Human Brain Evolution: A Search for Units, Models and Synthesis[1]

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Abstract: The challenge of trying to understand human brain evolution requires a constant synthetic integration between comparative neuroanatomy and paleoneurology. Each has its strengths and weaknesses, but only paleoneurology can provide insights into an evolutionary lineage's brain evolution. The challenge in this realm is to move from "paleophrenology" to a paleoneurological domain that is empirical, quantitative, and hopefully replicable. Paleoneurology can provide at least six levels of neurobiological information. Absolute (and relative) brain size is but one level. This paper will focus on those kinds of evidence which hopefully address the issue of brain **organization** and **hierarchical** development, which might be considered as additional "phenotypic windows" worthy of study. Thus far, the evidence from paleoneurological investigations suggests that cerebral organization toward a human pattern preceded the well-authenticated increase in absolute brain size, and possibly occurred in *Australopithecus afarensis*. This organizational change is reflected in convolutional patterns, hemispheric asymmetries, and size-shape morphometric patterns as analyzed through multivariate statistical techniques. Given these aspects, analyses which examine brain size *alone* are very likely to provide misleading and possibly erroneous conclusions regarding the past dynamics of human evolution, e.g., the nature of human mosaic evolution and "punctuated equilibria" and/ or "gradualism."

Résumé: C'est sur l'intégration synthétique constante des disciplines de neuroanatomie comparative et de paléoneurologie que repose la compréhension du cerveau humain. Bien que chacune ait ses avantages et ses lacunes, seule la paléoneurologie peut pénétrer de manière empirique le développement de l'évolution cérébrale d'une lignée en pleine évolution. Le défi est de savoir passer du domaine "paléophrénologique" au domaine paléoneurologique, ce dernier étant de nature empirique, quantitative, et, nous ôsons l'espérer, reproduvisible. Plus de six niveaux d'information neurobiologique nous viennent de la paléoneurologie. Le volume cérébral absolu (et relatif) n'est que l'un de ces niveaux. Cet exposé porte en majeure partie sur les données se rapportant à la question de l'*organisation* du cerveau et de son développement *hiérarchique*, lesquels peuvent être considérés comme "fenêtres phénotypiques" et valent la peine d'être étudiées. D'après l'information paléoneurologique actuelle il semble que l'organisation cérébrale menant vers des aspects humains ait pu se produire chez l'*Australopithecus afarensis*. Ce changement au niveau de l'organisation cérébrale est traduit par l'aspect des circonvolutions, certaines asymétries hémisphériques, ainsi que par les aspects morphométriques de forme et de volume tels qu'analysées par les technqiues de statistiques à variables multiples. Comme on peut le voir, les études qui se concentrent *uniquement* sur le volume cérébral peuvent facilement projeter des conclusions trompeuses ou même erronées concernant les forces motrices de l'évolution humaine comme, par exemple, sur la nature de l'évolution humaine composée et "l'équilibre ponctué" et/ou le "gradualisme".

Keywords: **Human brain, evolution, neuroanatomy, paleoneurology.**

INTRODUCTION

Brain endocasts provide notoriously little information about brain organization, and yet their existences are often seized upon to discuss the evolution of the human brain. In essence, the most secure datum provided by an endocast (which is only a mold of the interior table of cranial bone) is its volume. And except for paleoneurological specialists, who could all fit in one telephone booth, **size** or **volume** of the brain would appear to be the sole phenotypic manifestation of any value to understanding human evolution. A roughly 3-to-4-fold increase in brain size during the past 4 million years, from some *Australopithecus* species (*afarensis*) to *Homo sapiens sapiens* cannot be taken lightly. That **was** a dramatic increase in the size of a very expensive metabolic organ, or better, set of organs. If this tendency to consider brain size alone

were applied to other morphological components of human and other primate evolution, e.g., the limbs, dentition, cranium, etc., imagine how impoverished our understanding of primate evolution would be. Is size the singular phenotypic manifestation of complex ontogenetic and phylogenetic processes ascertainable from comparative neuroanatomy and paleoneurology? Are evolutionary selection models predicated purely on "allometry" or "information processing" sufficient explanations of human brain and behavioural evolution? Are these models truly testable, i.e., refutable, when we have scarcely a single accurate body weight to associate with any particular hominid cranial capacity?

After years of collecting information from comparative neuroanatomy, do we even know **what** varies phenotyptically in different animal species regarding CNS structures, or how that variability relates to behaviour at the species-specific level, or how natural selection operates at the genotypic level affecting neural phenotypic variability?

Taking our own species as an example, I would challenge anyone to provide authentic, replicable, empirical evidence that can relate normal brain size variation to behavioural variation.[2] Yet the literature is replete with examples of the continual utilization of these two gross levels of distal phenotypic manifestations as if they were, in and of themselves, the only genotypic variations under pressure of natural selection, or other evolutionary mechanisms, such as drift, mutation, etc.

My purpose in participating in this symposium is not to provide a neat theory, but rather to express a number of reservations I have regarding the ways in which the problem of human brain evolution are approached. My purpose is to try to delineate some of the problems, as well as provide what I hope are some fresher insights from the paleoneurological evidence for hominid brain evolution during the past 3 to 4 million years.

EXPANDING THE PHENOTYPIC WINDOWS

I begin this paper with a fairly long quotation from a recent article entitled "Gene Expression in Brain" (Farquhar, et al. 1979) because it offers so much protein for thought:

> "Gene expression in mammalian brain is higher than in other complex tissue. DNA-RNA hybridizations studies with adult mouse, rabbit and human brain RNA have shown that 25% to 40% of single copy DNA...is expressed as RNA in brain compared to 10% to 12% in liver, kidney or spleen...Much of the transcribed RNA is degraded in the nucleus...;however, about 20% of the various sequences are transported to the cytoplasm for use in protein synthesis...the high level of transcription in the brain represents a capacity for expression of thousands of different DNA sequences...Studies of gene expression at different stages of normal and abnormal development suggest that brain development is associated with large changes in gene expression. Comparisons of RNA diversity in fetal and adult mice...,rabbits..., and humans...show that twice as many sequences are expressed in the adult as in the fetal brain...Studies of gene expression in rat brain have demonstrated differences based on environmental rearing conditions. For example, brain RNA from rats raised in impoverished environments show less sequence diversity from littermates raised under enriched conditions...Approximately 95% of (single copy) DNA sequences are homologous between chimpanzee and human and 85% are homologous between macaque and human...whereas less than 5% are homologous between rodent and human..."

First of all, the brain shows a 2 to 4-fold increase of DNA (single copy) expression over most other organs. This convincingly suggests more structural genes for natural selection to act upon. There is a 2-fold difference in expression of RNA between fetal and adult brains, and part of the diversity of RNA is attributable to environmental influences. In other words, a considerable amount of genetic switching "on and off," and integration takes place. Given a 95% homologous rate between ourselves and chimpanzees, one wonders what the 5% controls, particularly in view of the known prolonged growth of the human brain after birth in comparison to the chimpanzee. The majority of papers in the literature concerned with human and/or primate brain evolution give the implicit suggestion that the above 5% only regulates the size of the brain. There is not a single empirical demonstration that this is the case.[3]

Numbers have an almost magical quality about them, particularly for those concerned with phenotypic windows that lead to theories regarding brain evolution. Thus brain size, relative brain size, and derived statistics such as E.Q.'s (encephalization quotients) and Nc's ("extra neurons") (Jerison 1973) have been the most widely and persistently used phenotypic windows to express our wider ignorance of the total phenotypic expressions inherent in brain structure and function. To put it more bluntly, we must get beyond these phenotypic expressions of **size only**, if we are ever to have a coherent theory about human brain evolution. One could say the same for aardvark brain evolution, or brain-behavioural relationships in different breeds of dogs. I am not knocking or ignoring brain size; I am indicating that we must look for more than size, and give more thought to what natural selection actually works upon: the size of the brain, or all the complex unfolding of gene expression during differentiation, development, and growth of the brain in different species, the **most distal expression of which is brain size.**

In 1979, I tried to express my thoughts about these problems as follows:

> "By cathecting on size alone, all evolutionary paradigms become reduced to natural or genetic selection operating on incremental size increases and behavioural efficiency, which always has the underlying implicit structural argument that 'intelligence' equals 'brain size.' Thus, for example, all hominid evolution becomes 'scaling,' 'allometry,' or quantitative increases, whereas these are only distal manifestations of something more complex and important. In other words, all of individual variation, the very stuff that evolution works on, is reduced to a single dimension of either small or large. In fact, it is likely that the selection events in any animal's life depend more on the timing of maturational events, epigenesis within the central nervous system (CNS), and everyday events—that is, the 'nitty-gritty' life-death 'selection walks'—are matters of hierarchical organization, differentiation, and development, of which the outcomes through time can only be measured (thus far) as size increments. We should and can demand richer explanations." (Holloway 1979: 85).

