INTERPRETING THE EVOLUTION OF THE BRAIN

Author(s): HARRY J. JERISON

Source: *Human Biology*, September, 1963, Vol. 35, No. 3 (September, 1963), pp. 263-291

Published by: Wayne State University Press

Stable URL: https://www.jstor.org/stable/41448609

REFERENCES
Linked references are available on JSTOR for this article:
https://www.jstor.org/stable/41448609?seq=1&cid=pdf-reference#references_tab_contents
You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at https://about.jstor.org/terms

Wayne State University Press is collaborating with JSTOR to digitize, preserve and extend access to *Human Biology*

JSTOR

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

INTERPRETING THE EVOLUTION OF THE BRAIN[1]

BY HARRY J. JERISON
Behavior Research Laboratory, Antioch College
Yellow Springs, Ohio

A SYMPOSIUM on cultural determinants of human evolution must include some preoccupation with the evolution of the brain, because the brain as the organ of memory and knowledge is interposed in the transmission of culture across the generations of men. I came to the study of brain evolution as a student of comparative psychology, concerned not so much with the transmission of culture as with the nature of behavior over short time periods of the order of a life-time or less. More specifically, I was interested in the biological foundations of human behavior and realized that this must be found embedded, in part, in man's role among the animals. Perhaps naively, I looked to the differentiation of the human brain relative to the brains of other mammals as a major biological key to man's place in nature, and was much impressed with Lashley's (1949) remark that the only measure of relative brain development that was at all related to behavioral development was the index of cephalization, calculated from gross brain and body weight. My work has been on the analysis of brain size and its relation to body size (Jerison, 1955, 1961), and as might be expected, I was quickly captured by the fascinating problem of the evolution of the brain.

Our interests, therefore, intersect on the question of how much meaning can be attached to the gross brain size. This interest grows as much out of desperation in the face of limited data as out of a predisposition to work with gross measures like brain weight or volume. The fact is that all that we know directly about the evolution of the brain is its gross size and appearance as determined from the endocranial cavities in fossil animals. So whether we like it or not we are faced with the problem: what does the brain size mean?

My approach will be to examine relationships between brain size and the microscopic anatomy of the brain and to treat these with equations

---

[1] This research is supported by the U. S. Air Force Office of Scientific Research under Grant OSR 150-63.

I wish to thank Dr. W. I. Welker of the Laboratory of Neurophysiology, University of Wisconsin, for allowing me to use his material in the preparation of Figure 1C of this report.

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

in which brain size can be used to estimate more meaningful biological parameters. I will then develop a formal theory of brain size, because in any quantitative analysis one must take special care to explain the coefficients, and the explanation can come only from showing the place of the coefficients in an appropriate theory. In short, I begin with empirical data, use the data to establish a set of more or less elementary propositions about brain size, and then derive a numerical coefficient to estimate the "efficiency" of brains from those propositions. I will anticipate by indicating that the coefficient that will be developed is an estimator related to the total number of neurons in the cortex, and that the primates, including the hominids, will be differentiated by their values for that coefficient.

The justification for attempting a single coefficient associated with brain development is not presented in detail in the substantive parts of the paper, nor is there space to present it in detail here. I can explain it by indicating that my interest as a comparative psychologist is less in the ethologists' problem of species-specific behavior of non-human species than in non species-specific behavior of the human species. Thus, I am concerned with dimensions of behavior that may be common to many species, especially of the mammals, and more especially, of the primates. These would include learning and learning capacities (which are difficult to study because of species-specific aspects), attention and attentive behavior (which may be more sensible as a subject for study), time-binding and temporally oriented behavior, and so forth. It is probably the case that these "non species-specific" dimensions of behavior are associated with development of very extensive neural systems in the brain. These systems include a variety of projection systems for the special senses as well as the diffuse projection systems of recent notoriety that are of special interest for problems of attention (Lindsley, 1960). The efficiency of these physiological systems should be related to the properties of very large aggregates of neurons, because large parts of the brain are involved in their normal functioning. It is, therefore, appropriate to attempt to determine a measure associated with the availability of large numbers of neurons for participation in such systems.

I will now present an analysis that will permit us to go from direct measures on the size of brains of fossil hominids to estimates of the efficiency of these brains by treating them as storehouses of neurons. Thus the evolution of the hominid brain will be quantified by measuring gross brain weight or volume and using these measures to estimate the number of cortical neurons.

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

FOSSIL BRAINS AND ENDOCRANIAL CASTS

The direct evidence on the evolution of the brain comes from fossil "brains," that is, casts of the endocranial cavity. These endocasts, whether natural or artificial, often provide remarkable likenesses of the gross brain, as illustrated, for example, in Figure 1A which presents an endocast of a domestic cat and the dissected brain of the same animal. A copy of a natural endocast from an Oligocene sabertooth, *Hoplophoneus,* is shown in Figure 1B to illustrate how good an impression of the brain one sometimes gets from fossil remains.

Endocasts are available for many Tertiary mammals, and cover all of the 70 million years of the age of mammals (Edinger, 1929, 1948 1956). These are present in museums throughout the world. Unfortunately the record for primates including the hominids is one of the less complete ones. But there are some general relationships for the mammals as a class that can be derived from these endocasts, and in some instances the status and evolution of the primates can be understood as simple modifications of those relationships.

Certain limitations on work with fossil endocasts are obvious. One will never do any histology on the brain of *Hoplophoneus,* nor will its cortex be mapped for the projection of sensory systems, except by analogy (and assumed homology) with contemporary felids. On the other hand, however crude the available measures on fossil "brains," their importance is enormous, because they are the only direct record of the evolution of the brain.

Measures of endocasts are limited to (a) total volume, (b) linear measures that are sometimes combined to give indices of size, (c) measures of surface area including measures of portions of the surface relative to whole surface, and (d) diameter of nerve bundles as estimated from cranial foramina. Although many indices have been recorded, most judgments about the evolution of the human brain from hominid precursors use the first of these measures, the brain volume, as their main quantitative basis (*e.g.*, Clark, 1960; Coon, 1962). I will limit myself, here, to a consideration of the information that can be extracted about a brain if we know only its total volume.

Since the direct evidence on brain evolution comes from fossil endocasts we must first determine how accurate a model of the brain an endocast provides. Figure 1 has suggested that, qualitatively, the

