JAMES ARTHUR LECTURE ON
THE EVOLUTION OF THE HUMAN BRAIN
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Paleoneurologic, Neoneurologic, and Ontogenetic Aspects of Brain Phylogeny

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Frederick Tilney, *The Brain in Relation to Behavior;* March 15, 1932

C. Judson Herrick, *Brains as Instruments of Biological Values;* April 6, 1933

D. M. S. Watson, *The Story of Fossil Brains from Fish to Man;* April 24, 1934

C. U. Ariens Kappers, *Structural Principles in the Nervous System; The Development of the Forebrain in Animals and Prehistoric Human Races;* April 25, 1935

Samuel T. Orton, *The Language Area of the Human Brain and Some of its Disorders;* May 15, 1936

R. W. Gerard, *Dynamic Neural Patterns;* April 15, 1937

Franz Weidenreich, *The Phylogenetic Development of the Hominid Brain and its Connection with the Transformation of the Skull;* May 5, 1938

G. Kingsley Noble, *The Neural Basis of Social Behavior of Vertebrates;* May 11, 1939

John F. Fulton, *A Functional Approach to the Evolution of the Primate Brain;* May 2, 1940

Frank A. Beach, *Central Nervous Mechanisms Involved in the Reproductive Behavior of Vertebrates;* May 8, 1941

George Pinkley, *A History of the Human Brain;* May 14, 1942

James W. Papez, *Ancient Landmarks of the Human Brain and Their Origin;* May 27, 1943

James Howard McGregor, *The Brain of Primates;* May 11, 1944

K. S. Lashley, *Neural Correlates of Intellect;* April 30, 1945

Warren S. McCulloch, *Finality and Form in Nervous Activity;* May 2, 1946

S. R. Detwiler, *Structure-Function Correlations in the Developing Nervous System as Studied by Experimental Methods;* May 8, 1947

Tilly Edinger, *The Evolution of the Brain;* May 20, 1948

Donald O. Hebb, *Evolution of Thought and Emotion;* April 20, 1949

Ward Campbell Halstead, *Brain and Intelligence;* April 26, 1950

Harry F. Harlow, *The Brain and Learned Behavior;* May 10, 1951

Clinton N. Woolsey, *Sensory and Motor Systems of the Cerebral Cortex;* May 7, 1952

Alfred S. Romer, *Brain Evolution in the Light of Vertebrate History;* May 21, 1953

Horace W. Magoun, *Regulatory Functions of the Brain Stem;* May, 1954

Fred A. Mettler, *Culture and the Structural Evolution of the Neural System;* April 21, 1955

Pinckney J. Harman, *Paleoneurologic, Neoneurologic, and Ontogenetic Aspects of Brain Phylogeny;* April 26, 1956

PALEONEUROLOGIC, NEONEUROLOGIC, AND ONTOGENETIC ASPECTS OF BRAIN PHYLOGENY

It is an honor to have been invited to deliver a James Arthur Lecture on the Evolution of the Human Brain. Our discussion is the twenty-fifth in an annual uninterrupted series which began in 1932, so that it may be of interest to refer at the outset to the topics discussed in previous lectures, in an attempt to distill some of the spirit of the series.

One finds, of course, that the phrase "evolution of the human brain" has been afforded a rather wide interpretation. The majority of the previous speakers seem to have followed the lead of the inaugural lecturer, the late Professor Tilney, and have discussed behavioral aspects of brain structure and function. Several speakers were neurophysiologists and dealt with recent findings (often their own) on the way the brain carries out its manifold operations. A third group discussed one or another of the three different ways of looking at brain evolution, which receive consideration in this presentation, namely, the study of brain history as revealed by a consideration of fossil brains (paleoneurology); of comparative anatomy of contemporary brains (neoneurology); and of the embryological development of the brain (ontogeny).

Both comparative anatomy and embryology have long been regarded as evolutionary sciences, in the sense and to the extent that both give us information about the ancestry of the animals studied. In comparative neurology we often arrange the brains of animals in what we call a phylogenetic series. It is common to hear, read, or utter such phrases as "the brain from amphioxus to man," or "up from the ape," or "from fish to philosopher." Certain of the smaller modern primates are commonly referred to as "prosimians," with the implication, at least, that the predecessors of the monkeys resembled the lemuroids of today, and that when we study the brain of the bush baby or the potto, it is tantamount to studying an ancestor of the rhesus monkey or the Hamadryas baboon. Embryology, in accordance with the well-known if now somewhat repudiated law of biogenesis, is certainly an evolutionary science if "Ontogeny recapitulates phylogeny." If such were the case, man in his embryological development would pass through stages which would accurately recall his evolutionary history.

But the law of biogenesis is in sufficiently bad repute nowadays that, out of consideration for our embryological colleagues, it is only fair to state that the dictum as originally expressed by Haeckel (1847) has been considerably modified by the embryologists of our time. It seems also fair to say that the general idea of recapitulation still has a powerful effect in the directing and interpreting of embryological as well as evolutionary studies. As with many generalizations, the reception accorded the biogenetic principle has been colored by the emotions and attitudes of the times. When originally propounded, biologists were sufficiently eager to embrace it that many did so rather uncritically. Later, when the fire of controversy surrounding the evolutionary concept had moderated somewhat, a reëvaluation was in order, and the weight of opinion against its obvious defects threatened to destory the usefulness of the "law" altogether. At the present time it seems that a middle ground has been approached,[1] and it is rather generally recognized

[1] A good discussion of the current status of biogenesis is by Hobart M. Smith (1956).

that, although ontogeny does not recapitulate phylogeny, *sensu stricto,* there is nonetheless likely to be a connection between certain phylogenetic events and certain of the ontogenetic events that have been preserved for posterity in embryology. In such cases, embryology provides phylogenetic insight of crucial significance and is indeed evolution reënacted.