BRAIN SIZE AND TIME

There have been a number of attempts to plot the known increase in hominid brain size vs. time. The attempts are worthy, motivated by the desire to see graphically tempo and mode in the evolutionary history of this complex organ, and thus hopefully glean some insight into the selection dynamics operating in the past. Figure 1, adapted from Holloway (1972), shows one such attempt to provide a conceptual basis for trying to depict such changes, and offers a number of possibilities. I believe it is only fair to say that such efforts are very premature, given the paucity of endocranial brain volumes and truly reliable absolute chronometric dates. The fossil hominid record does not presently suggest any single line of evolutionary development that is without controversy, making it thus impossible to put what few early endocranial volumes that exist into some neat and orderly phyletic sequence of pleasing anagenic simplicity.

The earliest hominids yet discovered date to about 4 mya (million years ago), and are from the Hadar region in Ethiopia (Johanson, et al. 1982), and Laetoli, Tanzania.[4] The range of size difference in postcranial bones and dentitions is immense, but there is only **one** cranial portion that permits a reasonable **guess** at this creature's brain size. It is about 500 ml, based on a preliminary reconstruction I have made at Columbia University. That is, unfortunately, not enough to go on, as the body size estimates are quite variable. I will discuss certain morphological aspects of this endocranial brain cast somewhat later, but for the purpose of this section, it might tentatively be suggested that if the

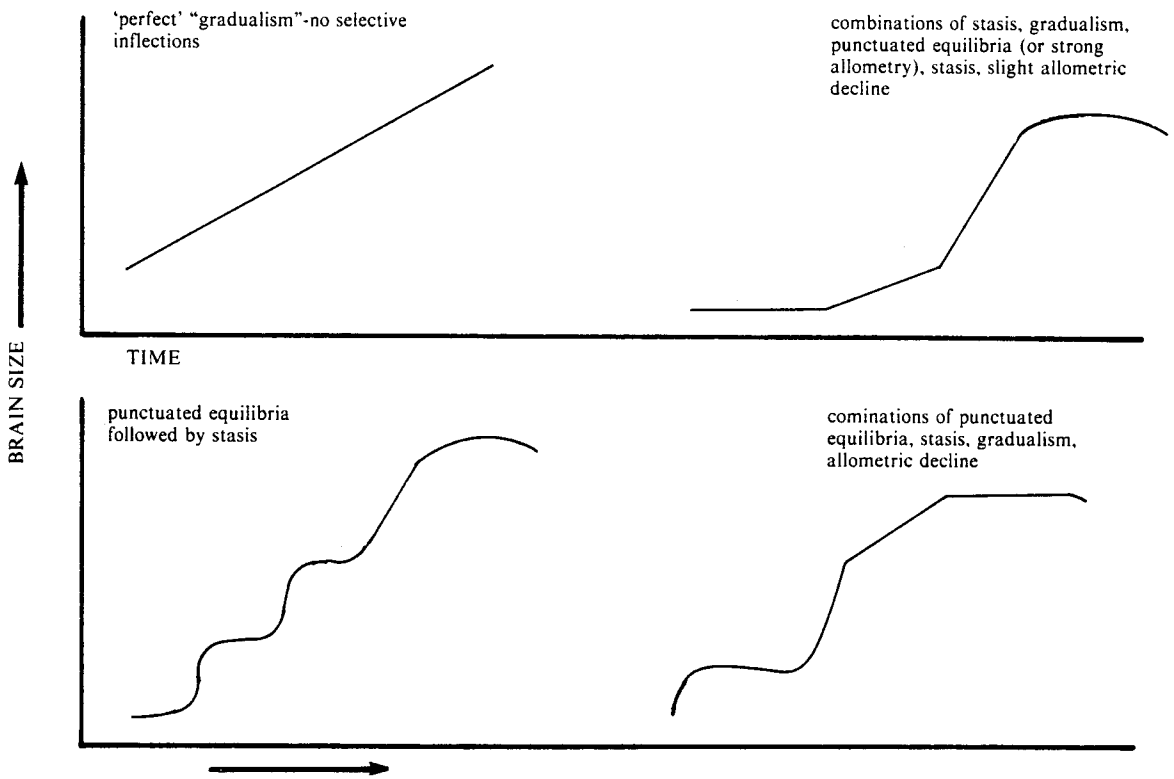

Figure 1. These hypothetical brain size versus time curves depict four possibilities during hominid evolution (adapted from Holloway 1972). Curve A would obtain if only allometrical change took place within a single hominid lineage, and at a constant rate, reflecting increasing body weight. Curve B is a composite, reflecting initial stasis, a gradual increase through allometry, and then "punctuated equilibria" where brain size increases dramatically, either through "strong" allometry, brain size increase without significant body size increase, or both. The slight allometric decline is suggested for the Neanderthal to modern *Homo sapiens* decrease. The first segment might represent *A. afarensis* with a gradual allometric (or isometric brain increase) to *A. africanus*. The strongly inclined segment could represent a *Homo habilis* to advanced *Homo erectus* evolutionary period. **However**, without secure knowledge regarding body size changes which would affect relative brain size, or reorganizational changes (e.g., increased parietal association cortex, hemispheric asymmetry, etc.), or changes in hierarchical development, these curves could be entirely misleading, as only the most distal phenotypic manifestation of neurogenetic processes is being plotted, i.e., brain size. Furthermore, the possibilities of different co-existing lineages are not drawn. Curves C and D are simply additional possibilities. The point is, we do not have the requisite knowledge to draw such curves, let alone understand their meaning in terms of evolutionary dynamics, and the paleoneurological evidence is suggesting that other changes besides brain size took place.

body-size estimate of about 75 lbs. is correct, the relative brain size of this Hadar adult *Australopithecus afarensis* is advanced beyond the chimpanzee level.

But it should be a matter of some reflection as to what brain size vs. time tells us; given a plethora of brain endocasts, all accurate with regard to volumes, and highly accurate body weights, and times, what would we have? We would have a basis for speculating about the reasons behind the **inflections** (or lack of them) in our curves of brain weight vs. time. We might speculate that at time X_1, brain growth was purely allometric, i.e., related to body size; while at time X_2 it was isometric; or at time X_3, increased without concomitant increase in body size. We could say the speed of change was fast here, slow there, constant here, etc., etc. and invariably, we would be trying to relate the **adult** volumes to behavioural efficiency and adaptation, and our model would still be one of natural selection operating on brain size only. The implicit or explicit assumption behind all of this would be: "bigger **adult** brains, better **adult** behaviour." Behaviour might be fragmented into modes of cognitive functioning, such as "memory," "foresight," "planning," "delay between stimulus and response," etc., etc. Any differences between brains in either cerebral organization or hierarchical development would not be included in the plot, and thus significant selection points possibly missed.