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

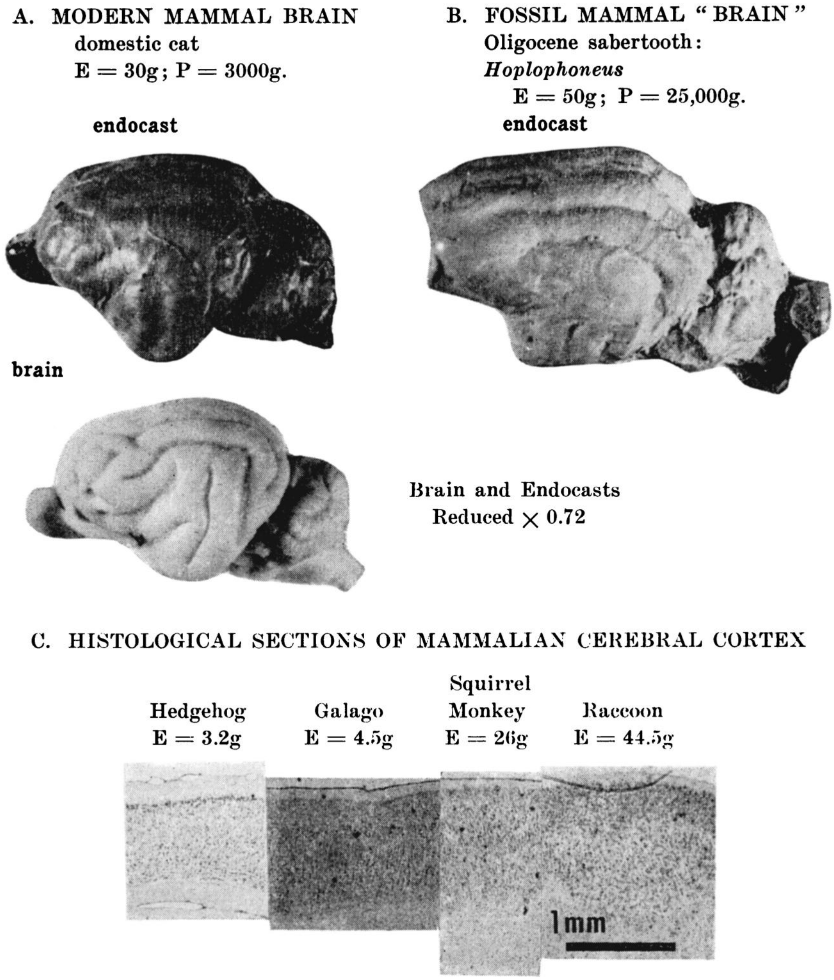

FIG. 1. MATERIAL USED IN THE ANALYSIS OF BRAIN EVOLUTION. A. Plastic endocast of domestic cat tipped slightly toward the observer (note the longitudinal fissure at top), and the dissected brain of the same animal in normal lateral orientation. Brain and body weights (E and P) in round numbers. B. Natural endocast of the sabertooth, *Hoplophoneus* from the White River Oligocene (30-35 million years ago) of South Dakota, with estimated brain and body weights. Its orientation is similar to the cat's endocast. Specimen No. 22538, U. S. National Museum. C. Photomicrographs of cerebral cortex (Somatic area?) of mammals sectioned at 25 μ and stained to show cell bodies. Sections are aligned with respect to the outermost layer of cortical cells; note that cortical thickness ranges from about .5 to 1.0 mm. The series of progressive mammals: galago (a small lemur), squirrel monkey, and raccoon show the decrease in neuron density (N_d—reflected in "graininess" of cortex at this magnification) with increasing brain weight (E) described in Figure 2 and equation 1. The hedgehog, a relict form, does not show this tendency, at least in this preparation. (Histological material from the Laboratory of Neurophysiology, University of Wisconsin.)

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

model can be very good indeed. This is true for primates (Connolly, 1950) as well as other mammals. Quantitative comparisons are also impressive and suggest that weight (grams) and volume (cc) can be used interchangeably. For example, the domestic cat in Figure 1 had an endocranial volume of 30 cc, and its brain, after several months in formalin before being removed from the skull, weighed 29.1 grams. Thus in this case the volume overestimated the brain weight by about 3%.

The most frequently seen gross measure of brain size is the brain weight, but in fossil materials as well as in Recent mammals the endocranial volume is also a common measure. It is, therefore, important to reach an understanding on the relationship of these two measures. It is not clear, for example, how much a brain weighs. Should it be weighed with or without the cerebrospinal fluid? Should the dura be left intact or should it be removed? Should the brain be weighed fresh or after fixation, and if after fixation, how long should it be pickled? These and other methodological questions have, at best, arbitrary answers, and the answers that are chosen may result in changes of as much as 20% in the measurements (Ariëns Kappers, 1929; Hrdlička, 1906; Mettler, 1956).

Estimates of volumes of fossil endocasts may also have large errors. A natural endocast that results from the replacement of soft tissues during the period of fossilization is only rarely retrieved in perfect condition, although it may be nearly perfect as in the case of the *Hoplophoneus* cast shown in Figure 1B. Very frequently the anterior parts of the olfactory bulbs are missing, as in the specimen of Figure 1B. Artificial endocasts will have other errors related to the skill of the preparator who clears out matrix from the endocranial cavity. A notorious example of an error in this regard that persisted in the paleontological literature for many years occurred in a cast described by Marsh (1876) of the endocranial cavity of *Coryphodon,* a large pantothere of some 50 million or more years ago. In this specimen the entire auditory bullae were apparently removed when preparing the skull for an endocranial cast, and Marsh remarked on the extraordinary cerebellum—most of which was created by the preparator during his excavation of the endocranial cavity! The error was finally pointed out by Tilly Edinger (1929) and by Tilney (1931), more than 50 years later.

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

In view of these and other limitations on the accuracy of measurement, it is, perhaps, wisest to consider both weight and volume measures as having rather large random errors associated with them that should be estimated by statistical procedures. I have normally used measures of volumes or weights of endocasts or brains interchangeably with minimal correction for artifacts. The random errors of measurement may approach perhaps 20% of the absolute magnitude of the measurement, and the constant errors have never been properly determined, but may be as high as 10%. We can tolerate these large errors of measurement, because the effects attributable to the variables that will concern us are large enough not to be masked by these sources of error.

BRAIN SIZE AND NUMBER OF CORTICAL NEURONS

The weight of the brain is, of course, the sum of the weights of its constituent parts. If we take the cell as the biologically significant unit, then the brain weight can be partitioned into contributions from each of the various types of cells in the brain and from the body fluids in the brain. Biologists may be reluctant to use a gross measure like the brain weight, because of the complexity of the brain's composition and the variety of its components, but it should be realized that if the contribution of any subset of cells to the total weight is orderly, then the gross brain weight could be used to estimate the number of cells in the subset. It will be shown in this section that the number of cortical neurons in the brains of mammals from a variety of orders can be estimated with fair accuracy from the brain weight alone. Stated another way, it will be suggested that even if one knows no more than that a particular number is a weight or volume of the brain of a mammal, it is possible to make a reasonable estimate about the number of cortical neurons in that brain.

The estimate is made from an equation relating the number of cortical neurons (which will be designated N) to the brain weight or volume (designated E). Such an equation will be developed from published reports on neuron density (number of neurons per unit cortical volume, N_d), and on the total volume of the cerebral cortex (V). Figure 1C, which will be discussed in greater detail later, illustrates the raw data for such an analysis. It shows frontal sections through the brains of several mammals, probably somatic cortex, with the brain weights of each specimen.

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

Neuron density has been determined empirically by counting neurons per unit cortical volume, and Figure 2 shows the relationship between neuron density and brain weight as reported by several investigators (Bok, 1959; Shariff, 1953; Tower, 1954). The lines are least-squares fits to the data in logarithmic form, and the equations of the lines are all of the form

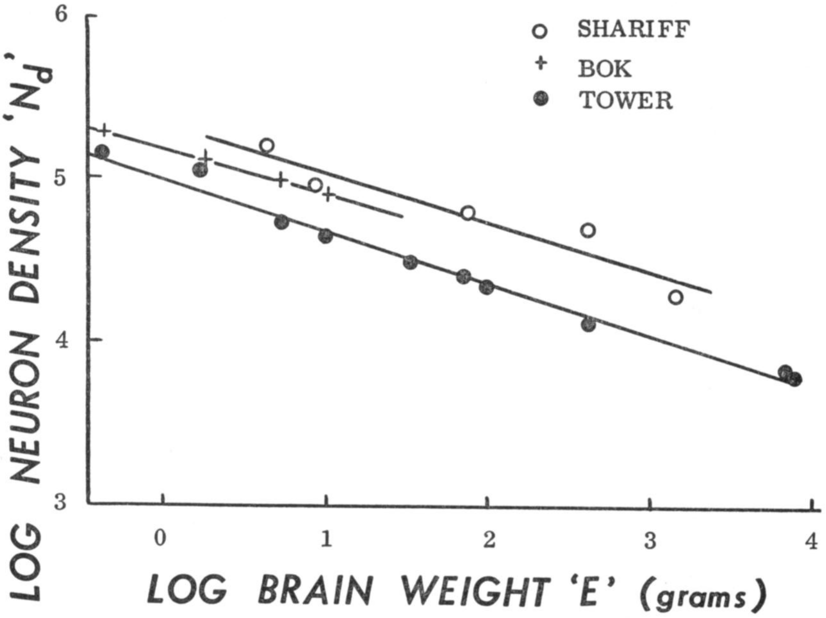

Fig. 2. Neuron Density as a Function of Brain Weight, both Measures Transformed into Logarithmic Units. Data from Bok (1959), Shariff (1953), and Tower (1954). N_d in neurons/mm^3.

$$\text{Log } N_d = a \log E + \log b_1$$

The slope, a, ranges from —.28 to —.35, or about —1/3. Written as a power function the equation is therefore:

$$N_d = b_1 E^{-1/3} \qquad (1)$$

For the present purpose there are two important things to keep in mind about Figure 2 and equation 1. First, the data were collected on brains from a variety of orders including, in Tower's data, rodents, carnivores, primates, elephant, and even whale, yet the neuron density

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

was not noticeably changed as a function of species. Second, although the curves are displaced vertically according to shifting values of b_1, the slopes of the curves (the exponent in equation 1) are remarkably consistent.