If comparative neurology and embryology could tell us what the facts of evolution really are, it should be possible to give a fairly satisfactory account of the evolution of the human brain; or, for that matter, of many animal brains representative of the major classes and orders of the vertebrates. But, just as embryologists have come to realize the limitation of biogenesis, so also have biologists come to appreciate that modern animal types do not form a phylogenetic series. Rather, these represent the end products of evolutionary processes which may have been proceeding along independent lines for, in some instances, millions of years. According to current concepts, the various orders of placental mammals have had a separate evolutionary history for as long as 70 million years. To regard the series rat, cat, monkey, and man as phylogenetic is warranted only if rat, cat, and monkey stages can actually be verified among human ancestral types. The demonstration of such ancestral types depends ultimately on the science of paleontology and cannot be separated from it. In like manner, the sequence from embryo to fetus to newborn to adult is not *per se* a phylogenetic sequence, regardless of how many ontogenetic facts there may be which relate to phylogeny. The important point is that we cannot tacitly assume this relationship. We can only inquire whether a particular ontogenetic change has any phylogenetic counterpart or not. Embryology is an evolutionary science only to the extent that known embryological stages have been compared with the facts of phylogeny as revealed in the fossil record. In like manner, comparative anatomy is an evolutionary science only after it has been integrated into the science of paleontology.

The data of comparative neurology, then, and of neuroembryology provide only indirect evidence concerning evolution. In such circumstances, we can hardly discuss the evolution of the human brain in any rigorous sense and not refer to the direct evidence of paleoneurology—that segment of science that rests on the solid rock of fossil remains.

Fossil Brains

Of course, the brain, like other soft parts, does not really fossilize. Nonetheless, there exists during life such an intimate relationship between the exterior of the brain and the interior of the skull, that the latter may be molded to the brain's image. If an ancient skull came to rest in a muddy stratum, which subsequently hardened into rock, the rocky interior of the cranium may form a natural cast, with similar contours and surface markings to those of the brain. Such a natural cast can be exposed by the chipping away of the cranial bones, and is one form of fossil brain. Artificial endocasts may also be made after removal of the cranial contents, with the use of a variety of molding materials. In either case, the study of endocranial casts provides the basic data for the paleontology of the brain, although, in addition, considerable information about the size of the brain may be obtained from a study of the skull itself, and inferences about habits or behavior may often be drawn from a study of other portions of the skeletal remains.

Fossil brains were first described by Cuvier in 1804[1] and

[1] The author is indebted to Dr. Tilly Edinger (1956) for this reference which was discovered by her and had not been previously published.

received sporadic attention during the nineteenth century. It has been only in the present century, however, that paleoneurology has come into its own as a productive and appreciated branch of science. Even at the present time many workers in the field of neurology seem largely unaware of the contributions that paleoneurology offers. There does appear to exist, however, an increasing awareness on the part of the general public of the promise of paleontology in general and paleoneurology in particular—related, no doubt, to educational programs such as those carried out in the American Museum, as well as to the publicity afforded by the press to recent fossil finds.

The longest rigorously documented ancestry among mammals is that of the horse, and, thanks to Dr. Tilly Edinger, the brain of this animal is also better understood from the standpoint of its history than is any other form. The usefulness of generalizations concerning the evolution of the brain derived from comparative anatomy and embryology can actually be tested because of the many years of patient study by Edinger, which is summarized in her monograph on the evolution of the horse brain (1948). Edinger has, in fact, provided us with a model for the study of brain phylogeny by demonstrating that once paleoneurological data are available, one can speak with authority about evolution and at the same time test the working hypotheses inherent in the facts of comparative anatomy and embryology. Edinger found that certain evolutionary trends indicated by the study of modern forms are, in fact, substantiated by paleontology; other trends, however, are only partially verified and require modification. A rather significant number of observations revealed by the study of fossils would not have been expected from the study of contemporary animals.

Edinger's work is significant, not only because it has contributed new facts, but also because it has done so much to provide a place for paleoneurology. A tendency to be superficial about phylogeny had grown up in comparative anatomy, and her studies have required us to be more realistic. Neoneurology and neuroembryology have much to contribute to evolutionary science, if we retain our critical faculties while constructing our hypotheses and synthesize our findings with those of the paleontologist. In fact, both neoneurology and embryology have actually been strengthened by paleontology, in that the broad generalizations derived from the study of modern forms have been largely validated by reference to fossil remains arranged in historical sequence.

Let us see, then, what the bold outlines of the evolution of the human brain appear to be.

The Phylogenetic Record[1]

Until rather recently, the fossil record of the primate order was very fragmentary. The resurgence of interest in primate paleoneurology, however, as well as several recent rich strikes of fossils, now permits the following tentative sketch of man's history.

Precursors of the primates are thought to have been small, arboreal, shrew-like creatures which gave rise to the primitive tarsiers and lemurs of the Eocene. The lemurs rapidly became a specialized and separate group and persist today as lemurs. According to one view, the many tarsiers of that period evolved, independently of the lemurs, from the shrew-like precursors of the primates. In the opinion of these specialists, however, the tarsiers are derived directly from lemurs before specializations had appreciably modi-

[1] In this outline, I have drawn freely from the works of Sir Wilfred E. Le Gros Clark, an anatomist who has become sufficiently at home in paleontology to be generally recognized as the international authority on the history of the primates.

fied their generalized structure. In any case they progressed to forms that foreshadowed the monkeys during the 25 million years of this period. The succeeding period, the Oligocene, witnessed the appearance of the true monkeys which branched out throughout the world, but the descendants of which are likewise simian rather than anything else. It appears, then, that the monkeys, as the lemurs, became an offshoot and that they have thrived away from the main line.

