are mere comparisons of gross brain size. It is a great pity that we do not as yet have a way to determine accurately the body weights of our hominid ancestors. If we did, we could plot these for particular lineages and, possibly, relate the resulting exponents to evolutionary selection pressures.

Figure 17 and table 5 show a range of possible brain:body weight relationships, based on current estimates of hominid body weights (Tobias, 1967; Lovejoy and Heiple, 1970) that might have characterized stages of hominid evolution. Interpretation of selection pressures for increasing brain size varies, depending on whether the exponents linking the fossil hominid lineages are > 1.0 , 1.0 , 0.66 , or less. The exponent 0.66 characterizes most nonhominid mammals (Jerison, 1973),

TABLE 1
Some Crude Indices for Hominid Endocasts^a

Specimen	Volume in Milliliters	$\frac{D \text{ arc}}{L \text{ arc}}$	$\frac{D \text{ arc}}{L}$	$\frac{L}{H}$	$\frac{H^3}{V}$
Taung	404	1.13	1.48	1.41	1.41
STS 60	428	1.00	1.35	1.40	1.29
STS 5	485	1.08	1.39	1.42	1.27
OH 5	530	1.47	1.37	1.45	1.20
SK 1585	530	1.73	1.42	1.43	1.37
ER 732	506	1.06	1.42	1.48	1.13
OH 24	590	1.01	1.29	1.40	1.32
OH 13	650	1.17	1.49	1.48	1.16
OH 9	1067	1.05	1.31	1.55	1.18
OH 12	727	1.11	1.41	1.60	0.97
HE I ^b	943	1.10	1.33	1.59	1.02
HE II ^b	815	1.06	1.35	1.53	1.08
HE IV ^b	900	1.00	1.31	1.64	0.94
HE VI ^b	855	1.05	1.33	1.68	0.97
HE VII ^b	1059	1.07	1.41	1.65	0.92
HE VIII ^b	1004	0.98	1.25	1.61	1.00
ER 1470 ^c	770	1.04	1.37	1.36	1.30
Omo 338s	427	1.02	1.37	1.54	1.03

TABLE 1 - (Continued)

Specimen	Volume in Milliliters	$\frac{D \text{ arc}}{L \text{ arc}}$	$\frac{D \text{ arc}}{L}$	$\frac{L}{H}$	$\frac{H^3}{V}$
<i>Pan paniscus</i>					
(n = 8)					
average	325	0.99	1.33	1.46	1.04
range	284-363	0.97-1.01	1.28-1.37	1.36-1.54	0.86-1.21
<i>Pan troglodytes</i>					
(n = 29)					
average	394	0.96	1.28	1.47	1.09
range	334-474	0.88-1.01	1.20-1.34	1.39-1.59	0.95-1.23
<i>Gorilla gorilla</i>					
(n = 36)					
average	498	0.98	1.26	1.53	1.04
range	383-625	0.94-1.04	1.19-1.33	1.39-1.67	0.85-1.24
<i>Homo sapiens</i>					
(n = 4)					
average	1442	1.10	1.43	1.40	1.25
range	1324-1586	1.04-1.14	1.39-1.46	1.35-1.46	1.11-1.42

Symbols: D arc = dorsal measurement between frontal and occipital poles; L arc = lateral measurement between frontal and occipital poles; L = chord length between frontal and occipital poles; H = chord length from vertex to lowest plane of temporal lobe; V = volume.

^aThese figures clearly show that most hominid fossils (*Homo erectus* excepted) have a greater degree of cortical height relative to both length and volume than do the African pongids tested.

^bThe well-known platycephaly of the Indonesian *H. erectus* is clearly shown by the L/H value, the low D arc/L arc, D arc/L and H³/V ratios.

^cThis specimen does not show a typical *H. erectus* pattern.

“basal insectivores,” and most lower primates (Stephan, 1972). This exponent suggests an allometric increase, where brain weight increases at a smaller rate than body weight. An exponent of approximately 1.0 indicates a constant brain:body weight ratio, suggesting selection pressure for brain weight to match body weight. An exponent greater than 1.0 suggests selection pressures for brain weight greater than that for body weight.¹

¹Of course, an exponent of 1.0 in hominids does mean an increase in brain size when compared with either a “basal” insectivore or vertebrate line where the exponent is about 0.66.