The cortical volume is determined empirically by planimetric measurements on histological serial sections. The relationship between the total cortical volume and brain size (volume or, equivalently, weight) is shown in Figure 3. The equation for these lines is:

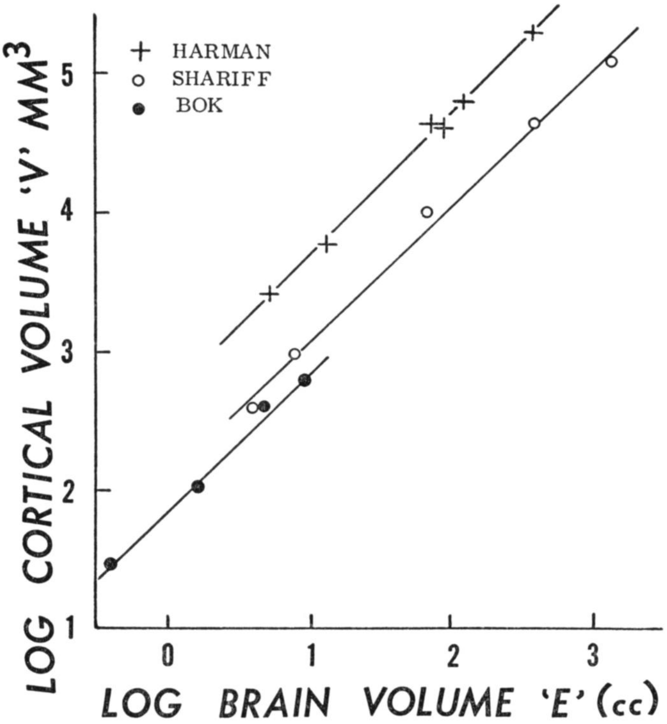

FIG. 3. CORTICAL VOLUME AS A FUNCTION OF BRAIN VOLUME (OR WEIGHT), BOTH MEASURES TRANSFORMED INTO LOGARITHMIC UNITS. Data from Bok (1959), Harman (1943), and Shariff (1953).

$$\log V = \log E + \log c_1$$

and the slope, in this case, is unity. This is, therefore, the linear equation

$$V = c_1 E \tag{2}$$

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

The value of c_i varies as b_i did in neuron density. The largest variation is attributable to Harman's use of brain volume, determined planimetrically from the cross-sectional areas of the mounted slides, as the abscissa; the other investigators used brain weights. Histological procedures usually result in consistent shrinkage of the mounted sections, a shrinkage that is usually assumed to be about 20-30%, and these and other artifacts in Harman's measurements (personal communication) probably produced some transformations of his data-points, but his results remain comparable to Bok's and Shariff's with respect to the slopes in Figure 3. As in the case of the neuron density and brain size relationship, the important feature of the data for the present argument is the similarity of the slopes in Figure 3 which permits one to write equation 2 as the general equation relating cortical volume to brain size.

For the remainder of the argument one must assume that the values of b_i and c_i in equations 1 and 2 are constants. This is readily acceptable for b_i in equation 1 (Figure 2) relating neuron density to brain weight, because one of the sets of data (Tower, 1954) is based on seven different orders of mammals, and yet the points fit well on a single line, that is a line with a single value for b_i. The displacement of the lines in Figure 2 which corresponds to differences in b_i is probably attributable to differences in the artifacts introduced by each investigator—either in the amount of shrinkage in their histological preparations, in their criteria for choosing "homologous" cortical regions in different species, or their criteria for counting a cell as a nerve cell.

It is less clearly acceptable to consider c_i as a constant in equation 2 (Figure 3) relating cortical volume to brain weight or volume, because there is a much narrower range of taxa in each group (Rodentia and a lagomorph for Bok; Primates and an ungulate for Harman, and only Primates for Shariff). Furthermore, there is some suggestion (Harman, 1957) that the primates and carnivores have consistently more cortical volume at a given brain volume than do rodents and marsupials. The most one can say is that the available evidence as shown in Figure 3 neither rejects nor supports the differentiation of the function relating volume to brain size by a taxonomic parameter. In this report we will accept the null hypothesis that the orders of mammals are not differentiated from one another in Figure 3, because it simplifies the argument considerably. If new evidence requires equations with parametric values attributable to mammalian taxa, the analysis will have to be more elaborate, but the basic argument will remain tenable.

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

It is now possible to state a relationship between neuron number and brain weight using the information in equations 1 and 2. The total number of cortical neurons is given by the product of cortical volume and neuron density or

$$N = (V)(N_d) \tag{3}$$

Substituting equation 1 and 2 in equation 3 we have

$$N = (cE)(bE^{-1/3})$$
$$N = bcE^{2/3} \tag{4}$$

or in logarithmic form

$$\log N = \log (bc) + 2/3 \log E \tag{4a}$$

Since b and c are constants this equation indicates a linear relationship between the logarithms of the number of cortical neurons and brain weight (or volume). The primary purpose of this section, to find an orderly relationship between the brain weight and a biologically significant subset of brain cells, is therefore accomplished.

Some additional results of Shariff (1953) provide a partial check on the validity of the relationship. Shariff calculated the total number of cortical neurons by sampling throughout the cortex to establish neuron density for different types of cortex (agranular, eulaminate, and koniocortex), and measured the volumes of each type of cortex. Shariff's estimates of total number of neurons in the brains of five primates are shown in Figure 4; the line is a "least-squares" fit to the points, and its slope is 0.62 ± .09. This is reasonably close to 2/3 and therefore supports the validity of equation 4a.

I have a few reservations about this analysis. First, its histological foundations should be strengthened. Figures 2 and 3, in which data from different laboratories could more reasonably be differentiated on the basis of laboratory of origin than on the basis of biological criteria, are instances of persistent artifacts contributed by the histological analysis. The recent resurgence of interest by competent biologists (see Tower and Schadé, 1960) provides grounds for optimism that this problem will disappear.

A second limitation of the analysis is due to the almost complete absence of data on differences in the number of cortical neurons among individuals of the same species and the apparently small differences between closely related species that have similar brain sizes. Information on individual differences and race differences in brain size and number of

This content downloaded from
217.91.150.187 ff:ffff:ffff on Thu, 01 Jan 1976 12:34:56 UTC
All use subject to https://about.jstor.org/terms

cortical neurons is urgently needed, because at the very least this would indicate the range of variation that can be expected for these measures, in effect, the error of measurement. At this time, with the appearance of apologists for "scientific" racism who rely on an alleged relationship between brain size and intelligence in modern man for some of their argument (see Comas, 1961), it is especially important to emphasize this major gap in knowledge. The point, of course, is that no inferences from the present argument can be drawn about differences in brain weight, whether real or due to artifacts (see Mettler, 1956), among races of a single species including the races of man.

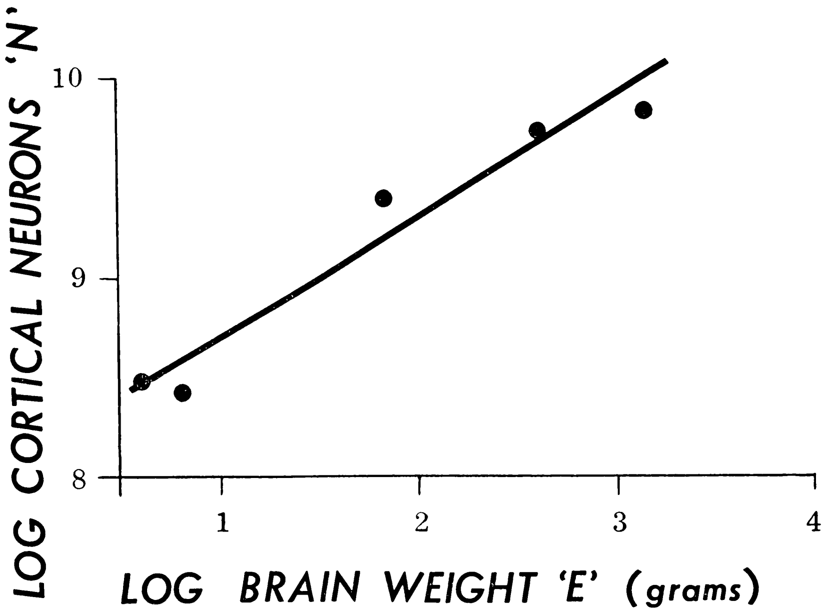

Fig. 4. Relation Between Number of Cortical Neurons and Brain Weight in Five Primates: Tarsier, Marmoset, Mona Monkey, Chimpanzee, and Man. Data from Shariff (1953).