The earliest apes also appeared in the Oligocene and can be found in each succeeding period. They are believed to have taken two separate lines: one, the now familiar side-line that leads to the highly specialized apes of today; and the other, the more conservative generalized line from which human precursors are derived. At some period between the Miocene and the Pleistocene (perhaps in the intervening Pliocene), the human stock is believed to have started its own specializations—brain, skull, and upright posture. Current opinion favors the possibility that Miocene apes gave rise to Pliocene intermediates that resemble, perhaps, *Australopithecus* which, in turn, developed into the Java and Peking hominids of the Pleistocene. These forms were eventually transformed into types similar to modern man. An interesting point about this sequence is that at almost every step of the way (except for the final stages) the brain has progressed less rapidly than the body.[1] There have been apes with monkey brains, and *Australopithecus* had remarkably human general skeletal characteristics but an ape-like brain. One can single out, from the general fossil records, tarsier-, monkey-, and ape-like brains in what appears to be the line of human development and

[1] The final steps of human evolution took place in a relatively short time, geologically speaking, during which the brain expanded at a more rapid rate than it had in its previous history.

thus provide some solace to the comparative neurologists who have been seeking to unravel the secrets of primate evolution over the years by a scrutiny of "graded series" of contemporary brains.

The Ontogenetic Record

We may continue with human embryology. Here we will have recourse mainly to the studies of the Minnesota school of anatomists which provide us with a good general picture of the ontogeny of the human brain. Most of this material was collected under the leadership of the late Professor Scammon (1933) and has been well summarized in the studies of Dunn (1921) and of Grenell and Scammon (1943).

A number of interesting facts have emerged from this work which seem pertinent to our present discussion. As is well known, the brain parts do not develop with equal speed. The older portions (as we are accustomed to think of them from both paleontology and comparative anatomy) are relatively larger in the beginning and become superseded (in size, at least) as ontogeny proceeds. Thus, the hind brain and midbrain represent a preponderant bulk of the encephalon in early development, only to be overshadowed by the forebrain later. Likewise within the forebrain itself, the older parts, such as the "rhinencephalon," are not only relatively, but apparently in certain instances also absolutely, smaller in the adult than in the embryo and fetus. The emergence of the forebrain and its newer parts is not the only striking feature of human neuroembryology. It is matched, and to a certain extent surpassed, by the evolution of the cerebellum as well. The cerebellum not only becomes dominant in later fetal life, but in point of fact enjoys its greatest period of relative growth during the last stages of the fetal-newborn period which in the human actually represents a terminal developmental phase, for the fundamental brain plan in the human is well established by the end of the first year of postnatal life.

If phylogeny is recapitulated in ontogeny, one should expect that the fossil record would show a relatively great development of both forebrain and cerebellum. However, the forebrain should slacken in development at the end, and the cerebellar increase would persevere to provide the finishing influence in the production of the brain of modern man. It is important to note that so much attention has been paid to the forebrain in general, and to the neopallium in particular, that the late relative emergence of the cerebellum, which is one of the most conspicuous volumetric events in ontogeny and has been clearly described both by Dunn and by Grenell and Scammon, seems very little appreciated. On this basis, the cerebellum appears to merit as much attention and study in the human evolutionary scheme as the forebrain itself. Interestingly enough, the late emergence of the cerebellum as a predominant structure in mammalian and primate evolution receives considerable support from both comparative anatomy and paleontology. If one takes particular note of the expansion of the lateral parts of the corpus cerebelli in primates, it is evident that, particularly in anthropoid apes and man, the so-called hemispheres reach their greatest size and complexity. As the scale is ascended, this lateral expansion develops concurrently with, and probably under the influence of, newly developed incoming pathways to the cerebellum, such as the cortico-ponto-cerebellar connections.

Paleoneurology tells a similar story. Brains of the prehuman predecessors, so far as these can be identified, are less well developed in both forebrain and cerebellum than are those of modern man. Unfortunately, however, the final stages are not clear. When more fossil material is available and when this particular point is subjected to inquiry, we may expect an answer to the question raised by the ontogenetic data, i.e., Did the forebrain as a whole retain its pre-