Let me put this another way. Imagine a line of finite length, L, representing the time of conception at the beginning, the time of death at the end, and in between we could mark off particular landmark events representing the ontogeny of a single individual. At some point, we would make a mark for reproduction, since that is the most critical time which the organism must exceed if its genes are to be replicated in the future. For a male, it may or may not matter whether the time extends further. For the female, it definitely does. Now that whole line, however long it is drawn, is subject to natural selection, and what bothers me most frankly is that most of our thinking is directed toward that line segment which extends beyond reproductive capability. To my mind, in species such as primates, and ourselves in particular, there is a relatively **long time** during which the organism must survive if it is to pass on its genes, and most of that time the organism is dependent on other social actors in its group. There is no point in denying that natural selection can operate on behaviour in the adult. My point is that natural selection also operates on a most complex interactive and interdependent set of developmental processes during the maturation of the brain **and its social and material nourishment.**

Our pictures of brain size vs. time cannot contribute to those developmental complexities in any meaningful way, except by realizing that the most distal expression of those processes is adult brain size, and that **sum**, I would argue, is really far less interesting than the parts that went into making the whole. I hope my intention is clear; by all means, we must and will continue to study brain size, but let us not lose our perspective as to what **that** phenotypic expression implies. For one thing, it implies a large number of supportive or complementary social behavioural adaptations and biological sequelae to accommodate the final product. The blood supply, pelvic diameters and flexibility during parturition, social care and nourishment, "learning," behavioural patterns emergent with extended growth and developmental periods, both in terms of extracting adequate energy resources from the environment (gathering and hunting), and a socially responsive network of caretakers, are only some of the most obvious supportive adaptations one can imagine.

ALLOMETRIC CONSTRAINTS

I believe that much more serious thought must be given to our allometric models.[5] For example, consider Jerison's (1973) magnificent chart in which 198 vertebrate species are plotted, brain weight against body weight. A polygon emerges, and by a critical geometrical choice, a slope of .66 is drawn through the array. Some of the species plotted are closely related to each other, others are not. The conclusion reached is that the brain and body are allometrically related in all species, and different brain sizes emerge from selection on body size. The question arises, or at least should arise, "how can one test the proposition that the relationships between brain and body weights is allometric for any group of phylogenetically related species?" Does every instance of a point laying on a trend line, or close to it, necessarily mean that only two variables are causally interacting? Could not some points lie on the line because indeed the former is the case, while others approximate the line for different reasons? How can one test the question? If we look at the scatter of points, particularly when log-transformed, it has a pleasing "groupiness" to it. But empirically, one should calculate the difference between the observed and predicted values for each species, and indicate closeness of fit. As far as I am aware only Passingham[6] and myself have tried to do this task for the primates. And when it is done, neural structure by neural structure, against either body weight or brain weight, there are some interesting departures between expected and observed values.

This does not deny value to the allometric concept, its definition, and its application to diverse data to take into account size increases. But I detect a tendency to reify such expressions to an almost genetically real level. Facetiously, I once said (1979: 64): "While I have never seen reference to a '.66 gene,' I believe most people think in those terms." I regard allometry as a preliminary descriptive depiction of the **correlative** nature between two complicated phenotypic characters, e.g., brain weight and body weights, or volume of primary visual cortex and brain weight, etc., etc. I do not regard it as a cause-effect analysis. For me, any allometric trend line is a **constraint, about which real organisms vary.** I regard the variations as no less important than the overall constraint, for it is the species-specific departures from trends which interest me, and for the time being, that interest happens to be focused on the human species. Perhaps tomorrow, it will be the aardvark, hyaena, or whatever species.

Surely by now, after decades of fascinating behavioural observations of different animal species

both in their natural and laboratory settings, we have come to realize that each species is somehow unique in its total behavioural repertoire, and yet there are very broad regularities, samenesses, universals if you prefer, which also exist, for example, in the mammals. These are not trivia, they are the substance of natural selection working over millions of years to produce variations upon which future selection will continue to work. They are not thoroughly explainable through allometry. All that can **possibly** be explained through allometry is adult brain size, a phenotypic characteristic which can be obtained through a diversity of developmental processes. If we were to plot all of the mammal species on a large diagram and throw in the values for cocker spaniels, great danes, basenji hounds, terriers, collies, and poodles, would anyone seriously expect them to deviate significantly from a mouse-whale plot of brain size and body weight? If you added alley and Siamese cats, would you expect any radical departures? If you added brown, black and the S-1 strain of rats, would it make a difference? Would you seriously propose that allometry "explains" their various behavioural and temperamental profiles?

Why then, should *Homo erectus* simply be an allometrically scaled version of *Australopithecus*, when the former made stone tools to standardized patterns and hunted large game animals, while there is no evidence that the latter did the same? Why should *Australopithecus robustus* be merely an allometrically larger version of *Australopithecus africanus* simply because brain size and body weight are larger in the former? Their teeth are not simply allometrically different, nor are their pelves, nor are the taphonomic relationships similar in the different beds in which they are found. Nor does the shape of the dorsal portion of their endocranial casts lend itself to such an interpretation (Holloway 1981), or the venous drainage through a marginal or accessory sinus in the robust and *afarensis* groups (see below).

Some extremely interesting and controversial work has been done by D. Freedman at the University of Chicago on ethnic differences in newborn behaviour in humans (Freedman and DeBoer, 1979). Are these differences, mostly in temperamental attributes and motor development to be related to brain size, or slight variations in the timing sequences of differentiation, development, and maturation of different parts of the newborn central nervous system? How much of the 25% to 40% of single copy DNA is involved in such variation? How much of the 20% of transcribed RNA sequences are involved? How much of the 5% difference between ourselves and chimpanzees single-copy DNA is involved? Intriguing questions perhaps, but no answers are available. The point is, there does exist some evidence for phenotypic variation of brain-behavioural interrelationships, and this work, if replicated and enlarged, could throw some much needed light on neurological variables other than size[7].

If, as de Lacoste-Utamsing and Holloway (1982) suggest, there is a statistically significant, measurable sexual dimorphism in the human corpus callosum, how much is allometric and how much controlled by genetic and epigenetic events during maturation of the brain? And when, out of a sample of almost 150 primate endocasts, we find striking differences in asymmetry patterns between pongids and humans in their cerebral hemispheres are we to regard these variations as only examples of allometry? (Holloway and de LaCoste-Larymondie, 1982)[8].

Allometry is a proper **first** approximation for testing the mathematical relationships between two variables, and thence for framing testable hypotheses about the causal (not merely correlative) association between them. This is the value of Jerison's work, and that is admirable. My point, however, is that any full evolutionary description of brain evolution will have to include more than allometry, and we must find ways of exposing **other** phenotypic windows on the brain and its development to achieve any holistic, synthetic theory between behaviour, brains, and evolution.

THE PALEONEUROLOGICAL EVIDENCE FOR HOMINID BRAIN EVOLUTION

Endocasts are very imperfect sources for detailed studies of brain structural changes through time. After all, one cannot hope to study more than surface details on the cerebral cortex, **if** these impress themselves on the internal table of bone of the surrounding cranium.[9] Cranial nerves, meningeal patterns, asymmetries, morphological shape **and size** are additional phenotypic expressions of interest to the paleoneurologist. I will not detail here the appalling lack of cerebral convolutional detail that is found on most hominoid (pongid and hominid) endocasts, as that has been discussed elsewhere (e.g., Holloway 1978b, 1975).

It is an ironic fact, at least with regard to my earlier discussions about brain size, that **that** phenotypic character is simply the most available or determinable character of them all. The point is **not** to ignore size, but to attempt to use it judiciously.

In outline, there are at least six "kinds" of information available from endocasts:

1. Absolute size
2. Relative size, when postcranial remains exist;
3. Convolutional patterns; sometimes present, but rarely so;
4. Lobar division, depending on the presence of convolutional patterns;
5. Morphometric properties, such as indices, radial and linear distance, asymmetries, etc.;
6. Meningeal (and other blood supply) patterns.