A final limitation is associated with the uniformitarian hypothesis that the neuron-number: brain-size relationship found in contemporary mammals also held true for the fossil forms in which endocranial volumes can be determined. The contemporary species used in this analysis, though representing a broad and taxonomically diverse range of mam-

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

mals, were all members of "progressive" orders. It will be important to perform the same kind of analysis and to determine analogous empirical equations for relict forms such as the opossum, the hedgehog, the tapir, and so forth. There are essentially no published data on this question, but Figure 1C suggests that in relict forms with obviously primitive brains (*e. g.*, the hedgehog), neuron density is much lower than would be predicted from equation 1. Thus brain volume measures would overestimate brain development in some primitive mammals, if the criterion for brain development is the number of cortical neurons.

Some of the argument and one of the reservations may be appreciated better by viewing the photomicrographs in Figure 1C. The series, made up of galago (a small lemur), squirrel monkey, and raccoon, shows the trend toward decreasing neuron density with increasing brain size. This is especially clear in comparing galago with either squirrel monkey or raccoon, because from equation 1 the predicted ratios of neurons per unit volume in these three cases are 2.0 : 1.16 : 1.0. The similar apparent neuron densities in squirrel monkey and raccoon is not surprising in view of the 1.16 : 1.0 expected ratio for these two species. The reservation about possible discrepancies in neuron densities for relict forms is illustrated by the hedgehog cortex, which is clearly less densely populated by neurons than the section of the larger galago brain, and therefore contrary to the prediction of equation 1.

Appreciation of the evolution of the brain is, at best, difficult when the basic material available for study is a handful of fossil endocasts. It has been my purpose in this section to determine whether biologically significant meaning can be attached to one measure that is sometimes available from fossil remains, the endocranial volume. Keeping the various reservations cited earlier in mind, it appears reasonable to consider the brain weight or volume as a kind of biological statistic that can be used to estimate the number of cortical neurons. Further analysis of the kinds of estimates that can be made for contemporary mammals with varying evolutionary background may require a direct measure of the "progressiveness" of a brain. This might be done by measuring surface features, such as the relative extent of cortex above and below the rhinal fissure. (It will be shown later that an indirect measure of progressiveness of brains is also possible.) Our purpose should be to refine and improve our ability to estimate the microscopic anatomy of the brain from gross measures, and it may be necessary to complicate the equations that permit such estimates. The argument presented here is that this kind of estimation is both possible and profitable.

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

BRAIN SIZE AND BODY SIZE

We can now appreciate the relationship between brain size and the number of cortical neurons, but we also know that like all organs of the body the brain will tend to be larger in larger animals. That is, as body size increases the expected brain size increases. A single equation, a power function, provides an adequate description of the relationship within contemporary mammals (Rensch, 1959), and the same kind of equation yields an adequate description of the brain: body relationship in mammals at Eocene and Oligocene levels (Jerison, 1961). The equation that relates mammalian brain size to body size is

$$E = k_1 P^{2/3} \tag{5}$$

in which E is brain weight or volume, P is body weight or volume, both in grams or cubic centimeters. The constant, k_1, is about .12 for contemporary mammals, .06 for Oligocene, and .03 for non-progressive Eocene mammals and the opossum. The significance of equation 5 for this argument lies in the uniformity implied for the description of brain size in the mammals, and its specification of evolutionary changes by the parameter k_1.

The function for contemporary mammals,

$$E = .12 P^{2/3} \tag{6}$$

probably holds for the Pleistocene and could therefore be used to help establish the position of the available fossil hominids with respect to the mammals as a class. It will first be desirable to see how well equation 6 fits data for contemporary mammals, including primates, and for this purpose the brain weights and body weights of all of the clearly adult individual mammals included in Crile and Quiring's (1940) tables were graphed in Figure 5, and equation 6 was drawn on the same graph. Figure 5 can be thought of as a successful experiment in which the predictive power of equation 6 was tested with another sample of brain and body weights.

Because of our interest in the evolution of the primates, and specifically of the hominids, the points in Figure 5 representing primates have been distinguished from the others. The primates are all above the line of best fit for mammals reflecting the well-known fact that primates are big-brained mammals. A larger sample of primates, including data from Crile and Quiring (1940) used in Figure 5, data from Kennard

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

and Willner (1941a, 1941b), reports on several gorillas (Noback and Goss, 1959; Schultz, 1950), and estimates on endocranial volume of various hominids (Coon, 1962), are presented in Figure 6, along with the line representing equation 6. The tendency for the primates to form a group lying above the general mammalian line is shown strikingly in this figure.

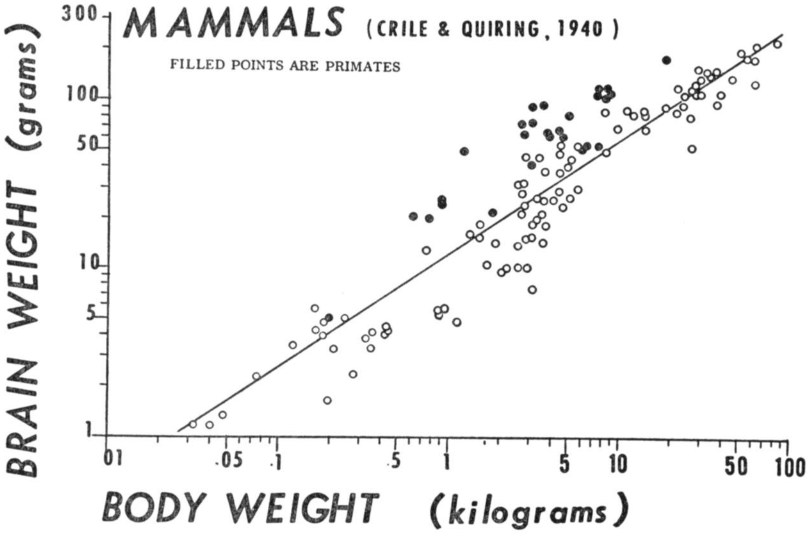

Fig. 5. Brain Weight as a Function of Body Weight. Each point represents a pair of values for mature mammals (Crile and Quiring, 1940). The line is the equation, $E = .12\ P^{2/3}$. The apparently random displacement of the points about the line can be considered as verification of the equation as a descriptive device for the analysis of mammalian brain weight, because the data points were "collected" independently of the equation.

A casual inspection of Figure 6 might suggest that the primate brain size should be estimated by a line parallel to equation 6, such as:

$$E_{\text{primates}} = .24P^{2/3} \tag{7}$$

Equation 7 when compared with equation 6 states mathematically that the "typical primate brain" is twice as large as the "typical mammalian brain" for any given body size. The implication is that brain size increased by multiplicative steps as mammalian species became more highly cephalized, an approach to brain allometry (Dubois, 1924; Brummelkamp, 1940) that has been questioned on several counts (*e.g.*, Sholl,

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

1948; Jerison, 1955). Some of the difficulties are illustrated by the data in Figure 6 on the great apes, in which the letter "C" was placed above a cluster of chimpanzee weights, and the letter "G" in the midst of gorilla weights. If equation 7 were correct, then one would have to account for the fact that the gorilla points are much closer than the chimpanzee points to the contemporary mammalian line (equation 6) that is drawn in the figure. The only justification for this would be if the gorillas were somehow describable as less cephalized or less intelligent than almost all other primates, a point that is hardly supported by comparative neurology (Tilney, 1928), or comparative psychology (Riesen *et al.*, 1953; Yerkes and Yerkes, 1929).

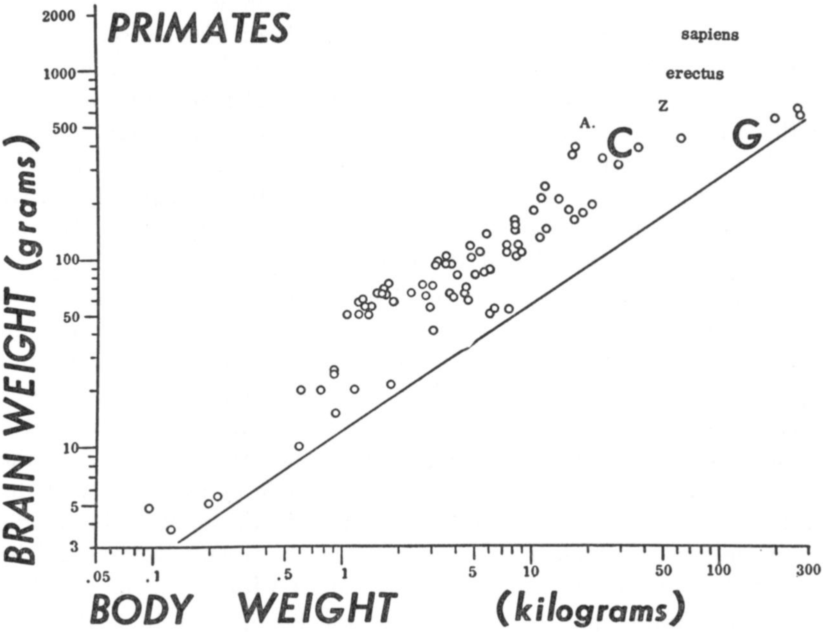

Fig. 6. Brain Weight as a Function of Body Weight in Primates. Data from Crile and Quiring (1940), Kennard and Willner (1941a and 1941b), and Schultz (1950). Chimpanzee points are near C; Gorilla points are near G. A, Z, for *A. africanus* and Zinjanthropus, and sapiens and erectus represent hominid estimates from Table 1, below. The line is the equation, $E = .12 P^{2/3}$.