TABLE 2
Endocranial Volumes of Reconstructed Hominid Specimens

Specimen	Taxon	Region	Endocranial Volume in Milliliters	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 732	<i>A. robustus</i>	East Africa	500	A	1
ER 1470	<i>H. sp.?</i>	East Africa	770 ^e	A	1
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

^aA, direct water displacement of either a full or hemiendocranial with minimal distortion and plasticine reconstruction; B, partial endocranial determination, as described by Tobias (1967, 1971); C, extensive plasticine reconstruction, amounting to half the total endocranial; D, determination based on the formula $V = f \frac{1}{2} (LWB + LWH)$, described by MacKinnon et al. (1956), 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.

^bAn evaluation of 1 indicates the highest reliability, 3, the lowest.

^cPostulated for adult—the value of the actual specimen is 404 ml.

^dPossible overestimate.

^eProvisional estimate.

^fThese values are as yet unpublished and should be regarded as provisional.

At the present stage of our knowledge, it is premature to go beyond this kind of simple exercise. Our samples are extremely

small, we have no good empirical evidence for any early hominid body weight and the values in figure 17 connect lineages that are geographically separated (i.e., the South African gracile *Australopithecus* with the East African *Habilis* with the East Asian *Homo erectus* with modern *Homo sapiens*). Nevertheless, these relationships between brain and body weight hold great promise for better understanding the dynamics of hominid evolution. Indeed, as is clear from figure 17, one can draw the lines in different ways, with constant slopes (i.e., 1.0) or with different slopes at different times. (See also Holloway, 1974a.) The implications are extremely important, even though the basic data are admittedly weak, for the lines in figure 16 demonstrate that a number of alternative hypotheses about hominid brain evolution can exist, and that any particular hypothesis is based on assumptions of body weight that cannot be empirically pinpointed. In any event they do show a human, rather than a pongid, pattern in terms of relative brain size and changes through time, which strongly suggests that hominid brain size increase and attending selection pressures were probably unique.

TABLE 3
Some Average Brain:Body Ratios for Various Animals^a

	Brain:body weight ratio
<i>Homo sapiens</i> ^b	1:45
Gorilla	1:200
Chimpanzee	1:185
Macaque, Rhesus	1:170
Marmoset	1:19
Squirrel monkey	1:12
Elephant	1:600
Whale	1:10,000
Porpoise	1:38

^aFrom Cobb, 1965.

^bGood tabulated data on ranges for healthy human adults is lacking. The exception is one study on Danes by Pakkenberg and Voigt, 1964, p. 297, in which normal brain:body weight ratios are shown to vary from approximately 1:28 to 1:80.

TABLE 4
Some Possible Brain Size: Body Weight Ratio and "Progression Indices"^a

Specimen	Average Brain Size (ml.)	Assumed Body Weight (Pounds)	Brain: Body Ratio	"Progression Index" PRG/BG
Gracile australopithecine	442	40	1:41	21.4
		50	1:62	18.7
		60	1:51	16.9
Robust australopithecine	530	50	1:43	22.3
		60	1:51	19.9
		75	1:64	16.9
		110	1:94	12.8
<i>Homo sapiens</i>	1361	150	1:45	28.8
<i>Homo erectus</i>	930	92	1:45	26.6
		125	1:61	22.0

^aBased on Stephan's, 1972, formula using a basal insectivore line (see text).

Note: Maximum PRG/BG for gorilla is about 7.0, and for the chimpanzee, about 12.0. See Stephan, 1972, for ranges.

Maximum body weight of average gracile australopithecine (442 ml.) with PRG/BG of 12, is 100 pounds. That is, if we allow the "progression index" of *Australopithecus* to be the maximum chimpanzee value, the body weight is calculated to be 100 pounds, which is clearly too heavy, based on the postcranial materials we have thus far discovered for the gracile form of *Australopithecus*.

4. Lateralization and Cerebral Hemispheric Dominance: Comparative neuroanatomy has not been able to demonstrate any definite difference between the human brain and the ape brain except on the basis of size. Absolute and relative brain sizes, plus quantitative differences in amount of cerebral cortex in certain lobes, such as the parietal and temporal, are all that have been defined. These are matters of continuity, as far as can be established at present. The cortico-cortical fasciculus occipito-frontalis, a long associational tract known to exist in the human brain, has not been distinguished in the chimpanzee or cercopithecoid brain (Bailey et al., 1943). This does not mean that an associational system does not exist between the posterior and frontal segments of the chimpanzee cortex, but only that it is probably not so developed as it is in *Homo sapiens*. Many more pongid specimens should be dissected before its presence or absence can be proved.