One could add a seventh kind of information if one wanted to include cranial foramina, and cranial nerves. All of these "kinds" of information depend on the completeness of the endocast, the degree of cranial deformation during and after death, and the intactness of the internal table of bone.

Presently, there are only some 40 to 50 endocasts of fossil hominids available for study, and most of these are incomplete. The number of these endocasts bearing any sulcal-gyral relief are much, much less. The "perfect" endocast, one that is complete, with good convolutional relief, has yet to be discovered.

TABLE I
Endocranial Volumes of Reconstructed Hominid Specimens

Specimen	Taxon	Region	Endocranial Volume in Milliliters	Method[a]	Evaluation[b]
Taung	*A. africanus*	South Africa	440[c]	A	1
STS 60	*A. africanus*	South Africa	428	A	1
STS 71	*A. africanus*	South Africa	428	C	2-3
STS 19/58	*A. africanus*	South Africa	436	B	2
STS 5	*A. africanus*	South Africa	485	A	1
MLD 37/38	*A. africanus*	South Africa	435	D	1
MLD 1	?	South Africa	500+20	B	3
SK 1585	*A. robustus*	South Africa	530	A	1
OH 5	*A. robustus*	East Africa	530	A	1
OH 7	*H. habilis*	East Africa	687	B	2
OH 13	*H. habilis*	East Africa	650	C	2
OH 24	*H. habilis*	East Africa	590[d]	A	2-3
OH 9	*H. erectus*	East Africa	1067	A	1
OH 12	*H. erectus* (?)	East Africa	727	C	2-3
ER 406	*A. robustus*	East Africa	510+10	D	2
ER 407	*A. robustus*	East Africa	510[e]	B	2-3
ER 732	*A. robustus*	East Africa	500	A	1
ER 1470	*H. sp?*	East Africa	752	A	1
ER 1805	*A. sp.?*	East Africa	582	A	1
ER 1813	*A. sp.?*	East Africa	510	A	1
ER 3733	*H. erectus*	East Africa	848[f]	A	1
ER 3883	*H. erectus*	East Africa	804[f]	A	1
OMO 338	*A. sp.?*	East Africa	427	C	1-2
HE 1	*H. erectus*	Indonesia	953[f]	A	1
HE 2	*H. erectus*	Indonesia	815[f]	A	1
HE 4	*H. erectus*	Indonesia	900[f]	C	2-3
HE 6(1963)	*H. erectus*	Indonesia	855[f]	A	2
HE 7(1965)	*H. erectus*	Indonesia	1059[f]	C	1-2
HE 8(1969)	*H. erectus*	Indonesia	1004[f]	A	1
Salè	*H. erectus*	Morocco	880	A	1
Solo I	*H. erectus soloensis*	Indonesia	1172	A	1
Solo V	*H. erectus soloensis*	Indonesia	1250	A	1
Solo VI	*H. erectus soloensis*	Indonesia	1013	A	1
Solo X	*H. erectus soloensis*	Indonesia	1231	A	1
Solo XI	*H. erectus soloensis*	Indonesia	1090	A	1
Spy I	*H. sapiens neanderthalensis*	Europe	1553	A	1
Spy II	*H. sapiens neanderthalensis*	Europe	1305	A	1
Djebel Ihroud I	*H. sapiens neanderthalensis*	Morocco	1305	A	1

[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=f½ (LWB+LWH), Holloway (1976), where L=maximum length, W=width, B=length, bregma tex to deepest part of temporal 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.

Table 1. provides a list of endocasts this author has studied, giving the location (discovery), taxonomic assignment, volume, and comments about the reliability of such figures. The earliest hominids of Hadar, Ethiopia, and Laetoli, Tanzania, are still in the process of study. Laetoli, rich in footprints and mandibular and dental fragments, is without an "endocastable" cranial fragment. The Hadar region has provided three cranial fragments, none complete, of which one yields a reliable estimate. (See above.)

Taken all together, this collection indicates that absolute brain size roughly tripled during the past 3 to 4 mya, from about 450 ml (as an average Australopithecine value) to roughly 1400-1450, ml among our own modern species, *Homo sapiens sapiens*. Neanderthals, existing approximately 40 to 50 thousand years ago, did (on the average) appear to have slightly larger brain volumes, with the male average being around 1540+ ml. They also had a massive musculo-skeletal framework, suggesting a high degree of lean body mass, and from known relationships between brain size, stature and weight in modern *Homo sapiens* (Holloway 1979b), it would appear that the Neanderthal average excess above our own in brain size was probably related to its greater lean body mass, i.e., a true allometric relationship. Certainly, no significant convolutional details, or shape patterns, differ between ourselves and Neanderthals.[10]

Relative brain sizes, i.e., the ratio of brain weight (g) to bodyweight (g) can only be estimated in most cases. Our own relative brain size is large among mammals, but not the **largest**, being exceeded by a number of animals, including some primates. The Australopithecines, whether *afarensis*, *africanus*, or *robustus* species, are problematical, given the incompleteness of postcranial remains in **direct** association with the cranial fragments that permit brain volume to be determined. Estimates of body size do not appear to be an area where physical anthropologists share much agreement.[11] But I do believe that the

available evidence is very suggestive that relative brain size is somewhat greater than the chimpanzee, our closest living primate relative. If my calculations are correct, even the *afarensis* taxon had a higher relative brain size than pongids, although its absolute brain size is overlapped by modern pongid values.

These observations have considerable relevance to other neural measures, such as E.Q.'s (encephalization quotients), which take into account both absolute and relative brain weight. The E.Q.'s scores are of course dependent upon the data bases chosen to calculate the E. Q. 's, e.g.,

$$\text{E.Q.} = \frac{\text{brain-weight}}{0.12 \text{ body wt.}} \quad .66$$

The above equation was offered by Jerison (1973). Holloway and Post (1982) have reviewed the uses of different data bases recently, and we find one constant fact, regardless of which taxa are used in the data base, or which E.Q. equation is derived. The earliest hominids are always intermediate between present-day pongids and ourselves. We believe this to mean, minimally, that natural selections did operate on brains quite early in hominid evolution. I have said "brains" rather than "brain size" quite purposefully, because it is not possible to rule out organizational changes of the early hominids beyond a pongid level. With equal force, one cannot prove that anything else but size did change. In any event, the evolution of absolute brainsize is **not** a terminal dynamic in hominid evolution, although its importance was probably greater toward the middle and end of our evolutionary development.

Convolutional detail is difficult to extract from endocasts, and controversy is still in progress regarding Dart's (1924) original Taung discovery *Australopithecus africanus*. The major controversy centres about objectively demonstrating the position of the infamous lunate sulcus, or "affenspalte." If anterior, as Falk (1981) claims, the lunate is in a pongid position.[12] If posterior as I claim (Holloway 1982) and as did Dart, Schepers and Le Gros Clark, it is in a hominid position. The lunate sulcus is roughly the anterior boundary of the primary visual striate cortex.[13] If the lateral extent of that cortex appears reduced, it suggests an increase of the adjacent parieto-temporal "association" cortex. If that could be unequivocably demonstrated in *Australopithecus*, it would indicate that natural selection **did** operate on the **organization** of cerebral cortex, as well as its size, *early in hominid evolution.*

Preliminary studies on the Hadar *A. afarensis* endocast materials are provocative in at least two aspects. First, the small adult AL 168-28 portion is the best preserved specimen for endocranial detail in the posterior parietal and occipital regions. There is very clear evidence for a furrow or groove running obliquely from just anterior to the lambdoidal sutural remnant, diverging slightly from the midsagittal plane, for approximately 2 cm. It could be one of two critical sulcal landmarks: the lateral calcarine, or the interparietal. Comparisons, both morphological and metrical, with five *Pan troglodytes* brain casts (not endocasts) suggest very strongly that this feature is the interparietal sulcus. If correctly identified, the posterior portion of this groove is located in a posterior, decidedly non-*Pan* orientation. That is, since the posterior end of the interparietal **always** abuts the lunate sulcus in *Pan*, this latter feature should be more posteriorly oriented, i.e., in a human-like position, rather than anterior as in all *Pan* brains ever examined.