It is worth noting, in passing, that with the exception of *Homo sapiens* all of the hominids would probably be included within the range

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

of "error deviations" from the primate line of equation 7. In short, an approach using equation 7 to represent primates implies that there is no differentiation of relative brain size within the order Primates, with the exception of *Homo sapiens*. This proposition has been presented seriously by eminent authorities (T. Edinger, 1960; von Bonin, 1941), but in view of the rather general agreement that there is differentiation in behavioral capacities (*e.g.*, Shell and Riopelle, 1958) anatomical measures associated with brain structure should also be capable of differentiating the groups of primates. Gross brain size should, in fact, be sensitive enough to measure the difference, in view of the evidence cited here that relates gross brain size to the number of neural elements in the brain or at least the cerebral cortex. The data of figure 6 will therefore be analyzed in such a way as to provide a criterion for discriminating among the groups of primates, and the measure of relative brain development can be judged by its compatibility with estimates of the behavioral capacities of the groups.

In an earlier analysis of the problem (Jerison, 1955) I was able to discriminate among the major primate groups on the basis of a brain weight factor that was assumed to be independent of body weight and dependent on relative brain development. The total brain weight was assumed to be the result of the addition of this factor (which was called E_c) and a second brain weight factor (E_v) which was dependent on the body weight. The analysis was made quantifiable by assuming that the second brain weight factor was exactly equal to the total brain weight of a primitive mammal, in other words that the second factor could be estimated from the body weight by equation 5 with $k_i = .03$.

The implicaton for the evolution of the hominid brain is that the variable factor, E_v, could be estimated for fossil hominids from guesses about their body size, and the level of brain development achieved by these hominids could then be stated quantitatively by calculating the constant factor for the endocranial volume. The relationship described in equation 4 between brain weight and number of cortical neurons modifies the analysis and makes it somewhat more elegant as an exercise in theoretical biology. The new analysis that is possible of the brain size problem will be presented now and will be followed by an application to primate data. This will also illustrate the kind of information that can be extracted from the fossil record on the evolution of the human brain by using a very elementary theory relating the gross and microscopic anatomy of the mammalian brain.

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

A THEORY OF BRAIN SIZE

The following hypotheses developed from an earlier statement of this approach (Jerison, 1955) are used:

Hypothesis 1. The mammalian brain size (weight in grams or volume in cc) can be analyzed into two independent components, one of which, E_v, is determined by body size and the other of which, E_c, is associated with improved adaptive capacities. The total brain size, E, is the sum of these two components. Thus,

$$E = E_v + E_c \tag{8}$$

Hypothesis 1a. Analogous measures are available for the total number of cortical neurons, N, and the neurons in E_v and in E_c which will be designated, N_v and N_c;

$$N = N_v + N_c \tag{8a}$$

Hypothesis 2. The relationship between N and E is given by

$$N = 8 \times 10^7 E^{2/3} \tag{9}$$

I have here adopted the empirical result of equation 4 as a hypothesis, because at this time I prefer not to attempt to derive it from more elementary statements. The exponent, 2/3rds, in equation 9 means that the number of cortical neurons is proportional to the cortical surface. This is reasonable, because the cortex is an outer or surface layer of cells, no more than a few millimeters thick (see Figure 1C), and the cortical neurons are all in that "outer layer" or cortex.

If equation 9 holds for the total brain weight and neuron number it cannot hold for both N_v and N_c. It is, therefore, necessary to state:

Hypothesis 2a. Equation 9 also holds for N_v as follows:

$$N_v = 8 \times 10^7 E_v^{2/3} \tag{9a}$$

The reason for hypothesis 2a is apparent when one considers that primitive mammals have a brain size, $E = E_v$, sufficient to maintain vegetative, sensorimotor, and related behavior, and equation 9 or 9a states the number of neurons in such a brain. When we assign a portion of the brain size (weight or volume) of a progressive mammal to activities that it has in common with primitive mammals it is natural to assume that the number of neurons associated with these activities should be the same in the progressive as in the primitive animal.

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

It may not be obvious that E_v in the progressive mammal's brain will have to be more massive than in the primitive mammal. This "theorem" is derived as follows. From hypothesis 1, additional neurons in the E_c component would increase the total number of neurons in the progressive mammal's brain, and by equation 9 the total brain weight would be greater by a corresponding amount. From equation 1 (or less directly from equation 9) we note that neuron density is lower in larger brains, and therefore the number of neurons, N_v, in the progressive mammal would be less tightly packed, and hence would have to be fitted into a larger mass of brain tissue than E_v, the total amount of brain tissue in the primitive mammal of similar body size.

Hypothesis 3. In all mammals, a brain weight factor, E_v, can be estimated from equation 5 with $k_1 = .03$; thus

$$E_v = .03P^{2/3} \tag{10}$$

In contemporary mammals this brain weight factor can be used to estimate the number of cortical neurons associated with primitive behavioral functions, following the argument of hypothesis 2a, and applying equation 9a.

These three hypotheses provide the basis for precise statements about relative brain development, because N_c, as developed here, is a numerical measure of progressiveness in brain development beyond the level required by increasing body size. N_c can be estimated when information on gross brain and body weight is available. Of the three hypotheses, only the first has no direct empirical correlate. The second hypothesis is based on the empirical result presented earlier as equation 4. The third hypothesis as stated in equation 10 is related to an empirical result obtained on a sample of archaic Eocene mammals and the opossum (Jerison, 1961).

The first hypothesis, despite its failure to be associated with a direct empirical result, is a very common one in discussions of brain development. It may have first been stated by Manouvrier (1885), and in evolutionary but nonquantitative terms by L. Edinger (1885); Dubois (1920) argued against the additive aspect, preferring a multiplicative jump by a factor of 2 of the sort discussed and rejected earlier in this report. Bok (1959) stated it as follows: ". . . our measurements clearly point to the conclusion that the total number of cortical nerve cells in the various animal species is defined by two influences: the size of the body and the degree of cephalization." (p. 241). In this report it has been stated as a simple quantifiable additive hypothesis.

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

It must be the case that mammals with highly developed brains differ from their less cephalized relatives in the number of cortical neurons, but it seems unlikely that they would also differ significantly in the manner of functioning of large aggregates of cortical neurons. The more advanced forms might be more competent in storage of information, in decision-making behavior, in sensorimotor coordination, and so forth, but the neural mechanisms for such activities should be similar in progressive and primitive mammals. Thus the efficiency of the brain should be reflected in the number of neural elements, and additional components (neurons) in the progressive brain can be considered merely as additional elements of the same type as those that occur in a primitive brain. The point is essentially the same as made by von Neumann (1951) that the capacity of a computer can in a general way be stated by the total number of elements that it contains.

I am not, at this time, prepared to consider the differentiation of brains either grossly in terms of relative contributions of different sensory, motor, and other projection systems (*cf.* Woolsey, 1958), or microscopically in terms of relative frequency of different types of neurons (*cf.* Sholl, 1956). I am willing to accept the assumption that within large enough aggregates of neurons the various species-specific effects of equally cephalized mammals are balanced. For example, the extensive development of sensorimotor systems associated with the manus in raccoon (Welker and Seidenstein, 1959) may be equivalent to the sensorimotor systems associated with the snout in the pig (Adrian, 1947; Woolsey and Fairman, 1946), despite the ordinal separation of these two mammals. Mammals would be differentiated on N_c when they differ in relative amount of development of their respective specializations.