TABLE 5

Brain:Body Weight Double-Log Relationships Based on the General Formula $h = bk^x$, with Possible Slope Differences Depending on Brain and Body Weights Used^a

Specimen	Brain Volume (ml.)	Body Weight (pounds)			Slope
<i>Australopithecus</i>	450	40	50	60	1.0
<i>H. erectus</i>	930	83	103	123	
<i>H. sapiens</i>	1361	123	150	180	
<i>Australopithecus</i>	450	40	50	60	0.6
<i>H. erectus</i>	930	115	143	180	
<i>H. sapiens</i>	1361	200	200	250	
<i>Australopithecus</i>	450	85-86	—	—	1.92
<i>H. erectus</i>	930	123	—	—	
<i>H. sapiens</i>	1361	150	—	—	
<i>A. africanus</i>	450	50	—	—	1.0
<i>H. habilis</i>	775	86	—	—	
<i>H. erectus</i>	930	114	—	—	
<i>H. sapiens</i>	1361	140	—	—	1.75

^aBrain weights are held constant, the slopes varied and the resulting body weights determined by projection to the abscissal axis, which is the body weight.

The most singular difference known to exist at present is that the human brain is characterized by cerebral hemispheric dominance and a high degree of laterality. In general the left hemisphere seems dominant, in terms of language phenomenon, in the inferior parietal lobe (Wernicke's area), in the gyri and sulci of Heschl and in the third inferior frontal convolution, often known as Broca's area. The right hemisphere, particularly the parietal lobe, seems "dominant" for spatiotemporal and

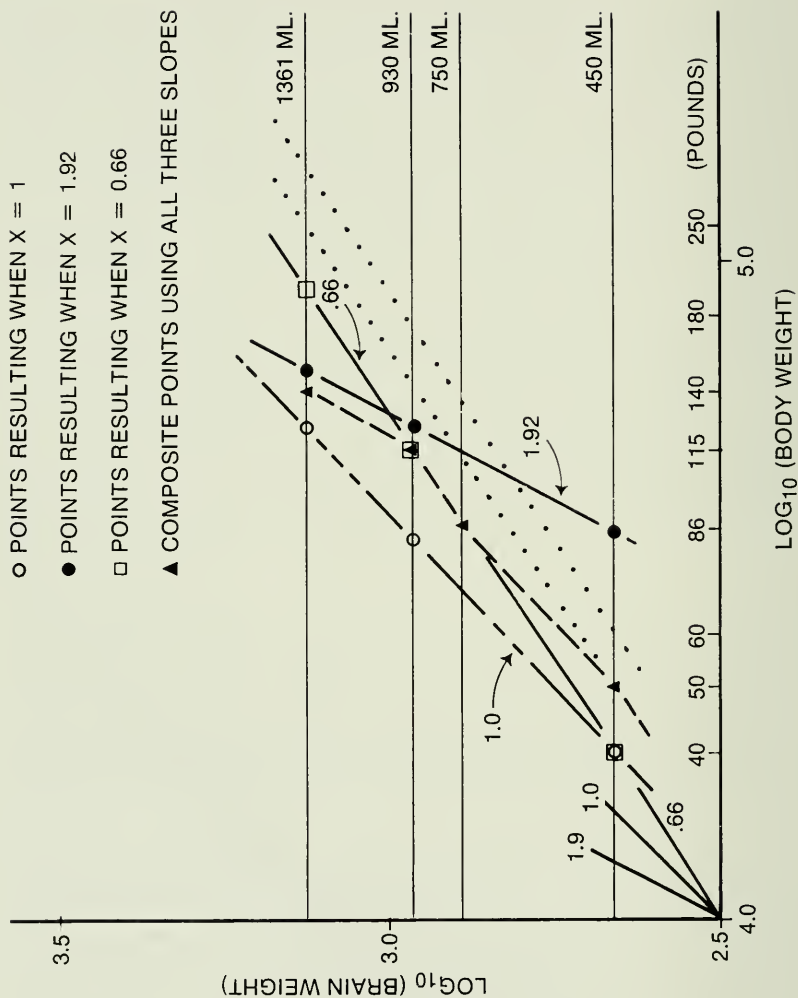


FIG. 17. Double-log (base 10) graph showing some possible regression lines, depending on assumptions of body weight, and allometric growth equation of exponential form $h = bk^x$ or $\log_{10} h = \log_{10} b + x \log_{10} k$, where h = brain weight in grams, k = body weight in grams, and x = slope of line. Average for gracile australopithecines is taken as 450 ml., *Homo erectus* as 930 ml. (based on my unpublished determinations for six endocasts) and 1361 ml. as the average for modern man, based on Tobias (1971). A slope of 0.66 is usually regarded as the best slope for all mammals (see, for example, Stephan, 1972).