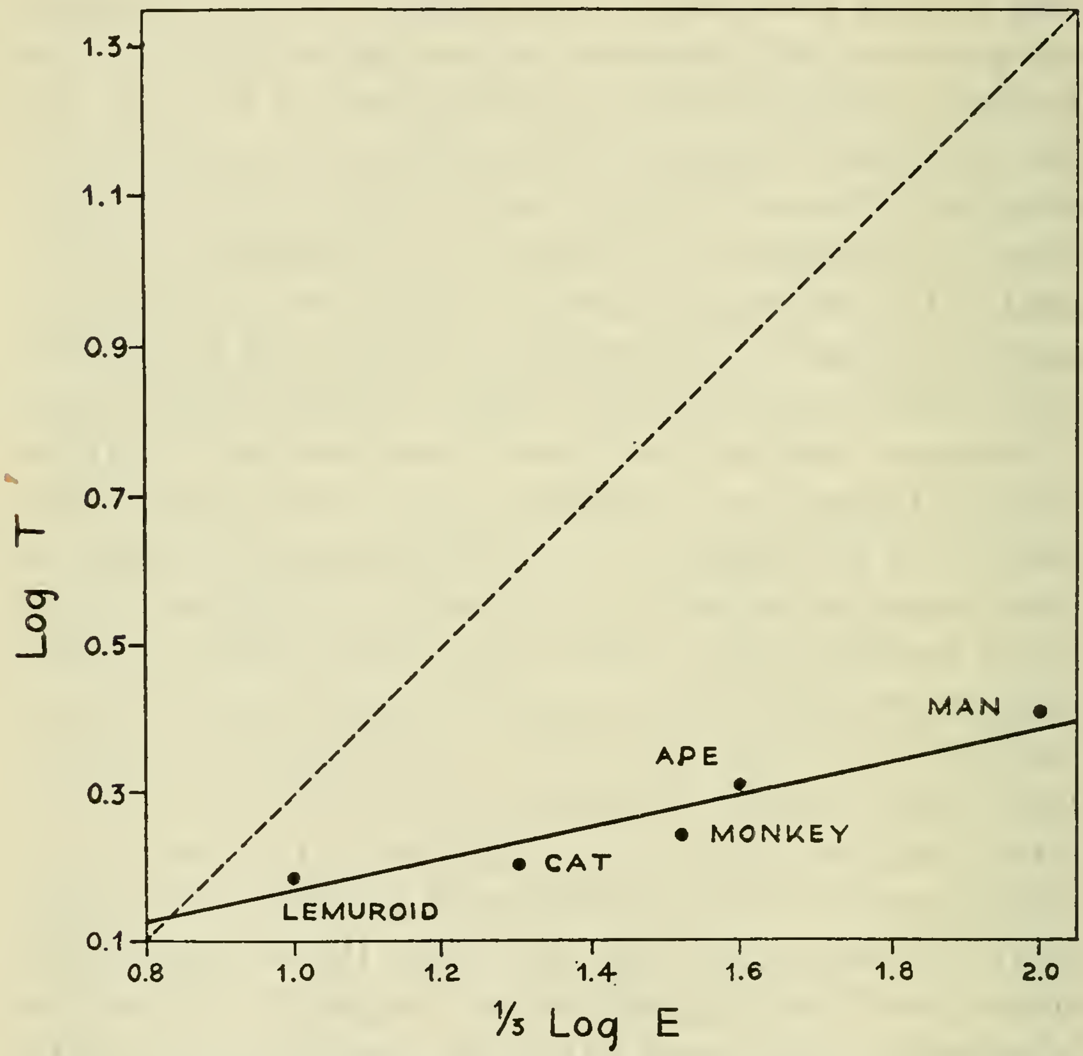

Fig. 1. Double logarithmic plot showing the relationship between increase in thickness of the isocortex to the increase in size of the brain. Logarithms are employed in order that relative change can be emphasized. The logarithm of thickness (log T) is plotted against a comparable dimension of the brain; i.e., one-third of the logarithm of the brain weight (1/3 log E). It will be seen that the rate of increase of isocortical thickness, although steady from lemuroid to man, is relatively slight, falling well below the slope of the dotted line which indicates value-to-value expansion. (From original in Harman, 1947a, p. 163, fig. 1.)

ponderating tendencies throughout evolution, or did it yield this vaunted privilege to a "downstream" structure, the cerebellum, during the terminal period when the brain of *Homo* finally became indistinguishable from that of *Homo sapiens?*

The emergence of the forebrain and cerebellum in embryology is associated with a marked furrowing or fissuration of the outer surface of these structures. Although many parts of the brain are increasing during this period, such fissuration is a familiar developmental phenomenon in only some of them. Those brain parts that exhibit increased fissuration, however, do so not only during embryological development, but also in the phylogenetic series of both the comparative anatomist and the paleontologist. The significance of fissuration appears to depend on the structural plan of the brain parts in question; that is to say, fissuration occurs in an enlarging brain part when increase in volume is accomplished without significant increase in thickness. The phenomenon is consequently especially characteristic of brain parts which form the surface or cortex, although certain interior structures (e.g., dentate nucleus and inferior olive) also exhibit the same phenomenon. Data documenting this explanation of fissuration have been supplied from comparative neurological studies, as illustrated in figures 1, 2, and 3.

Why should the cortex increase more in its surface than in its thickness? Apparently, the thickness of the cortex is a rather constant dimension, just as cell size is a rather constant dimension. Once a certain degree of maturity is attained, the brain enlarges by multiplication of cells or by expansion of intercellular space, rather than by increase of the individual elements. Further, the cerebral and cerebellar cortices achieve a relatively stable vertical structure early in development before much fissuration has occurred. Increases in the cortex thereafter are accomplished largely by lateral expansion, rather than by enlargements in depth. This means that the cortical, or fissurating, parts of the brain expand by means of an increase in the number of vertical units and/or by a sidewise swelling of such units. One would expect, then, that increase in brain size would be correlated, especially in later development, with increased fissuration. Such is actually the case with the cortex as judged by paleoneurologic, neoneurologic, and ontogenetic criteria.

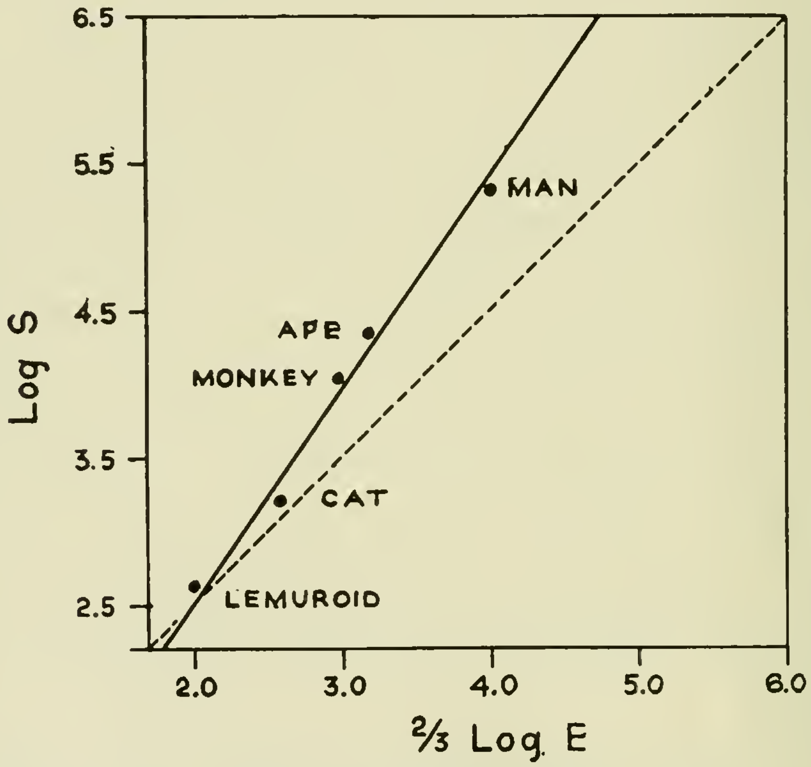

FIG. 2. Double logarithmic plot showing the relationship between increase in surface of the isocortex to the increase in surface of the brain. The logarithm of isocortical surface is plotted against two-thirds of the logarithm of brain weight. It will be seen that the rate of increase of isocortical surface is relatively great as compared to the corresponding dimension of the brain. (From original in Harman, 1947a, p. 164, fig. 2.)