It will eventually be necessary to account for specializations within the mammals associated with special adaptive niches, and perhaps the most radical aspect of the first hypothesis is its assumption that the variety of special adaptations in the mammals can be considered equivalent for the purpose of determining a "general factor" in brain development. The analogy to a general factor in human intelligence (Spearman, 1927) cannot be missed, and raises issues analogous to the debate on whether a notion of general intelligence really makes sense for man (Thurstone, 1947). Nevertheless, as a first approximation it is appropriate to think about general intellectual ability, independently of, let us say, spatial ability, language ability, cultural specificity and so forth. Similarly in the mammals as a class it may be appropriate to think of general mammalian capabilities and the degree to which these are per-

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

fected, independently of the special abilities of the varieties of mammals. The approach is essentially that of a taxonomic key in which the mammals are first distinguished from other vertebrates, then the orders of mammals are distinguished, then families within orders, and so forth. I think of the present approach as associated with the first levels of abstraction of the characteristics of the mammals. For example, one might consider the appearance of the exponent of 2/3 in equation 10 (or in empirical forms of the equation) as a defining characteristic for the mammals. The rest of the theory is concerned with a measure of the primitiveness-progressiveness dimension, and N_c is developed for this purpose. More specific adaptations within the mammals are not yet considered.

ANALYSIS OF BRAIN SIZE IN PRIMATES

The theory permits us to analyze brain size in mammals and to determine the number of neurons, N_c, that should be associated with

TABLE 1

Estimates of "extra neurons," N_c, in combinations of brain and body size in primates

	(1) E	(2) P	(3) N	(4) E_v	(5) N_v	(6) N_c
[Rhesus]	100	10,000	1.7	14	.5	1.2
[Baboon]	200	20,000	2.7	22	.6	2.1
[Chimpanzee]	400	45,000	4.3	38	.9	3.4
[Gorilla 1]	540	200,000	5.3	103	1.8	3.5
[Gorilla]	600	250,000	5.7	119	1.9	3.6
[*A. africanus*]	500	20,000	5.0	22	.6	4.4
[Zinjanthropus]	600	50,000	5.7	41	1.0	4.7
[*H. erectus*]	900	50,000	7.4	41	1.0	6.4
[*H. erectus*]	1,000	50,000	8.0	41	1.0	7.0
[*H. sapiens*]	1,300	60,000	9.5	46	1.0	8.5

NOTE. E and P are round figures for brain and body weights or volumes typical of the primates, in brackets at left. Data for Gorilla 1 are rounded from Noback and Goss (1959) and illustrate the calculations on "live" data. Fossil hominid data are by guess and by Coon (1962). E, P, and E_v in grams or cc; N, N_v, and N_c in billions of neurons. Computational procedures follow successive applications of following formulae (numbered as in the text):

$$N = 8 \times 10^7 \times E^{2/3} \quad (9)$$

$$E_v = .03\, P^{2/3} \quad (10)$$

$$N_v = 8 \times 10^7 \times E_v^{2/3} \quad (9a)$$

$$N_c = N - N_v \quad (8a)$$

This content downloaded from 217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

the evolution of behavior beyond the primitive mammalian level. Results of an application of the theory to data that might have come from the primates including the fossil hominids in Figure 6 are shown in Table 1.

The figures for brain weight, E, and body weight, P, in Table 1 were deliberately chosen round numbers that would, nevertheless, be appropriate for the particular primates listed in the brackets for each row. The hominid weights, including *Australopithecus,* Zinjanthropus, Pithecanthropus, and modern man are "generally accepted" figures (Coon, 1962), although one can perform the indicated operations with any pairs of numbers. At the bottom of the table the formulas that were used to derive the data of columns 3-6 from the data of columns 1 and 2 are listed. The constants in those formulas are not dimensionless; thus, 8×10^7 is in cm^{-2}, and .03 is in cm or grams. Although this is academic for the present, there are dimensional problems associated with this kind of theory that will eventually have to be resolved (Kavanagh and Richards, 1942).

The results in Table 1 are readily obtained by the sequential application of the formulas in the table. As an example, the data in the top row begin with the pair of measures, $E = 100$ grams and $P = 10{,}000$ grams. The number of cortical neurons is determined by inserting $E = 100$ into the first equation (equation 9), and we have:

$$N = 8 \times 10^7 \times (100)^{2/3} = 1.7 \times 10^9$$

The value for E_v is obtained by inserting $P = 10{,}000$ into the second equation (equation 10):

$$E_v = .03\,(10{,}000)^{2/3} = 13.9 = 14$$

The value for N_v is then obtained by inserting $E_v = 14$ into the third equation (equation 9a):

$$N_v = 8 \times 10^7 \times (14)^{2/3} = 4.65 \times 10^8 = 0.5 \times 10^9$$

The value for N_c which is the measure of prime concern is obtained with the final equation in Table 1, equation 8a of this report, by subtracting N_v from N: $(1.7 \times 10^9) - (0.5 \times 10^9) = 1.2 \times 10^9$. It will be noted that all numbers were rounded to no more than two significant figures, and rounding was carried further if a failure to round out numbers would have implied more than two significant figures in N_c.

The most interesting feature of Table 1 from the point of view of this symposium is the way that the australopithecines (*A. africanus* and

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

Zinjanthropus) are distinguished from the anthropoid apes despite the fact that their absolute brain size is in the anthropoid range. The usual qualitative statement that body size differences can account for a hominid brain in the anthropoid ape brain size range is given clear and quantitative meaning by Table 1. A second example of the role of body size is illustrated by the "Chimpanzee" and "Gorilla" in Table 1. These anthropoid apes are similar in terms of the value of N_c despite the large difference in brain size.

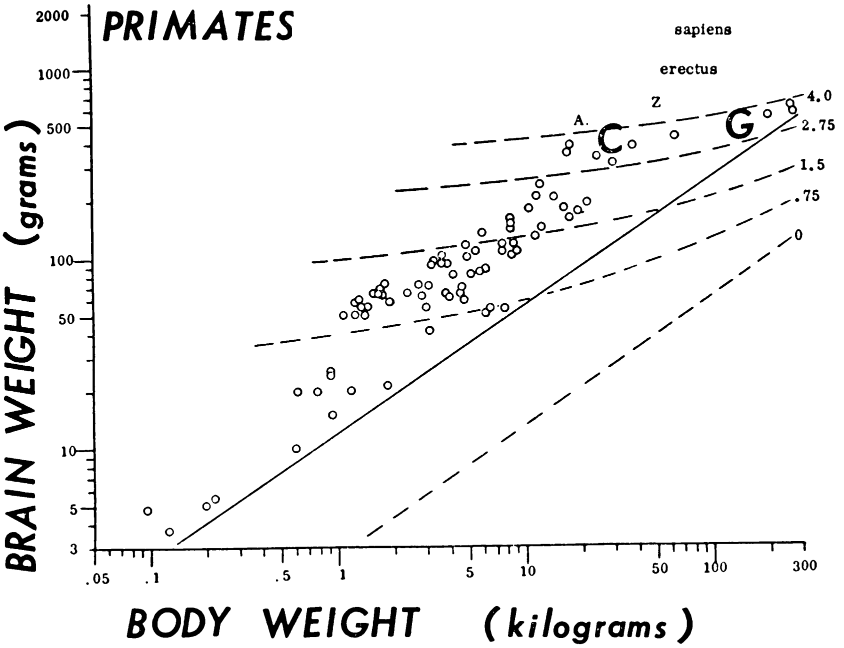

FIG. 7. THE SAME INFORMATION AS IN FIGURE 6 WITH THE DASHED LINES ADDED TO REPRESENT BRAIN WEIGHTS AT GIVEN BODY WEIGHTS FOR EQUAL VALUES OF N_c. Bottom dashed line is the "primitive mammalian line" with $N_c = 0$ and represents equation 10: $E = .03\ P^{2/3}$. Parameter for the other lines is also N_c in billions of neurons. All hominids are above the top line (4×10^9 neurons in E_c). The points lying between $N_c = 2.75$ and $4 (\times 10^9)$ represent every anthropoid ape in this sample. The points lying between $N_c = 1.5$ and $2.75 (\times 10^9)$ represent every baboon in the sample and one sooty mangabey described by Kennard and Willner (1941b). The points between $N_c = .75$ and $1.5 (\times 10^9)$ include the gibbon and most of the new and old world monkeys. The point below $N_c = .75 \times 10^9$ are for the Squirrel monkey (*Saimiri*), marmosets and lemurs.