This diagram shows that a number of possibilities exist and that the general slope of 0.66, if maintained throughout hominid evolution, results in body weights for modern *Homo* that are too heavy. Most slope possibilities suggest genuine selection for heavier brains. It should be realized that a number of alternative lines can be drawn. For example, the line of slope = 1.0 is based on a 40-pound body weight for the gracile australopithecine. Shifting that line over to 50 or 60 pounds gives more realistic body weights for *Homo erectus* and modern man. The composite line through the triangles has three different slopes, indicating changing selection pressures for allometric growth relationships through time. Another limitation to keep in mind is that the basal values for brain weight come from three different types of populations, the higher values coming from Asian fossils and a world-wide average for modern man. All of these slopes and figures are approximations only, taken from graph projections.

visual integration. These attributes have long been discussed in the literature, but they have never been demonstrated by gross measurements, either on the brain or on endocasts of modern *Homo sapiens*. However, Geschwind and Levitsky (1968) have shown that when the temporal and parietal lobes are cut away, the left side shows strikingly enlarged convolutions, the gyri of Heschl, underneath. Astakhova and Karacheva (1970) have shown that differences between left and right hemispheres are present before birth. It is not possible to go into all the functional details, but they can be taken as a species-specific attribute of human brain structure, and by extension, of behavior.

Do the fossil hominid endocasts show such differences? Unfortunately the endocasts of the South and East African australopithecines are seldom bilaterally complete, which precludes any direct measurements. Gross measurements, such as lengths, arcs, breadths and heights, do not demonstrate any consistent asymmetries on complete endocasts. LeMay and Culebras (1972) have suggested that the Neanderthal brain cast from La Chapelle-aux-Saints shows laterality, but this depends on how carefully the Sylvian fissure is defined in its posterior course, a feature generally impossible to observe on most endocasts.¹ LeMay and Culebras's angioradiography of living humans does, however, show consistent left-right differences, but until a more accurate and sensitive method to measure endocasts of fossil hominids is found cerebral dominance in fossils cannot be proved. I am currently working on some of the newer *Homo erectus* fossils from Indonesia, on the basis of which a case may be made for cerebral dominance, but it is too early to be certain. The presence of stone tools, of primitive, but nevertheless standard patterns, at least 2.6 to 3.0 million years old, is suggestive of both lateralization and of primitive communication by a language based on symbols (Holloway, 1969).

¹I have not been able to see this fissure clearly on any fossil hominid endocasts I have examined.

SUMMARY OF DIRECT AND INDIRECT EVIDENCE

In summary, we find among the early australopithecine examples fairly clear-cut evidence for human, rather than ape-like, brain organization. This is based on the following evidence:

1. The endocasts show a more human shape, particularly in the posterior migration of the lunate sulcus, which separates the primary visual cortex from the parietal association cortex, signifying an expanded associational cortical zone. The temporal lobe, so often implicated in memory mechanisms, is expanded in the anterior pole and in the inferior posterior region. The orbital rostrum is very unlike that of the apes, and there is a suggestion of an enlargement in the third inferior frontal convolution, the so-called Broca's area, which is involved in motor control of speech.

2. Indirectly, the locomotor, manipulatory, dental, and total skeletal evidence indicates a human musculoskeletal organization that presumably required neural reorganization to operate in human behavior patterns.

3. The faunal associations suggest an adaptation based on scavenging and/or hunting for animal protein. The stone tools known from this early period are made to standard patterns. Both the faunal associations and stone tools are indications of human behavior requiring reorganization at almost all levels of the brain (Holloway, 1970), from sensorimotor integration and finesse, through set and attention variables, to memory (the organization of experience and the storage, recall and reconstitution of elements).