This is a preliminary judgement. A fuller description is currently in progress, but if correct, the significance is very great. It would mean that by roughly 3 mya, the cerebral morphology of these earliest bipedal hominids was already moving toward a truly hominid disposition, **despite the small size of the brain** (i.e. within modern *Pan* limits).

The second interesting aspect of the Hadar endocranial remains is that two specimens, the adult AL 333-45, and the infant, AL 333-105, show unambiguous evidence for marginal (or accessory) sinus drainage, which skirts the lateral internal margins of the foramen magnum. This feature, amongst hominid fossils, occurs **only** in robust forms of *Australopithecus* from S. Africa (Swartkrans, SK 849, SK 1585), Tanzania (O.H.5. — see Tobias 1967 for a detailed study), and Kenya (KNM-E.R. 407, 732). The KNM-ER 406 specimen is filled with matrix so this feature cannot presently be seen. The heart-shaped foramen magnum is so similar to that for O.H.5, that I would be quite amazed if KNM-ER 406 did not show a marginal sinus pattern also.

I do not wish to enter into taxonomic disputes at this stage, since this work is of a preliminary nature. But I do find it very difficult to accept the hypothesis put forward by Johanson, et al. (1982) that *A. afarensis* first evolved into *A. africanus*, and from the latter arose *A. robustus*. There is no evidence for a marginal sinus in any *A. africanus* specimen that I have seen. The feature, which presumably has some genetic developmental basis, would have had to appear independenty in *A. robustus* after the loss of the feature in *A. africanus*. Consequently, I favour, for the time being, an hypothesis in which both *A. africanus* and *A. robustus* are splitting off from *A. afarensis* somewhat earlier. But where is there early (i.e., ca.3 mya) evidence for a *robustus*-like lineage, unless perhaps, *A. afarensis* is ancestral to it, *or* the Hadar dates are too early?

But this is not the whole picture. Morphometric studies published elsewhere (Holloway, 1981) are showing considerable promise in more objectively ascertaining which regions on the dorsal brain endocast surface appear to show the greatest shape changes between taxa, once size is taken into account. In this regard, dorsofrontal and parieto-temporal-occipital regions appear to show the most differences in shape between extant pongids and early hominids (see Figure 2.). That is, once allometric corrections are made for radial distances from the surface to a homologous centre point, these regions still show the highest F-ratios of between-group variance to within-group variance, and can help discriminate taxa of endocasts with high degrees of correct classifications. This is provocative, but many caveats are in order, and the reader is urged to examine the original report

Figure 2. One of several endocast contour maps derived from stereoplotting studies (Holloway 1981a). This particular map shows the distribution of 171 univariate F-ratios, after each location was allometrically corrected (i.e., size removed). The darkest regions have the highest F-ratios (e.g., 8.5 to 12.7), significant at the .00001 level, and are located in the parietal, occipitoparietal, and middle dorsofrontal regions. This map combines information for 92 endocasts of living and fossil hominid species. The extant species were *Gorilla*, *Pan* (*troglodytes* and *paniscus*) and modern *Homo sapiens*. In essence, this map shows that the ratios of between-group to within-in group variances are very high at particular locations. Each group or set of groups compared generates a different contour map, and the reader is advised to consult the original publication for the explanation of techniques and caveats.

(Holloway 1981a). Other regions **do** show some allometric increase, and thus the studies strongly suggest that **both** size and shape were critical components during hominid brain evolution.

Moreover, studies of petalial asymmetries on a large sample of pongid and hominid endocasts (Holloway and de La Coste-Larymondie 1982) are showing significant differences in asymmetry patterns. We find that pongids, (in particular *Gorilla*), do show occipital petalial asymmetries, but seldom show the typical left-occipital, right-frontal torsion petalial asymmetry pattern so common in modern *Homo sapiens*, as Lemay[14] and her colleagues have shown. The fossil hominids, perhaps from *Australopithecus* on, but certainly *Homo*, show the human pattern with such frequency as to be indistinguishable from modern *Homo sapiens*, at least as far as Chi-square statistics are concerned.

While this finding was not totally unexpected, its strength was **not** anticipated. Considerable caution is necessary in interpreting these findings. On the one hand (to be somewhat facetious), these patterns show a high statistical correlation with right-handedness (albeit the relationships between petalias and handedness are not obligatory) and cerebral dominance. This suggests cognitive patterns of symbol-manipulating on one side, and spatiovisual and manipulovisual integration on the other, and all that **that** implies from the split-brain research of Gazzaniga, Sperry, etc.[15] These kinds of findings are ripe for synthesis with the archaeological evidence for behavioural patterns that existed among our hominid ancestors, such as tool-making, social communication (verbal and nonverbal), and skills in spatial orientation relating to throwing objects at moving targets with accuracy and force, locating game and other natural resources, and finding one's way back to camp, homebase, water source, or sleeping trees, wherever one's group was. The other hand, of course, is how to empirically demonstrate these relationships, and apply them to prehistoric populations in an evolutionary paradigm. The sample sizes for the various hominid taxa are not large enough to be certain, and in many cases, the endocasts are not complete enough to allow totally unambiguous determinations of laterality and