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

The analysis in Table 1 would group the primates of Figure 6 in the way shown in Figure 7. It is clear here that the australopithecines fall somewhat above the anthropoid apes, that is, that the australopithecine level is to be considered divergent from the anthropoid line in terms of brain development as well as in terms of other characteristics, and although the divergence is relatively small it is readily recognizable by the kind of analysis performed here. The lines added in Figure 7 connect points representing brain weights that yield equal values of N_c for various body weights, and they can be considered as lines representing equal degrees of progressiveness of brain development in terms of the theory presented in the previous section. The particular ones presented in Figure 7 were chosen to discriminate groups of primates from one another with essentially no overlap. The highest line is based on the highest value for N_c calculated from published brain and body size data on anthropoid apes, and it can be seen that estimates of australopithecine points fall above that line.

DISCUSSION

This entire report has been concerned with the kind of information that can be extracted from a statement about the gross size of the brain of a mammal. The reason for this concern is that the evolution of the hominid brain as well as other mammalian brains can be studied directly from fossil endocasts, and one of the quantitative measures available from this material is the endocranial volume. I have translated the available literature relating the microscopic anatomy to the gross anatomy of the brain into a set of simple equations. The common notion that brain size is associated with body size as well as intellectual functions was translated into another simple mathematical expression, and finally, I have joined a distingiushed company by assuming that the basic brain size: body size relationship is a primitive one for the mammals and that subsequent brain development was independent of body size.

The approach, then, was to construct a theory that combined these fairly common propositions. The most speculative steps were taken in writing equation 8a as additive and assuming that N_v could be computed with equation 9a. But steps like these have to be taken if the assumptions are to be precise enough to be tested. This permitted a brain factor associated with body size and a brain factor associated with intellectual functions to be described in quantitative terms.

One aspect of the present approach as opposed to earlier and different analyses such as produced by Dubois (1928), by Count (1947), or by

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

Bok (1959) is in the relationship suggested between numerical parameters and biological events. I am particularly concerned with the effects of apparently small changes in the basic hypotheses on the numerical values of computed coefficients (such as N_c), and until one can develop direct measurements of biological quantities that correspond exactly to those coefficients one should be aware of the interposition of one's theory between the coefficients and the things the coefficients are supposed to represent. For this reason a fairly explicit statement of the hypotheses associated with the development of numerical estimators is necessary to permit the evaluation of a quantitative analysis. This is both the strength and the weakness of quantitative approaches; they are easy to test and easy to reject, but acceptance is always provisional.

The effect of working from a theoretical analysis to an empirical analysis should be good, because the theory should be capable of suggesting relationships that go beyond the original data. In the present instance a number of theorems can be derived from the theory. One fairly obvious one is that if contemporary mammals lie on a line best fitted by equation 6, then large mammals must be relatively more cephalized than small mammals. This result agrees with Rensch's (1956) position derived from a different approach. As another theorem, one would derive a slope less than 2/3 if one fitted a line to a double logarithmic plot for closely related mammals. The theory could also be used to predict results of studies of animal behavior. Figure 7, for example, predicts that among the monkeys and apes one should find similar behavioral capacities in a group consisting of rhesus monkey, spider monkey and gibbon, greater capacities in sooty mangabeys and baboons, and still greater capacities in anthropoid apes. (It was in an effort to arrive at such a generalization that I first became concerned with the kind of problem discussed in this report.)

Before concluding I would like to point out an important problem for the theory when it is used to estimate N_c in two, particular mammals, the elephant and the porpoise. In the elephant, taking $E = 6{,}000$ gm and $P = 7 \times 10^6$ gm, reasonable estimates that are close to the figures offered by Tower (1954) and by Crile and Quiring (1940), we get a value of $N_c = 1.8 \times 10^{10}$ neurons, or about twice the value for modern man. In the porpoise, taking $E = 1750$ gm and $P = 150{,}000$ gm (Crile and Quiring, 1940), we get $N_c = 10^{10}$ neurons or about the same value as for modern man. If we demand that the values of N_c correspond to an ordering in terms of behavioral capacities we must assume either that the assumptions used in determining N_c are insufficient or that we

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

are grossly underestimating the behavioral capacities of the elephant and porpoise. I would guess that both errors occur, but I would prefer, for the present, to emphasize the second type of error. The problem is the fundamental one of accounting for cross-species differences in behavioral capacities.

I have no ready solution for the problem implied by the existence of mammals with more "extra neurons" than man that are yet subjected to our dominance. It is worth noting that within their adaptive niches the elephant and porpoise have both had notable biological success. The elephant in its natural habitat was, perhaps, the dominant land mammal of most of the Tertiary when judged by the frequency, range, and variety of the recovered fossils of the order Proboscidea. Although similar criteria are not available for the porpoise, the recent, well-publicized, work on the behavior of porpoises and demonstrations of the capabilities of porpoises at public institutions like "Marineland" indicate that these animals have elaborate and as yet incompletely understood abilities and potentialities.

For the present, I think it best to face the challenge of these data from the elephant and porpoise by considering them in association with effects due to directions of evolution. As indicated in the substantive sections of this report, some acknowledgment of the role of the groups of mammals and their special adaptations will eventually have to be made. This should take the quantitative form of a set of parameters for the basic equations. Perhaps the point of entry of one such parameter might be at the relationship between brain and behavior rather than on the quantification of brain evolution. In this sense it may be appropriate to accept a common brain:behavior relationship only for groups of mammals that followed a common direction of evolution in other respects, and the comparison of elephant, porpoise, and man with equations lacking a "direction-of-adaptation" parameter would be inappropriate.

The order, Primates, may be considered as a group with a common direction of adaptation, because, with few exceptions, its taxa are relatively unspecialized except for their enlarged brains. A measure of relative brain development in primates could refer to adaptive functions that have been handled by the plasticity of behavior instead of by the evolution of appropriate body structures as in the case of other orders of mammals. The analysis of the evolution of the primates as an unspecialized order adapted toward adaptability in a variety of niches

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

can then take the form of the analysis of the evolution of the "organ of adaptability," the brain.

SUMMARY AND CONCLUSIONS

The main effort of this analysis has been to substitute quantitative for qualitative statements about brain size and evolution. No attempt was made to introduce radically new concepts or indices into the analysis; instead common concepts were analyzed for their quantitative implications. In the context of this symposium the contribution of this analysis has been to suggest ways to interpret measurements of gross characteristics of the brain in terms of aspects of its microstructure. The most concrete result has been to show, quantitatively, that the australopithecines who had been designated as hominids largely on the basis of other skeletal structures (Washburn and Howell, 1960) were clearly, if only slightly, in advance of the level of brain evolution achieved by the anthropoid apes of our time. Fossil hominids of the genus *Homo* could also be differentiated, with *erectus* lying below the level of *sapiens*. The quantitative specifications of these differences were presented in Table 1 and are suggested in Figure 7. An interesting and useful aspect of the results is that, excepting the smaller australopithecines, the similarity of body size in the hominids permits one to use absolute brain weight or volume as the measure of brain evolution.

The brain weight or volume was proposed as a kind of biological statistic to estimate a parameter, N, representing the total number of cortical neurons. It will be instructive to conclude the report by thinking in terms of such a statistic. There is, for example, the problem of determining the distribution of sampling errors, and in the body of the report it was suggested, somewhat obliquely, that these errors should be estimated from within-species variations in brain size and number of cortical neurons. This implies the assumption that the number of cortical neurons is *not* related to brain weight within individuals of a single species.[2] It would be inappropriate to present the statistical reasoning that requires this assumption, but it should be noted that it is another example of the benefits from mathematical precision in the analysis. It becomes easy to state significant propositions that are capable of being tested experimentally.

When comparisons were restricted to differences among species and

---

[2] One should exclude tests based on domesticated species where intensive selective breeding produced radical revision of some morphological characters.

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

higher taxa, the brain weight or volume was found to be a reasonable estimator of the number of cortical neurons. A further analysis, based on commonly accepted assumptions about the size of the brain resulted in the determination of a second useful parameter, N_c. This parameter was interpreted as the number of "extra" neurons that may be associated with the evolution and adaptation of brain: behavior mechanisms in response to the challenge of the environment. With this second parameter it was possible to differentiate the primates, including the hominids, on the basis of relative brain development.

LITERATURE CITED

ADRIAN, E. D. 1947 The Physical Background of Perception. Clarendon Press, London.

ARIËNS KAPPERS, C. U. 1929 The Evolution of the Nervous System in Invertebrates, Vertebrates and Man. De Erven F. Bohn, Haarlem.