4. Tentative brain:body ratios and encephalization indices support (but do not prove) a human brain organization.

THE STAGES OF HOMINID BRAIN EVOLUTION: A POINT OF VIEW

So far I have discussed both direct and indirect evidence to support the suggestion that the human brain had an early beginning regardless of its absolute size. All I have said thus far applies to endocasts, and thus to the brains of the early

hominids. Brains evolve in both material and social contexts. It is my contention that human social behavior has very old roots, not only in the sense that we have evolved from some primitive apelike lineage, but in the sense that human social behavioral evolution occurred early and was the major stimulus for further evolution since the time of the australopithecines. I would like to try to put together the story of the reorganization of the hominid brain, its great increase in size and the evolution of human behavior in a synthesis that avoids some of the simplistic one-to-one linear relationships that physical anthropologists are prone to make, such as that tools made the brain evolve or that tools replaced the canines.

In this section I wish to return to the original questions: How did the human brain evolve to its present state? How can we interpret the large increase in brain size from *Australopithecus* to modern *Homo sapiens*?

It is apparent that part of this increase must be related to increase in body size. Exactly how much is difficult to say, since it depends on which animal body and brain weights we compare with man and how we regard "extra" or "vital" neurons (Jerison, 1963, 1973). Taking the average human brain weight as 1450 grams and the average body weight as 150 pounds, the following different calculations can be made: (1) Using Jerison's (1973, p. 44) equation of $E = 0.07 P^{2/3}$ (E = brain weight, P = body weight) for higher vertebrates, we get an expected brain weight of 108 grams for *Homo sapiens*, leaving 1342 grams as "extra" (not related to body weight); (2) If we use Stephan's (1972) equation for "basal insectivores," the expected brain weight is 475 grams, leaving 975 grams as "extra"; (3) Jerison's (1973, p. 391) equation of $E = 0.12 P^{2/3}$ for higher primates gives an expected brain weight of 223 grams, leaving 1227 grams as "extra."¹ Both Jerison equations

¹I am using "extra" purely in the operational sense that it exceeds a weight based on a log-log regression with an exponent of roughly 0.6. I do not believe that any neural elements are in any other sense "extra," whether in terms of weight or numbers of neurons. The so-called extras are part and parcel of the animal's adaptive behavioral repertoire!

leave us with the same degree of encephalization as the dolphin.

Obviously these figures leave much to be desired, as the formulas are based on regressions relating only to living species. We would need to know the regressions for our fossil ancestors (*Ramapithecus*, *Australopithecus*, *Homo erectus*, etc.) to know what the increase in brain weight relative to body weight has been. If we use the mean of 442 cc. for the brain weight of the gracile australopithecines and 45 to 50 pounds as body weight, the brain:body weight ratio is about 1:45, roughly the same as modern *Homo sapiens*. If this ratio remains constant, i.e., at an exponent of 1.0, then none of the increase (ca. 1000 ml.) is "extra," at least in terms of the hominid regression equation.

As can be seen, the figures can be used in various ways. It is all the more curious, then, that, contrary to most opinions (Jerison, 1963, 1973), the present data on neuron numbers in the primate cerebral cortex (see, for example, Shariff, 1953) do not indicate that the increase in brain size in *Homo sapiens* is primarily a result of hyperplasia, or the addition of large numbers of neurons. From Shariff's (1953) data, modern man seems to have about 1.25 times as many neurons as a healthy chimpanzee. Jerison's (1963, 1973) calculated "extra" cortical neurons are at total variance with Shariff's data, the only empirical evidence existing for primates. According to Jerison (1963), *Homo sapiens* has 2.2 times as many cortical neurons as a chimpanzee, yet his equations for "extra" neurons are derived from Shariff's empirical histological counts (see Holloway, 1966a, 1974a, for a further critique).¹

From limited neuropathological data, there is a suggestion that healthy chimpanzees and gorillas might have fewer mature functioning cortical neurons than human microcephalics (Holloway, 1964, 1968; Lenneberg, 1964, 1967). The behavioral repertoire of microcephalics is certainly limited, but many of

¹This preoccupation on mass can also be found in Count (1973), who transformed neuron numbers from base 10 to 2; i.e., humans have 2^{33} neurons, while chimpanzees have 2^{31} neurons. Count suggested that thus only two mitotic divisions separates the chimpanzee from the human brain. I strongly disagree with this interpretation.

them can use language, and their behavior is hardly simian. This further suggests some basic reorganization of the brain.