The phenomenon of fissuration is relevant to the present discussion, not only because it is a striking feature of development, but also because, if our interpretation of the phenomenon is correct, we should be able to draw some inferences concerning what occurs within the fossil brain. If thickness of a cortical sheet is such a constant dimension in a fissurating cortex, then the degree of fissuration, the surface area, and the over-all size of the brain (all of which may be judged from endocasts) may provide enough data to allow a guess at cortical volume. If such is the case, a new dimension could be added to paleoneurology, a science that hitherto by its very nature has been largely a study of the brain surface.

So much for the folding of the neopallium. What of its phylogenetic growth and of the growth of other parts of the brain? Tentative answers to questions pertaining to phylo-

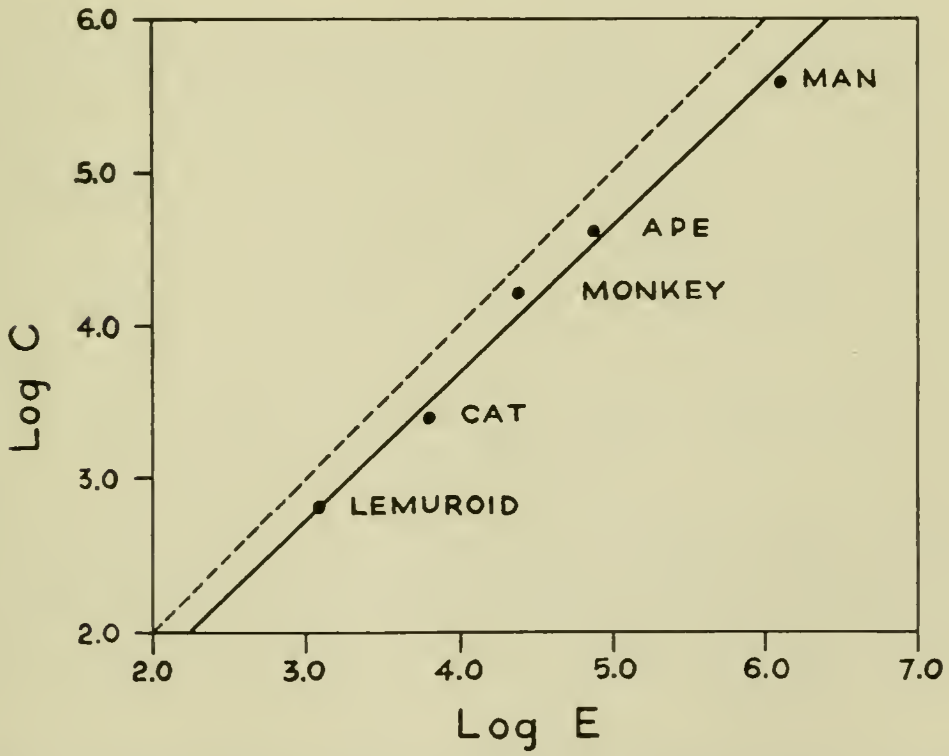

FIG. 3. Double logarithmic plot showing the relationship between increase in isocortical volume and increase in brain volume. The dotted line has been drawn at an angle of 45 degrees from the horizontal in order that the slope of log C to log E may be interpreted. It will be seen that the relative increase in isocortical volume matches the relative increase in the over-all size of the brain. (From original in Harman, 1947a, p. 165, fig. 3.)

genetic growth can be provided by comparative anatomy and seem to us to be best supplied by quantitative studies. We wish to place special emphasis on the importance of measurement to comparative neurology, because in the past all too many generalizations have been put forth in this area without recourse to data. Of course, many parts of the brain of many animals have never been subjected to quantitative analysis, but such data as are available appear to indicate certain trends which, in turn, may ultimately be correlated with fossil findings.

Neoneurologic Data on the Growth of the Brain

In figures 4, 5, and 6 are graphed some data reported by the present author some 10 years ago, which allow us to compare the "phylogenetic growth" of the neocortex as judged by comparative anatomy with the growth of the brain itself. One striking feature emerges from these data, i.e., within orders of mammals, the increase in size of the neopallium is a remarkably constant phenomenon, the neocortical volume tending towards a constant percentage of the total brain volume in both Carnivora and primates (figs. 4 and 5). A phylogenetic increase or hierarchy on a percentage basis is evident only if separate orders are compared, as is done in figure 6. For example, percentages for the Rodentia are approximately 30 per cent; for the Carnivora, between 40 per cent and 46 per cent; and for the primates, from 46 per cent to 58 per cent. It seems to me that these data are consistent with the paleontological fact that various orders have been separate for a long time, that years ago the brain plan within groups was roughed out, and that subsequent evolution took place without destroying the fundamental pattern. The same situation, indicated in these studies, which presents the interrelationships of brain parts as an orderly unfolding within groups, has also been found in our studies of the basal ganglia (Harman and Carpenter, 1950), and receives further support from the work of von Bonin (1948). The latter author has demonstrated that if the surface of the frontal lobe (a structure that is highly regarded for its preëminence in man)