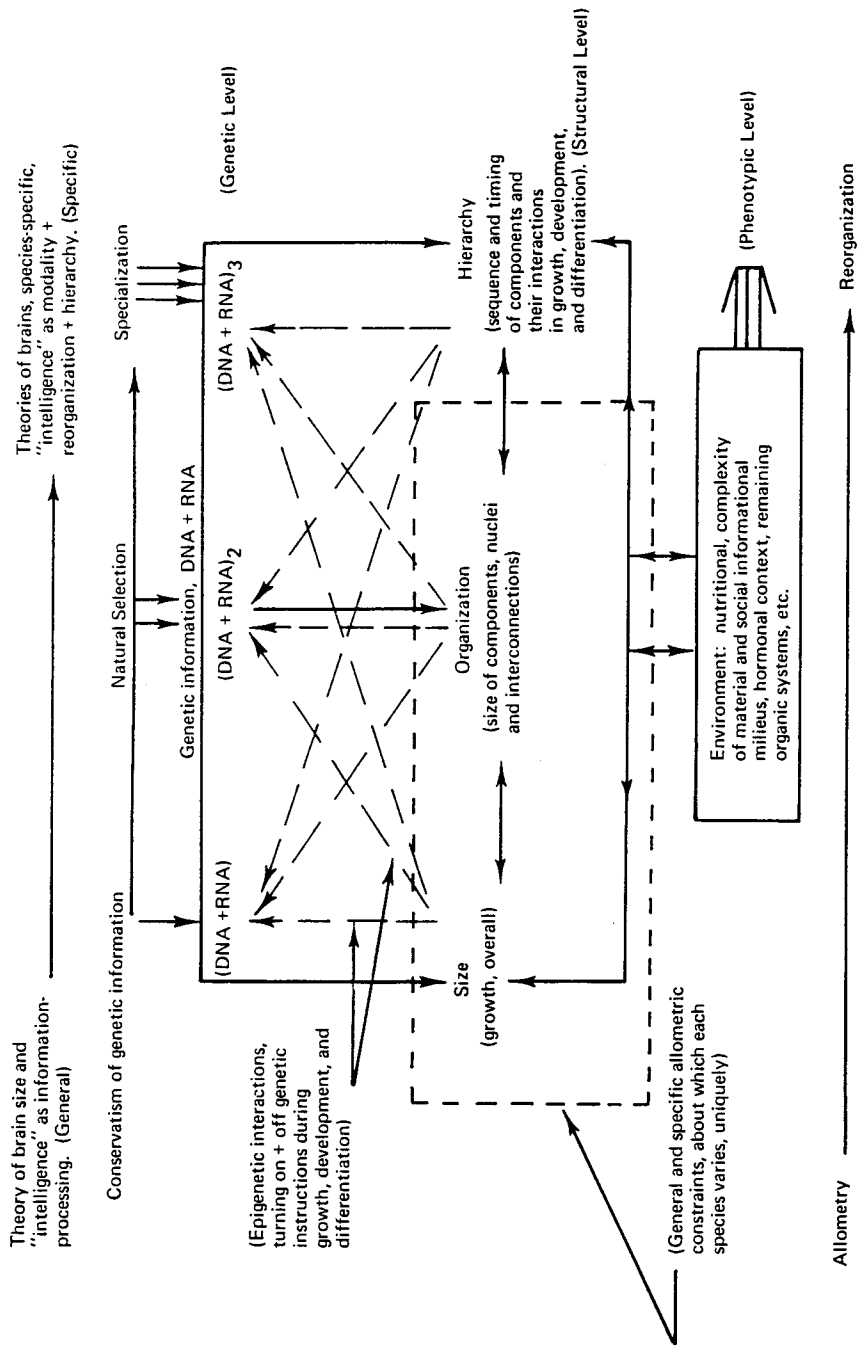

Figure 3. A model of how brain size (absolute), reorganization (differential sizes of components), and hierarchy might be conceived. The "Phenotypic Level" toward the bottom right portion of the diagram is almost exclusively regarded as brain size by most authors, but in this model is meant to include more than absolute size. For allometrists, only the left side appears to be of interest, the rest being "trivial." For anyone concerned about species-specific brain-behavioural evolution, i.e., *Homo sapiens*, the left portion cannot explain the totality that is the human brain (or any other animal's brain), as allometry is only the **constraint** around which other species vary, and brain size alone cannot be related to species-specific repertoires of behaviour, or unique evolutionary histories. This model **explicitly** regards the final phenotypic level as a complex orchestration between the neural events which unfold through the interaction of structural and regulatory genes, with natural selection operating upon at least three realms of genetic information. (This figure is adapted from Holloway 1979, where a fuller discussion can be found).

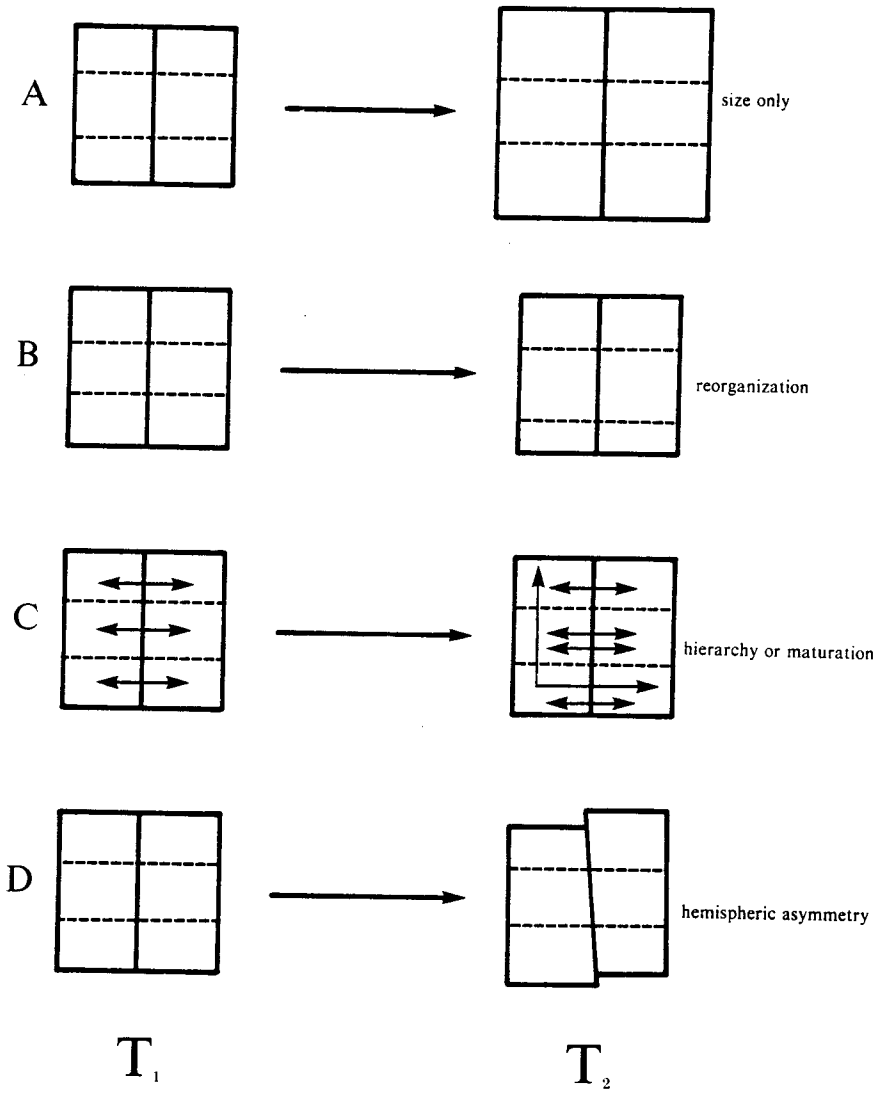

Figure 4. This figure shows four different possibilities of brain changes through time (T_1 to T_2). In A, the brain is shown with two hemispheres (left and right), and two transverse dotted lines which represent the central and lunate sulci respectively. The change from T_1 to T_2 is simply an increase in size (absolute) without any change between the size of components or connections between them. This change could occur isometrically or allometrically.

In **B**, the change from T_1 to T_2 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.

Model **C** depicts changes in **hierarchical** development without any change in absolute brain size from T_1 to T_2. The arrows represent fibre systems maturing at different rates and/or increasing in number between different cortical regions through the corpus callosum, although other brain structures and fibre systems could be involved.

In model **D**, absolute brain size remains the same from T_1 to T_2, 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 behaviour, and adaptation. Indeed, the shift from T_1 to T_2 in model B could represent a true case of "punctuated equilibrium," 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.

dynamics of human evolution. For example, when the bony postcranial remains of *Australopithecus afarensis* show clear evidence of musculoskeletal patterns indicative of bipedal locomotion (corroborated by Dr. Mary Leakey's discoveries of footprints in the tuffs at Laetoli, Tanzania), one cannot leave the nervous system in a vacuum, but must accept the fact that some re-structuring of the nervous system had to have taken place to permit the operation of a new locomotory system. One will never be able to look at the surface of an endocast for *A. afarensis*, at the precentral gyrus, and say, "See, bipedal locomotion!" But one must accept that the brain was somehow **reorganized** to accomplish the locomotory tasks, and **all that that implies in terms of adaptive behaviour**. That is, locomotory behaviour could not evolve in either a behavioural **or** brain-structure vacuum.

Stone tools, made to more or less standardized patterns, do not appear in the fossil record until ca. 2 mya. This is almost 2 my after *A. afarensis*. Perhaps wood, bone, and even stones were used in the interim, but one cannot prove it from the archaeological record as yet. Either late, more advanced versions of *australopithecus* or early true *Homo*, perhaps *habilis*, were responsible for the known stone tools from Omo, Ethiopia; Lake Turkana, Kenya; Olduvai Gorge, Tanzania; and both Sterkfontein and Swartkrans in South Africa.[18]

These artifacts show a consciousness that we identify as "human," as they indicate some operation of socially derived and transmitted sets of social consensus, or "rules." For some of us, the making of stone tools to standardized patterns suggests language was present (Holloway 1969, 1976a, b, 1981). For others it does not, as they see pongids (particularly the chimpanzees) capable of the same tasks. But more to the point, I believe these fabrications provide the earliest clues to the intellect of these early hominids and, moreover, suggest probable refinements in brain structures mediating fine manipulative capabilities, and the use of planning or foresight, and application of the tools to a number of functions involved in subsistence.