Most scientists agree that the major increase in brain size is most likely related to hypertrophy, or increase in size, of the elements. The cortical neurons are generally large in man, there is a reduction in their density and an increase in both dendritic branching of the receptive processes of the neurons and in the number of neuroglial cells supporting the neurons. Thus, one important aspect of the large increase in brain size seems attributable to the reorganization of numerous component structures. That is why I believe comparisons based on cranial capacities alone are meaningless. One cc. of chimp or australopithecine cortex is not equivalent to one cc. of modern human, Neanderthal or *Homo erectus* cortex. It is changes in the spatial relationships between elements that provide our great neural complexity, for these result in an enormous number of synaptic contacts, or switching points (Holloway, 1964, 1966b, 1967, 1968).

The great increase in brain size can best be related, I believe, to a matrix of interacting variables of neural and behavioral complexity during the Pliocene and Pleistocene epochs that had an essentially positive feedback structure (see Holloway, 1967). The matrix involved a change in endocrine-target tissue interaction, an increased postnatal dependence of offspring on parents, delayed maturation and the growing role of social programming on the brain. This interpretation is based on (1) observations regarding the effects of hormonal manipulations on such brain parameters as average cortical neuron size, neuron density, dendritic branching, glial/neural ratios, and cortically-mediated behavior; (2) phylogenetic and ontogenetic changes in cortical histology; and (3) the effects of enriched and deprived environments on cortical neuron histology. I (Holloway, 1964, 1968) have reviewed this elsewhere and will not repeat the discussion here. The basic concordance in mammals between phylogenetic and ontogenetic development and extra environmental training on the one hand, and neurological changes—decreased neuron density, increased dendritic branching and

increased glial/neural ratios in animals treated with growth hormone or thyroxin—on the other, is illustrated in table 6. The table suggests a concordant picture of increase in brain complexity and cortically-mediated adaptive behavior. Thyroidectomy and sensory deprivation, however, produce opposite results.

TABLE 6
Concordances of Different Lines of Evidence and Various Neural Parameters^a

Type of Evidence	Neural Parameters				Cortically-Mediated Adaptive Behavior
	Average Size of Neurons	Neuron Density	Glial: Neural Ratio	Amount of Dendritic Branching	
Ontogenetic (growth)	+	—	+	+	+
Phylogenetic (within primates, related to brain size)	+	—	+	+?	+
Physiological manipulation					
1. throidectomy	—	+	—?	—	—
2. administration of thyroxin	+	—	+	+	+
3. growth hormone	+	—	+	+	+
Environmental manipulation					
1. Sensory deprivation	—	+	—	—	—
2. Environmental complexity and training augmented (rats) (ECT vs. IC) ^b	+	—	+	+	+

^aAs the size of the neuron increases, so does its perikarya and cytoplasm, thereby requiring more neuroglial cells to service its metabolic needs. The additional size means reducing neural density, i.e., the number of neural nuclei in a standard size cube of cortical tissue. They are thus packed together less tightly. The increased neuron size also provides more cytoplasmic material for dendritic and axonal processes. Notice particularly that the hormonal evidence (all of it *in vivo*) matches the ontogenetic, phylogenetic, and environmental lines of evidence.

^bSee Holloway, 1966a, and Rosenzweig, 1972, for details.

Anthropological interpretations of the increase in brain size generally attempt to relate the increase in cranial capacity essentially to single aspects of evidence, such as tool-making,

hunting, language, etc. As the fossil hominids show an increase in endocranial volume, the archaeological record shows a concomitant increase in the range and sophistication of stone tool assemblages and in the size and kinds of animals hunted. A statistical correlation does not, of course, necessarily mean a causal connection. I find it very difficult, if not impossible, to draw a causal connection between brain size and stone tools or hunting habits. These must surely tie in more with social programming or learning than with an increase in neural elements.

It would be a great oversimplification, if not a mistake, to relate cranial capacity in any linear or causal sense to the increasing complexity of stone tools during the Pleistocene. Early hominids accomplished more than simply making stone tools for future archaeologists' digs. Their tools were used in a variety of different environments, and their cooperative social behavior was an important part of adaptation to a hunting and gathering existence. Hunting and associated activities require a complex organization involving not only perceptual and motor skills, but an understanding of animals and their habits, plants, terrain, spoor, tracks, anatomy, butchering techniques, and perhaps storage. It is the total range of cultural adaptations that relates to brain increase; the making of stone tools is only one example, and of course, the most permanently recorded one.