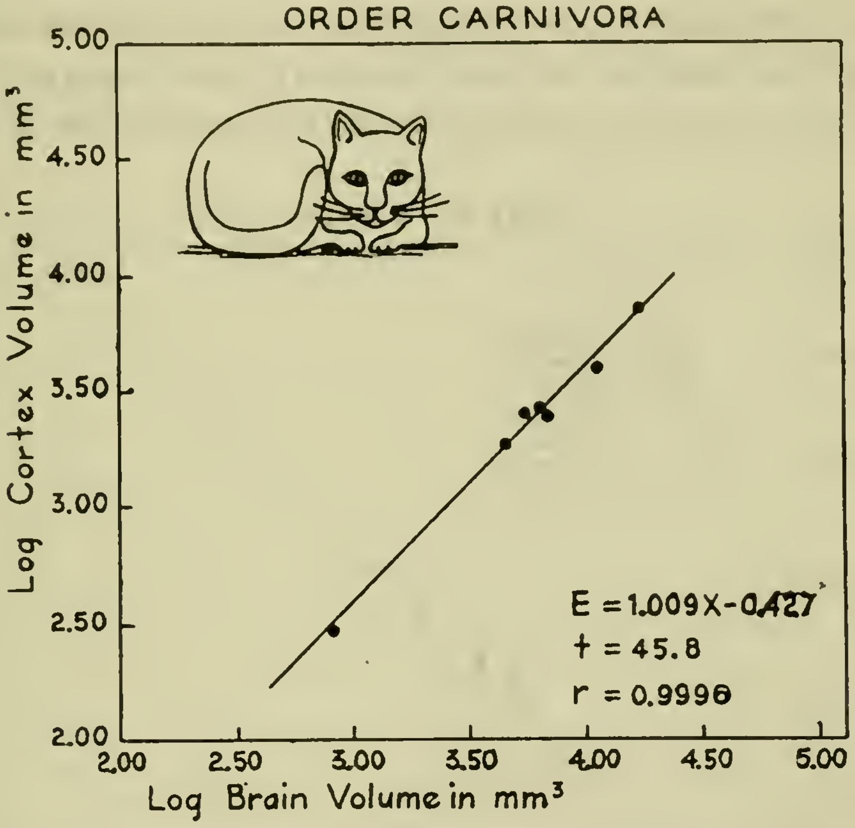

FIG. 4. Double logarithmic plot showing the relationship between isocortical volume and brain volume in Carnivora. It will be seen that the relationship is rectilinear and that the slope of the line approaches 45 degrees, indicating great internal consistency of brain parts within the carnivores. (Data from Harman, 1947b.)

is compared to the surface of the total cortex in a double logarithmic plot, a markedly rectilinear relationship exists from marmoset and lemur through monkeys and apes to man. However, in contrast to the neocortical-brain relationship, where percentages tend to remain the same within orders, there was a steady increase in the ratio (from 0.09 to 0.33) in favor of frontal cortex from marmoset to man. Thus, although the situation in frontal cortex and in neocortex as a whole may appear at first glance to be comparable, as the graphs are rectilinear, a basic difference exists in the slope of the lines. In both cases the rate of change appears to be governed by law, but the results are not the same. Man's isocortex is, by per cent, not remarkably different from that of other primates, but his frontal lobe is, although an analysis of how this may have occurred indicates that it was the result of a continuous change or trend

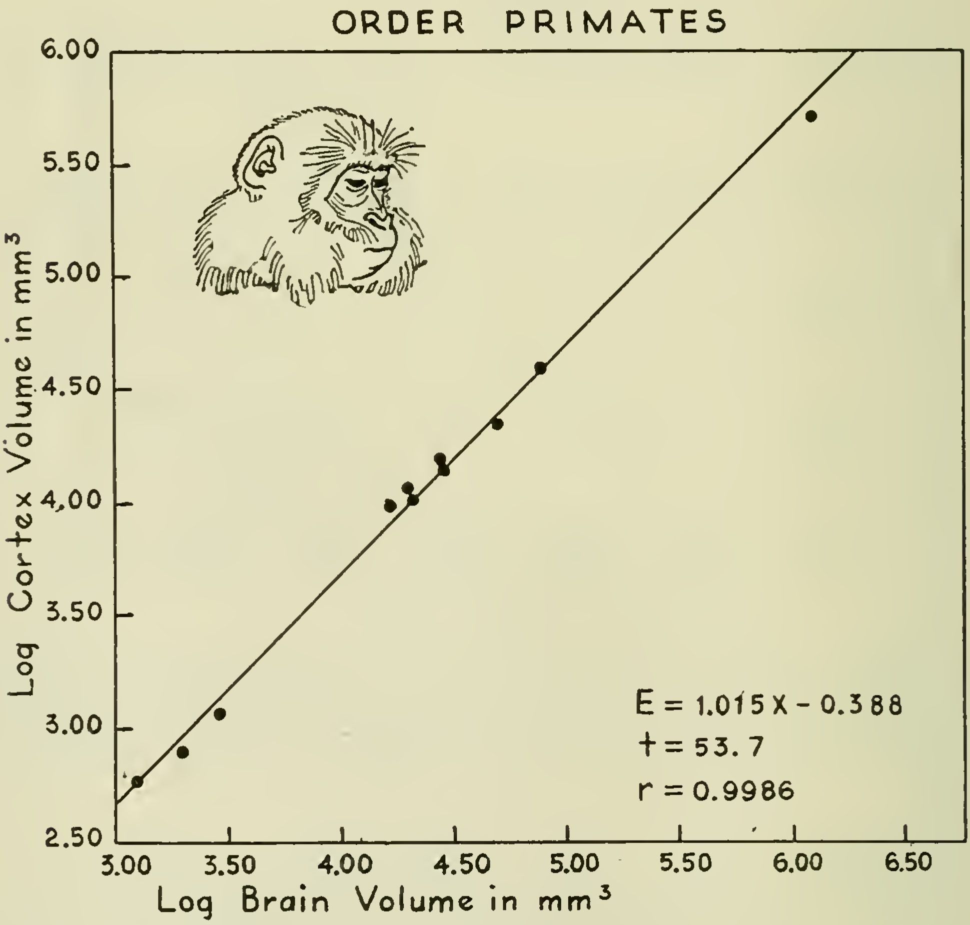

FIG. 5. Double logarithmic plot showing the relationship between isocortical volume and brain volume in primates. The similarity between this graph and that of figure 4 is evident. Apparently the isocortical-brain relationship within primates shows the same consistency as does this relationship within carnivores. (Data from Harman; 1947b.)

throughout the primate stock. Percentage-wise, then, Brodmann (1912) may have been justified in pointing to the "overwhelming development of the frontal lobe" in man, as also may von Bonin when he came to the seemingly contrary opinion that Brodmann's charts illustrated "a very simple case of relative growth, and that man has precisely the frontal lobe he deserved, by virtue of the overall size of his brain."