Again, one cannot look at an endocast and say, "See, this bump for the thumb on the precentral gyrus indicates tool-making," or, "Notice Broca's cap, and how it must signal that these beasts had language!" Indeed, the KNM-ER 1470 and 3732 endocasts, from Lake Turkana, Kenya, at about 1.8 mya, do have a protruding left Broca's cap, and that is corroborative, but only that.

Lastly, the dental evidence has suggested a developmental pattern of eruption that is human and not pongid-like, in the Australopithecines (Mann 1975). We cannnot know for certain the duration of growth and postnatal dependence times, but it seems most reasonable to interpolate between our own extended times and the shorter times of our closest living relative, the chimpanzee. The point I am trying to make is that natural selection had a long and complex interface of socially-nourished relationships between offspring and adults to work upon in the course of hominid evolution, and those variations in development and differentiation of the nervous system underlying those social relationships are not empirically visible (as yet) to anyone working on endocasts, and may or may not have been reflected as increases in brain size or organization of the brain.

In sum, brain size increase, both absolute and relative, were probably interspersed with evolutionary episodes of reorganization of the brain, and subtle shifts in hierarchical ontogenetic unfoldings of the complex DNA-RNA symphonic movements that are essentially constant for all mammals, but in which minor variations on the themes become the basis for species-specific behaviour patterns and brain evolutionary changes.

POSTSCRIPT

Since the preparation of this paper, newer discoveries and hypotheses regarding brain evolution have been published which require comment:

(1) In the 52nd annual James Arthur Lecture (1982) R. D. Martin has examined the issue of how big brains can be supported metabolically, and has underlined the fact that basic metabolic rate and body size, when plotted in log-log style, show a slope of 3/4 (See also Martin 1981, 1982). As Holloway and Post (1982) indicated, brain size vs. body size allometric equations vary considerably depending on the taxa chosen. While Jerison's (1973) slope of .66 is most often used, the fact is that using all primates (N=89) including *Homo*, provides a slope of .78. If *Homo* is omitted, the slope is .76 (N=88). Pongids (N=7) give a slope of .58 and Old World monkeys (N=36), a slope of .57. As we indicated on our paper, the empirical evidence does not suggest any one **single** causal explanation appropriate to all taxonomic groups. For some, the relationship between brain and body size could be related to metabolic constraints (per Martin's suggestion). In other taxa, the classical surface area-volume relationship of .66 might have been the constraint. I believe Martin's hypothesis linking large brains, metabolic demands, and a K-selective environment, i.e., "stable," is an important conceptual contribution, and one that underlines the important issues of postnatal growth and dependency, as a target for natural selection pressures in the past, as I have so often suggested.

(2) The question of cerebral asymmetries has taken on a new and provocative twist. **Not only** does the female of our species have a larger amount of corpus callosum relative to brain size than the male (de-LaCoste-Utamsing and Holloway, 1982), **but** also, this difference appears early in the prenatal embryo. Statistically significant differences are observed in the dorsoventral width of the splenium and in the ratio of corpus callosal area/brain weight in fetuses of 26-41 gestational weeks, the differences favouring the female (Baack, et al. 1982). It should be recalled that it is the splenium of the corpus callosum that contains much of the interhemispheric transfer fibres connecting the two parietal lobes. These observations, if replicated with larger samples, would corroborate: (1) much clinical data regarding differential impairment and recovery rates in females suffering cerebral insults; (2) purported gender differences in symbolic-analytic and spatiovisual-holistic task performance; (3) observations

of greater degrees of cerebral asymmetries, both functional and structural, in males. Aside from replication studies being necessary, these data suggest two important tasks: (1) extending the studies to other primates (particularly *Pan* and *Macaca*) to see if this is only a human phenomenon; (2) to integrate this data in an evolutionary context as per Holloway 1981, (Holloway and LaCoste-Larymondie 1982). This author would be amazed if sexual dimorphism in cognitive and manual skills were **not** a target for past selection pressures.

(3) The Hadar A. L. 162-28 specimen preserves a posterior portion of the cranium from which a partial endocast has been made by this author. The internal table of bone was relatively intact, and some convolutional details are visible. While my studies are in a preliminary phase, I do not detect any pattern typical of *Pan*, suggesting rather, that by 3.5 mya reorganization of cerebral cortex had occurred prior to either absolute or possibly relative brain size increase. In fact, linear arc and chord measurements, taken on the Hadar specimen and those of five chimpanzee brain casts, strongly suggest that the interparietal sulcus extends further posteriorly to a more *Homo*-like position. An alternative hypothesis was tested, i.e., that the groove was a remnant of the lateral calcarine sulcus rather than the interparietal. This hypothesis is refuted by the measurements taken from the midline to the groove. The groove is too medially placed to be a lateral calcarine groove. A third alternative, to regard the Hadar morphology as unique, sharing neither *Pan* nor *Homo* characteristics is obviously a possibility, but there is no way in which such a hypothesis could be tested without a fuller record of *Pan* brain evolution during Miocene-Pliocene times. Such evidence simply does not exist.

(4) In a most recent text, Passingham (1982) maintains that the major differences between human and other primate brains are allometric. This position apparently is endorsed by Eldredge and Tattersall (1982) and McHenry (1982). In his text, Passingham refers to my 1979 article, but dismisses the examples of departure from allometric constraints on the basis of small sample size. Curiously, he uses one of the smallest samples (i.e., Shariff 1953) to try and prove an allometric relationship for sensory cortex, after criticizing my attempts to show the departures from allometry for *Homo sapiens*. If pages 67 to 78 (Holloway 1979) are read carefully it will be seen that yes, sample sizes were small but **four independent studies provided the same overall result**, i.e., that the primary visual striate cortex in *Homo* is less than expected for a primate of our brain size.

McHenry's (1982) review of "encephalization" is interesting. First of all, the review ignores Holloway and Post's (1982) caution about the "relativity of relative brain size," although McHenry is aware that the .67 exponent has been challenged by Martin (1981). More curious, however, are the estimated body weights for the Australopithecines, which have been critically discussed in Holloway (1976a, 1981a). Once again it should be pointed out that when multiple regression is used on the actual thoracic and lumbar diameters (rather than averages) of McHenry's (1975) sample, three important things happen: (1) the residuals decrease, (2) the multiple R increases, and (3) the predicted body weights for Australopithecines (gracile and robust) are significantly less. If, in addition, one uses a .01 criterion for identifying outliers, the predicted values are even less. The effect is to lower body weights and thus increase relative brain size and thereby "encephalization". The increases do not move the australopithecines into the *Homo* range, but they do advance significantly over the pongids, i.e., *Pan*. This is not to be taken as an endorsement of McHenry's methods utilizing modern *Homo* and pongid thoracic 12 and lumbar 5 vertebrae, although I believe McHenry's study to be of great value and hopefully refined and replicated with a larger and more diverse data base. The conclusion reached is that brain size remained small for a considerable period of time, which is not in dispute. But there are tantalizing bits and pieces of evidence which suggest that more than brain size was involved (e.g., cerebral asymmetry, expansion of parietal association cortex, and possibly in the Hadar 162-28 specimen, a true hominid, disposition of the lunate sulcus). I simply regard it as premature to label this period of early hominid evolution as one of stasis based on one phenotypic manifestation i.e., absolute brain size. It is far more probable that as our fossil hominid sample increases, we will discover "mosaics" within the mosaic of the evolution of the brain. The possibility of strong and rapid selection pressures for organization could make true punctuated equilibria in brain evolution which would not appear in size vs. time plots. Selection for increased relative brain size could be gradual and appear as a punctuated equilibrium blip in such a plot. Strong selection pressures for increased body size, which in itself could be gradualistic, might result in a curve showing a punctuated equilibrium change in slope. An apparent stasis on a brain size vs. time plot could include a radical shift to cerebral asymmetry and a truly "punctuated equilibrium" in cognitive skills. The point should be obvious: beware single-variable-time curves, particularly when the variable (such as brain size) is the most distal expression of a complex unfolding of genetic-environmental interaction about which we remain curiously ignorant.