To the extent that the hunting of large animals involved cooperative enterprise, selection would certainly have favored behavioral mechanisms facilitating communication, including symbolic language. Language would have led to increased complexity of social interaction, involving appreciation of numerous related cues from social and material environments, and the control and inhibition of responses. In short, the increasing complexity of stone tools indicates other processes, but it cannot lead to more than educated guesses about the ecological complexity of selection pressures for human biosocial adaptations. (These relationships between tool-making and language, and hunting behavior and various levels of neural

structure have been examined in greater detail by Holloway 1964, 1969, 1970.)

Although the australopithecine brains were small, they were larger, both relatively and absolutely, than those of the chimpanzees, which probably had similar body weights. Between the chimpanzee or the gorilla and man there is a large difference in the duration of the growth period. Maturation is complete in a chimpanzee at nine to 11 years, whereas in man it takes about 20 to 25 years.

As yet we cannot look at a fossil and say at what age it became fully adult; but we must assume that growth rates and durations changed over the course of human evolution. One cannot get a brain to evolve in size without prolonging the period of its growth. Growth is a complex process involving interaction among genetic instructions for locus and timing, tissue differentiation, hormone environment (growth hormones, thyroxin, and androgens) and proper nourishment (including social nourishment). One of the organs most vulnerable to malnourishment is the growing brain, particularly during periods of mitotic division and nerve cell enlargement. The earliest evidence of increase in brain size in the fossil record coincides with the earliest evidence for utilization of protein-rich food (animal flesh). It seems an inescapable conclusion that there was an adaptive relationship between hunting and the evolution of the brain, mediated through longer periods of growth and dependence.

A SPECULATIVE MODEL OF HOMINID EVOLUTION

What follows is a set of speculations concerning the interrelations among a number of complex variables at different levels (anatomical, physiological, neuroanatomical, ecological, and social). The main purpose of this model is merely to show the matrix of variables that I believe must be considered if we are to have a clearer understanding of how the human brain evolved.

Beginning with *Ramapithecus* (10 to 14 million years ago)

one can postulate that adaptations based on a savanna environment (utilization of seeds, grass, and other vegetation) led to strong positive selection for bipedalism. I do not think we can speculate further without additional material. Consequently, my model starts after the *Ramapithecus* level of adaptation.

Stage 1: Early australopithecine phase. Major emphasis on social behavior adaptations, involving bipedalism, endocrine organization, and brain reorganization.

Stage 2: Late australopithecine-"habiline" phase. Major emphasis on consolidation and refinement of Stage 1.

Stage 3: Late "habiline"-early *Homo erectus* to Neanderthal-*sapiens* phase. Emphasis on elaboration of cultural skills through a positive feedback relationship and brain enlargement.

Stage 1 includes the rudimentary development of cooperative, sex-role-separated social groups resulting from endocrine changes involving hormones and target-tissues. There was a reduction of sexual dimorphism in tooth and skeletal size and an increase in epigamic features of secondary sexual characteristics such as permanent breasts and fat distribution. There were possibly other changes facilitating continuous sexual receptivity of the female and closer affective relations between the sexes. This complex of correlated anatomical, physiological, and behavioral changes led to greater sexual and social control associated with prolonged periods of postnatal dependence and learning. Changes in the interactions between hormones and target-tissues could have led to a reduction in aggressive components of behavior, sexual dimorphism in size and increased periods of growth with delayed maturation of skeletal development. These processes are mediated in a complex manner by the androgens and involve other hormones as well. The endocrine changes that led to the dimorphic features cited above could have played an important role in decreasing intragroup aggression, permitting groups to live more densely. In other words, the changes led to an increase in cooperative behavior (both among males and females and among males) that meant a stronger protection against both predators and other hominid groups. At the same time they affected growth rates,

accounting for longer periods of dependency and postnatal growth during which the brain showed an allometric increase. Associated with this complex of correlated changes are the developments of language (using a primitive symbol system) and hunting and scavenging (with a greater effective range due to more advanced bipedal locomotion).

I regard the development of language as more closely bound up with social affect and control than with hunting behavior involving signaling and "object naming," although this does not mean that hunting could not have been a strong positive selection factor for language.¹ In addition to reorganization of social behavior and bipedal adaptation, there was a reorganization of the brain involving, minimally, a decrease in primary visual cortex on the convex cerebral surface and an increase in parietal and temporal association cortex, allowing for greater discrimination among complex cues of the environment and for extension of foresight and memory to cope more effectively with the savanna-type environment. Associated with these is the early manufacture of stone tools to extend the economic base. The tools may have been used to break bones to secure marrow and to detach peices of flesh or skin. They may also have been used as missiles to drive off carnivores from their kills. The latter behavior involved not only cooperation among group members, but skill in coordinating hand-eye movements and a complex appreciation of spatial-visual calculation. It is very tempting to relate this kind of behavior with the right hemisphere, known to be dominant in such coordination.