Further contributions to a quantitative analysis of relative brain growth have been made by the extensive measurements on brain parts of different mammals carried out by Riley (1928) some years ago. He dealt entirely with ratios or coefficients, and restricted his attention to the midbrain, hind brain, and cerebellum. His method was to compare the cross-sectional area of a brain tract or group of nerve cells to the cross-sectional area of the region of the brain in which it was found, as has been done with the spinal cord by several authors who have compared relative areas occupied by the gray and the white matter at various levels. In all, Riley compiled coefficients for some 14 components and arrived at some suggestive conclusions. The increase in the new parts of the midbrain and hind brain and cerebellum is apparent if primates are arranged in the conventional series. The importance that many of the structures that exhibit relative growth have in the organization of motor behavior is quite evident; the pyramid, the ponto-olivo-cerebellar system, the neocerebellar nuclei, their outflow and midbrain connections, all reach their highest ratios in the human brain. Older structures, such as reflex centers in the midbrain for hearing and vision, and the older centers of the hind brain dealing with those primitive spatial orientations present throughout vertebrates, decrease throughout and are lowest in the human brain. The centers in the hind brain that serve to relay sensory information to higher cen-

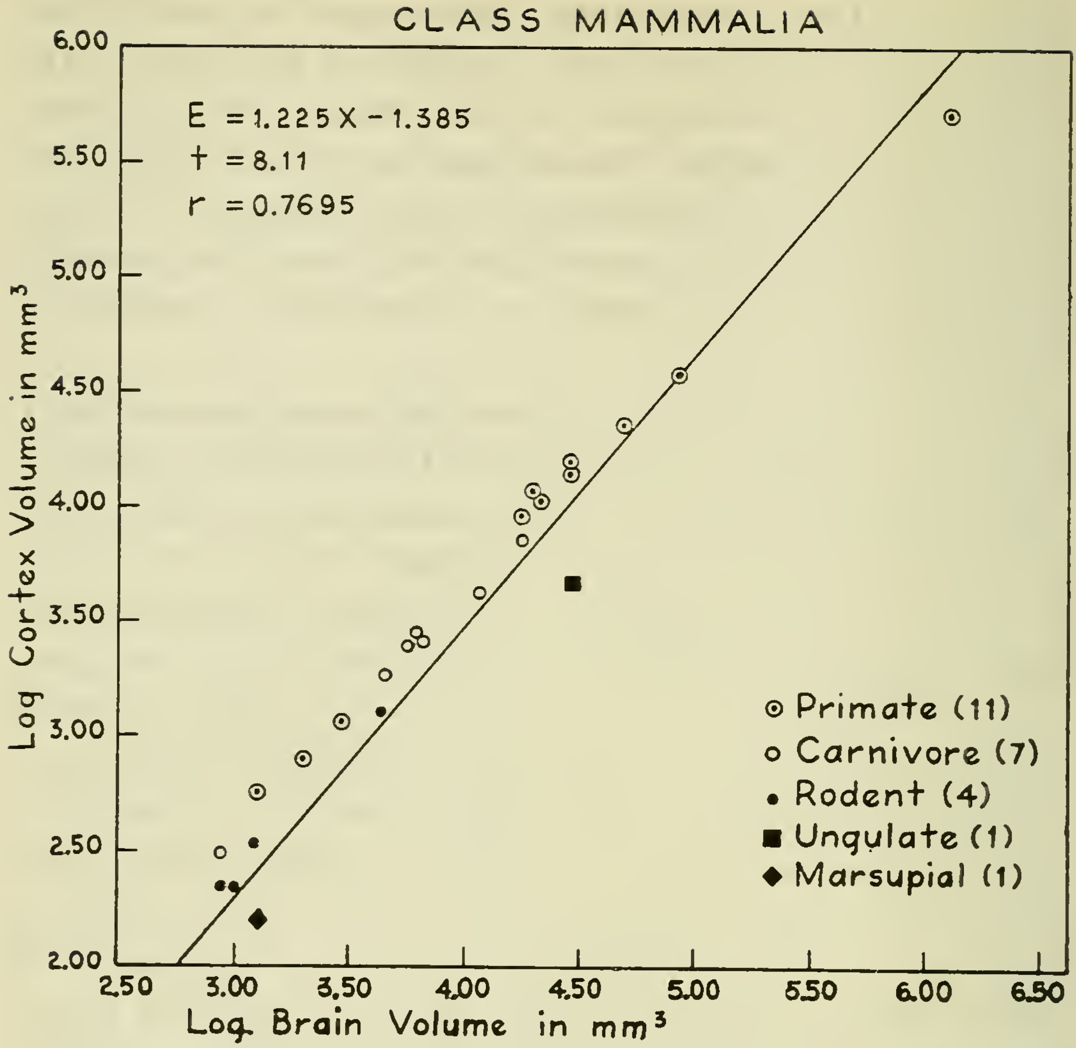

FIG. 6. Double logarithmic plot showing the relationship between isocortical volume and brain volume in different mammals. Although there is a general trend towards an increase of both cortex and brain throughout the mammalian class, if brain increase is used as the basis for comparison, considerable differences exist in amounts of isocortex between animals of different orders. Thus, in the lower left-hand corner a marsupial, a rodent, and a primate of the same brain size have markedly different cortical volumes. Throughout the plot, wherever points have the same position on the X axis, it will be noted that the values on the Y axis always favor the primate. (Data from Harman, 1947b.)

ters from the extremities are of interest. The relay centers for the lower extremities are relatively constant, whereas those for the upper extremities show a steady increase and, again, reach the highest value in the human brain. The fact that man became an armed hunter, tool maker, and fire maker early in history finds its correlation in the phylogenetic measurements compiled by Riley.