NOTES

1. This paper is a revised, updated and expanded version of an earlier paper entitled "Phenotyptic windows other than size in the evolution of the human brain," presented at the Tenth International Congress on the Unity of the Sciences, November 1981.

2. I emphasize "normal" in this challenge, purposefully ignoring known abnormalities such as microcephaly, or the well-known effects of aging and alcoholism in reducing brain weight and particular abilities, of which "memory" is but one.

3. I am aware that the obverse is also true regarding brain components and developmental maturational events. Clearly, something else than absolute size differentiates human from chimpanzee brains.

4. All earlier references to these discoveries can be found in volume 57 No. 4 of the *American Journal of Physical Anthropology*. (1982), which is devoted exclusively to these finds.

5. Those who believe allometry to be the saving empirical bulwark of evolutionary studies should carefully read the recent article ("Rethinking Allometry") by Smith (1980). I personally believe but cannot prove, that the wholesale application of allometry to all size considerations in every aspect of evolutionary biology, but human and non-human primates in particular, grossly oversimplifies the problems, and we thus lose much interesting complexity.

6. Please refer to references at the end of this paper. Passingham and I appear to view the quantitative evidence on primate brain structures very differently, as I have indicated in the "Postcript" to this paper. The newer data set provided by Stephan, et al. (1981) now includes some 40+ brain structures for 45 different primates, including *Homo sapiens*. It is impossible in this paper to go through the differences between **actual** and **expected** (allometrical) values of all of the various structures for *Homo*. Many follow a close approximation, such as the cerebellum, neocortex, septum, hippocampus, mesencephalon, etc. Other structures do not, such as the lateral geniculate, visual striate cortex, striatum, pineal, paleocortex, hypothalamus, amygdala, etc. As a full quantitative study of these departures is in preparation, it should be pointed out that viewing allometry as "constraint" rather than "law," is a useful initial distinction. The newer Stephan, et al. (1981) data confirms my 1979 findings of significant departures, particularly in the visual cortex, but in many other structures also.

7. Freedman's finding are generally unpopular among social scientists, particularly anthropologists who believe all human groups have zero variance in genetically-mediated behavioural variation, but about 33% in serum protein variation. I find Freedman's work, despite all proper caveats about ethnic or racial labels, sample sizes, etc., exciting because it hopefully opens some additional "phenotypic" windows on attributes of neonatal behavioural variation, which surely must have some structural bias, if only temporarily manifested in neonates. This is, I believe, one example of hierarchical development, which I defined as follows in the 1979 article:

   "Hierarchy refers to the unique timing of embryological and all further ontogenetic development of brain processes; (that is, myelinization, neural nuclei, and fibre tract maturational interactions) and transactions with the rest of the organism and environment. It is essentially hierarchy that results in species-specific patters of maturation of different parts of the brain at different times in relationship to some ethological paradigm of infant-mature interaction (particularly in social animals)." (Holloway 1979: 62). Please refer to the original article for other examples.

8. There are no complete *A. africanus* endocasts with both right and left sides intact, including both frontal and posterior portions. It would have been much more fortunate if our early hominid ancestors had died standing on their heads, rather than choosing sides....The *A. robustus* specimens (SK1585 and OH5) are more complete, and suggest the human petalial configuration. In our analysis, all small-brained hominids were included together, which includes KNM-ER 1805 and 1813 from Lake Turkana, Kenya. We are not certain these latter two specimens are *A. africanus*. Nor is it so easy simply to assign them to *Homo habilis*, since they are quite different from the OH7 of Tanzania which was the type specimen for this taxon.

9. It should be obvious that any cerebral convolutional detail is dependent on the impressions the gyri and sulci make upon the internal table of bone of the cranium, through the three meningeal layers. The fossil hominids from Africa are quite variable in this regard. Almost all of the E. African hominids from Lake Turkana show zero relief, due mainly to their eroded condition. The Olduvai Gorge, Tanzania, specimens tend to be better preserved, but more incomplete. Suprisingly, the best examples are from South African sites. The Hadar, Ethiopian adult (AL 333-145) specimen of *A. afarensis* is, for the most part poorly preserved with regard to the internal table. However, even intact extinct crania of modern *H. sapiens*, and the pongids, tend to show very few reliable sulcal patterns. This does not render paleoneurology useless, but it does mean that the opportunities to trace convolutional patterns in hominids is rare, and must be done with great care, utilizing measurements wherever possible to test alternative hypotheses regarding the identification of any one sulcus, i.e., the lunate, interparietal, lateral calcarine, etc.

10. See Holloway (1980) for a discussion of a possible allometric relationship, and newer data on Spy I and Spy II. Stereoplotting studies to date show no evidence of my significant regional shape differences between neandertals and modern *Homo* endocasts, except for some dorsal platycephaly.

11. The Hadar, Ethiopian hominids assigned to the taxon *Australopithecus afarensis* have a high degree of sexual dimorphism in body size, to judge from their postcranial remains. One estimate goes as far as 145 pounds, others around 75 pounds. Such variability, not only phenotypically but also in terms of estimate procedures, and the lack of clear association between individual's crania and limb bone fragments makes accurate estimate of relative brain size impossible. This fact notwithstanding, I find it amazing that McHenry (1982) is willing to use a 415 ml estimate from Johanson and Edey (1980) to provide a relative brain size for this taxon.

12. Actually, her placement of this sulcus is in a *cercopithecoid* rather than a *pongid* position, and Falk (1980) offers no quantitative justification for placing it where she does. McHenry's (1982) comments regarding Dart's mistakenly identifying the lunate as the lambdoid suture are inaccurate, as it was Schepers who made that error. While McHenry cites LeGros Clark's (1947) classic paper, it would appear that he read it as carelessly as did Falk (1980).

13. I am aware of the controversies over the interpretation of whether or not this cortex is purely "associative" or in fact a secondary integrative sensory area. My use of the term "associative" is meant to be more in accord with the latter interpretation.

14. In particular, see LeMay (1976).

15. I am assuming that these works are so well-known that citation is not necessary. To indicate adequately all of the relevant publications in this area of neurobiology would simply take too much space.

16. In fact, both the Hadar AL 333-45 adult, and the AL 162-28 specimens show very slight left occipital petalias. In the former case, there is some post-mortem damage and distortion which could play a role in the petalial information, thus my hesitation to emphasize such a finding. The latter example is very indistinct.

17. I am referring to *Microcephaly vera*, but am very aware of the inherent difficulties in utilizing pathological examples in any evolutionary context. The point is very simple, however; certain cases of microcephaly demonstrate the possibility of "nature" constructing a brain-machine lacking in size, but retaining species-specific repertoires of behaviour in base components.

18. I am aware from Professor Isaac's demonstration and slides shown during this symposium, that simply bashing two rocks together produces very useful and acceptable cutting tools. But all of the sites I mention **also** contain forms made to **standardized** patterns. Either early hominids went to far more trouble than necessary to do their tasks, or these standardized forms hopefully provide clues to cognitive patterns and communicative exchanges more complex than in other animals. (See Holloway 1969, 1981a, for a fuller discussion).

19. Language cannot be proven simply by indicating a pronounced Broca's cap, or a bulging 3rd inferior frontal convolution. But when such a pattern appears together with an expanded inferior

parietal lobule, and stone tools made to standardized patterns, the corroborative evidence becomes more additive.

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