Stage 2 includes refinement and elaboration of the changes in social behavior begun in Stage 1, as well as an increased dependence on social cohesion, language, and stone tools.

¹I do not agree that human cognition, and more particularly spoken and gestural communication are mainly cortical-to-cortical events, "liberated," so to speak, from limbic influences. Emotional involvement and tonus is always present in human communication, except perhaps in cases of psychopathology. This does not mean that evolutionary changes in cortical tissue and hemispheric relationships were not necessary. I only mean that those changes were not merely additive, but totally integrated with noncortical structures, particularly the thalamus, limbic structures, hippocampus, and reticular formation.

Bipedal locomotion was essentially fully human. There was both relative and absolute expansion of the brain, associated mainly with increased body size. There was greater efficiency of economic sharing and cooperation between the sexes,¹ providing the basis for longer periods of postnatal dependency and learning, which initiated a feedback system between brain and cultural behavior. Language behavior became more strongly developed, and cognitive behavior of a more nearly human type developed, where language and tool-making arose from the same psychological structuring. There were true stone tool cultures at this stage, and language had prime importance in maintaining social cohesion and control and in "programming" offspring. Dependence on hunting increased and there was more success in stalking and hunting larger game. There was a selection for increased body size, bipedal agility and predictive abilities for more successful hunting. The social behavioral changes outlined in Stages 1 and 2 permitted longer male-male association for persistent hunting and for the protection of a more secure home base for females and young, who were providing small game and vegetables. The "initial kick," or "human revolution," is fully set and leads to Stage 3.

In Stage 3 a positive feedback between brain development and cultural complexity was mediated through the increased periods of dependency and learning (which was taking place in a more complex and stimulating material and social environment) of the offspring. The major neural changes are those of size and refinement of the reorganized human brain (that is, sensorimotor, associative, extrapyramidal modulation, and cerebellar involvement in manual dexterity). This is not a stage of behavioral innovation, but an elaboration of "complexity-management" involving fineness of sensory discrimination and association between larger sets of past memories and skills (see Holloway, 1967).

¹No chauvinistic intents are harbored in the speculative model, in terms of either male or female superiority. I view the evolution of sex differences, both in behavior and morphology as complementary to human evolution, not as competitive or supraordinative.

It must be emphasized that I see these stages as gradual and continuous, with certain developments stressed more strongly in one stage than in another. My main point is to show that social behavior mechanisms have had a long development, beginning with the early hominids. In a sense, increase in brain size is minor compared to the evolution of the social matrix. Brain expansion finally depends on a solid behavioral foundation. My model takes into account both the skeletal remains and the cultural evidence and provides a base for synthesizing anatomical, behavioral (social and individual), physiological, adaptational, and ecological variables.

It is possible, I believe, to consider more molecular analyses within this model. At the level of neuroanatomy, one can suggest various brain regions that could be correlated with behavioral attributes such as set and attention, concentration, "memory" (permanence, quantity, facility, and strategy of recall), hand-eye and running coordination, mother-infant affect, babbling and reticular core reorganization, cerebral lateralization, play, curiosity, prolongation of prepubertal vividness of experience, memory, and so on. To do so, however, is far beyond the limits of this lecture.

It must be understood that the analysis of endocranial casts alone cannot play more than a limited role in elaborating my hypothesis, or in supporting my speculations. The external morphology of endocasts provides clues, not proof, about past selection pressures, and these clues are fairly gross. The judicious use of endocasts, both as clues to neural reorganization and to changes of growth variables must await further discoveries with firm dates. While studies of australopithecine endocasts are in progress, it should be apparent that the specimens have potential use, both as clues to general events in hominid evolution and as morphological patterns for taxonomic purposes. The analysis given thus far shows, I believe, that the evolution of the brain has always been an integral part of hominid evolution and was not something that took place following other changes in different morphological sectors of the hominids.

Let me close by asserting my belief that human behavior is a long-standing evolutionary development, possibly more than three million years old. Human thought, aside from its more sophisticated scientific recency, is no late invention, but instead is very old. The human brain is both the product and cause of the evolution of human social behavior, and we should recognize that our brains are both the instruments and products of our sociality, the genesis of which was long in the making.

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