To date, no correlations have been advanced that differentiate highly civilized man from more primitive races. Comparative anatomy and embryology have been able to account to a certain extent for differences between man and other primates but not among members of the human species. We are forced to the realization that the methods are probably of value only in the broad sense. So long as we remain in this wide realm and do not overtax our methods or stretch our data, quantitative studies on the growth of the brain may be expected to yield data of importance, if only to the question of evolution in reference to the origin of species.

A Look Ahead

Our previous discussion has presented data on the growth of the human brain drawn from embryology, comparative anatomy, and paleontology. As more paleontological information becomes available, we should be better able to single out the forms of modern animals that most closely simulate stages of evolution and to assess more accurately what steps in ontogeny recapitulate phylogeny. Yet it now seems evident that all these studies must of necessity be carried out at relatively coarse levels of observation and therefore will be able to give hardly more than a generalized account of what has occurred. In spite of this fact, it also seems likely that anatomists and paleontologists will persevere until the picture of man's development (rough though it may be) has been completed. We might conclude here, but we will not because we are tempted to look ahead a bit and inquire how the general picture obtainable by the above methods of study can be supplemented by other and new techniques.

During ontogeny and also phylogeny (as judged by comparative anatomy) a number of characteristic changes occur in the cells and tissues of the brain. Chief among these are blood supply, cell form, and that intriguing phenomenon called myelination. Judged both by ontogenetic and phylogenetic criteria, a general plan of increasing differentiation and complexity has been found in the way in which the blood vessels establish themselves with respect to the central nervous system. The phylogenetic and ontogenetic growth and modification of nerve cells and the cell bodies and processes also follow a general plan of increasing complexity. The formation of myelin, a lipoprotein complex laid down on the surface of the nerve fiber and having important interrelationships with it, appears to be related not only to the taxonomic position of the animal, but also to the stage of embryological development and the phylogenetic antiquity of the fiber in question. For reasons such as these, the microscopic structure of neural tissues may acquire phylogenetic significance, and, if such is the case, exciting times are ahead. The vision of the microscope as we have known it for most of the present century has now been significantly extended by the development of electron microscopy. We can only guess at what correlations will emerge when comparative cytology has had the use of this new, powerful tool for a few more years. Certainly this vista is an intriguing one, because the electron microscope can do much to bridge the gap between the level of microscopic observation and the molecular level and thus allow for elucidation, in a very fundamental sense, of those differences and similarities that have resulted from the formation of new species and that have been responsible for them.

The Molecular Level

A science that deals with the biochemical growth of organisms and of organ systems, including the nervous system, has now reached the stage at which symposia are beginning to appear. Had I been more courageous, I might have discussed the biochemistry of the developing nervous system in the present lecture. In spite of this lack of temerity, I am encouraged to point out that just as we are on the threshold of a science of comparative cytology at the ultramicroscopic level, so also are we now witnessing the development of this science at the molecular level, i.e., with respect to the physicochemical composition of protoplasm in animals of different species and at various stages in embryological development. The concept of brain evolution that lies ahead, then, is one that promises to deal with the very crux of the matter, and these new approaches should provide increasing insight into the basic mechanisms responsible for the production of the modern brain, that is, for the growth, differentiation, and development of the functioning nervous system within the functioning organism.

Conclusion

All the studies referred to in the present paper are cooperating towards giving us a comprehensive picture of the development of *Homo sapiens*. However, it must be evident that the human being we are attempting to recreate is something of an abstraction. As anatomists, we might be content to present the story of man's origin, which would apply to the first creature who could be classified as *Homo sapiens,* an event that may have occurred some 200,000 years ago. A great deal of evolution seems to have occurred since, and it is a matter of considerable regret that this most important aspect of man's development (civilization and its effect on its architects) has been dealt with here so lightly. Fortunately, Mettler (1956) and Shapiro (1957) have both considered this problem with insight and skill.

What, then, can we make of the human brain at the present time? It is something of a morphological anomaly, which has attained great size and complexity in a relatively short period of time. Yet throughout history primates have always been distinguished by the size of their brains. As Le Gros Clark points out, the increased brain power of the primates has allowed for the keeping of generalized and primitive features along the main line of human descent. The retention of these primitive characteristics has allowed for great structural plasticity and facilitated adaptation. Man's torso and extremities seemed to have been prepared in advance, so that in the final stages of development the brain and the skull were the structures chiefly involved.

In the course of phylogenetic development, as judged by paleontology, comparative anatomy, and ontogeny, certain structures (the neo-, or new, parts) have become more prominent, somewhat at the expense of older structures. However, such phylogenetic changes as have been analyzed appear to follow simple laws of relative growth so far as rates are concerned and can usually be correlated, by rather elementary mathematical procedures, with the over-all size of the brain. Ontogeny and comparative neurology are in good agreement with paleoneurology so far as general principles are concerned, but there is an obvious need for more complete paleontological information before many comparisons of a quantitative nature can be attempted. A happy thought in this connection for those who still concern themselves with the physical facts of development (and one developed here) is that the surface of the brain appears to be a very significant dimension so far as the neocortex is concerned. Because the cortex is such an important part of the brain, and because it is in respect to surface that most comparisons with fossil forms must actually be made, we await with renewed interest new fossil findings in the primate series.

It is not unreasonable to expect that man's brain will continue to study itself so long as *Homo sapiens* shall last. We must reserve to the imagination and judgment of man himself how long this shall be and what role the human brain will play in the determination of its duration.

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