BOK, S. T. 1959 Histonomy of the Cerebral Cortex. D. Van Nostrand Company, Inc., New York.

BONIN, G. VON 1941 Side lights on cerebral evolution: brain of lower vertebrates and degree of cortical folding. J. Gen. Psychol., *25*: 273-282.

BRUMMELKAMP, R. 1940 Brain weight and body size: a study of the cephalization problem. Proc. Kon. Ned. Akad. Wetenschap., *39*: 1-57.

CLARK, W. E. LEGROS 1960 The Antecedents of Man. Quadrangle Books, Chicago.

COMAS, J. 1961 "Scientific" racism again? Current Anthropol., *2*: 303-314.

CONNOLLY, C. J. 1950 External Morphology of the Primate Brain. Charles C. Thomas, Springfield, Illinois.

COON, C. S. 1962 The Origin of Races. Alfred A. Knopf, New York.

COUNT, E. W. 1947 Brain and body weight in man: their antecedents in growth and evolution. Ann. N. Y. Acad. Sci., *46*: 993-1122.

CRILE, G. AND D. P. QUIRING 1940 A record of the body weight and certain organ and gland weights of 3690 animals. Ohio J. Sci., *40*: 219-259.

DUBOIS, E. 1920 The quantitative relations of the nervous system determined by the mechanism of the neurone. Proc. Kon. Ned. Akad. Wetenschap., *22*: 665-680.

——— 1922 Phylogenetic and ontogenetic increase of the volume of the brain in the vertebrata. Proc. Kon. Ned. Akad. Wetenschap., *25*: 230-255.

——— 1924 On the brain quantity of specialized genera of mammals. Proc. Kon. Ned. Akad. Wetenschap., *27*: 430-437.

——— 1928 The law of the necessary phylogenetic perfection of the psychoencephalon. Proc. Kon. Ned. Akad. Wetenschap., *31*: 304-314.

EDINGER, L. 1885 Zehn Vorlesungen über den Bau der nervösen Zentralorgane. F. C. W. Vogel, Leipzig. Cited by H. W. Magoun. Evolutionary concepts of brain function following Darwin and Spencer. *In* Evolution after Darwin, 1960 S. Tax (ed.), *2*-199. Univ. Chicago Press, Chicago.

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

EDINGER, TILLY 1929 Die fossilen Gehirne. Ergeb. Anat. Entwgesch., *28*: 1-249.

——— 1948 Evolution of the horse brain. Geol. Soc. Amer. Memoir 25, Baltimore, Maryland.

——— 1956 Objets et résultats de la paléoneurologie. Annales de Paléontologie, *62*: 97-116.

——— 1960 Anthropocentric misconceptions in paleoneurology. Proc. Rudolf Virchow Soc., *19*: 56-107.

HARMAN, P. J. 1943 Volumes of basal ganglia and cortex in mammals. Proc. Soc. Exp. Biol. Med., *54*: 297-298.

——— 1957 Paleoneurologic, Neoneurologic and Ontogenetic Aspects of Brain Phylogeny. Monograph, James Arthur Lecture Series, Amer. Mus. Nat. Hist.

HRDLIČKA, A. 1906 Brains and brain preservatives. Proc. U. S. Nat. Mus., *30*: 245-320.

JERISON, H. J. 1955 Brain to body ratios and the evolution of intelligence. Science, *121*: 447-449.

——— 1961 Quantitative analysis of evolution of the brain in mammals. Science, *133*: 1012-1014.

KAVANAGH, A. J. AND O. W. RICHARDS 1942 Mathematical analysis of the relative growth of organisms. Proc. Rochester Acad. Sci., *8*: 150-174.

KENNARD, M. A. AND M. D. WILLNER 1941a Findings at autopsies of seventy anthropoid apes. Endocrin., *28*: 967-976.

——— 1941b Weights of brains and organs of 132 new and old world monkeys. Endocrin., *28*: 977-984.

LASHLEY, K. S. 1949 Persistent problems in the evolution of mind. Quart. Rev. Biol., *24*: 28-42.

LINDSLEY, D. B. 1960 Attention, consciousness, sleep and wakefulness. *In* H. W. Magoun (ed.) Handbook of physiology, section 1: neurophysiology. Am. Physiol. Soc., Washington, D. C. *3*: 1553-1593.

MANOUVRIER, L. 1885 Sur l'interprétation de la quantité dans l'encéphale et dans le cerveau en particulier. Bull. Soc. Anthropol., Paris, *3*: 137-323.

MARSH, O. C. 1876 On some characters of the genus *Coryphodon* (Owen). Am. J. Sci. Arts, *11*: 425-428.

METTLER, F. A. 1956 Culture and the structural evolution of the neural system. Monograph, Arthur James Lecture Series, Am. Mus. Nat. Hist.

NEUMANN, J. VON 1951 The general and logical theory of automata. *In* L. A. Jeffress (ed.) Cerebral mechanisms in behavior: the Hixon Symposium. John Wiley and Sons, Inc., New York.

NOBACK, C. R. AND L. GOSS 1959 Brain of a gorilla I. Surface anatomy and cranial nerve nuclei. J. Comp. Neurol., *3*: 321-343.

RENSCH, B. 1956 Increase of learning capability with increase of brain-size. Am. Nat., *90*: 81-95.

——— 1959 Trends toward progress of brains and sense organs. Cold Spring Harbor Symposia Quant. Biol., *24*: 291-303.

RIESEN, A. H., B. GREENBERG, A. S. GRANSTON AND R. L. FANTZ 1953 Solutions of patterned string problems by young gorillas. J. Comp. Physiol. Psychol., *46*: 19-22.

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms

SCHULTZ, A. H. 1950 Morphological observations on gorillas. *In* W. K. Gregory (ed.) The anatomy of the gorilla, pp. 228-253. Columbia Univ. Press, New York.

SHARIFF, G. A. 1953 Cell counts in the primate cerebral cortex. J. Comp. Neurol., *98*: 381-400.

SHELL, W. F. AND A. J. RIOPELLE 1958 Progressive discrimination learning in platyrrhine monkeys. J. Comp. Physiol. Psychol., *51*: 467-470.

SHOLL, D. A. 1948 The quantitative investigation of the vertebrate brain and the applicability of allometric formulae to its study. Proc. Roy. Soc., B *135*: 243-258.

——— 1956 The Organization of the Cerebral Cortex. Methuen and Co., Ltd., London.

SPEARMAN, C. 1927 The Abilities of Man. The MacMillan Co., New York.

THURSTONE, L. L. 1947 Multiple Factor Analysis. Univ. Chicago Press, Chicago.

TILNEY, F. 1928 The Brain from Ape to Man. Paul B. Hoeber Inc., New York.

——— 1931 Fossil brains of some early Tertiary mammals of North America. Bull. Neurol. Inst., New York, *1*: 430-505.

TOWER, D. B. 1954 Structural and functional organization of mammalian cerebral cortex: the correlation of neurone density with brain size. J. Comp. Neurol., *101*: 19-51.

TOWER, D. B. AND J. P. SCHADÉ 1960 Structure and function of the cerebral cortex. Proc. of the 2nd Internat. Meeting of Neurobiologists. Elsevier Publ. Co., Amsterdam.

WASHBURN, S. L. AND F. C. HOWELL 1960 Human evolution and culture. *In* S. Tax (ed.) 1960 Evolution after Darwin, *2*: 33-56. Univ. Chicago Press, Chicago.

WELKER, W. I. AND S. SEIDENSTEIN 1959 Somatic sensory representation in the cerebral cortex of the raccoon (Procyon lotor). J. Comp. Neurol., *3*: 469-502.

WOOLSEY, C. N. 1958 Organization of somatic sensory and motor areas of the cerebral cortex. *In* H. F. Harlow and C. N. Woolsey (eds.) 1958 Biological and biochemical bases of behavior. Pp. 63-81. Univ. Wisconsin Press, Madison.

WOOLSEY, C. N. AND D. FAIRMAN 1946 Contralateral, ipsilateral and bilateral representation of cutaneous receptors in somatic areas I and II of the cerebral cortex of pig, sheep and other mammals. Surgery, *19*: 684-702.

YERKES, R. M. AND ADA W. YERKES 1929 The Great Apes: a study of anthropoid life. Yale Univ. Press, New Haven.

This content downloaded from
217.91.150.187 on Sun, 15 May 2022 23:14:51 UTC
All use subject to https://about.jstor.org/terms