Brain to Body Ratios and the Evolution of Intelligence

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BRAIN evolution is the obvious correlate of the evolution of intelligence. A gross measure of the evolution of the brain is afforded by a comparison of total brain weights in contemporary species arranged as a phylogenetic series. However, brain weight is correlated with body weight, and comparisons among species must be considered in terms of expected brain weight for any given body weight. This paper (*1*) examines the differential evolution of the mammalian brain with special emphasis on the primates and suggests a specific brain-weight factor correlated with intelligence.

In contemporary mammals the brain weight can be related to the body weight by the function

$$E = kP^{\beta} \qquad (1)$$

in which E is the brain weight and P the body weight. The parameters, k and β, may be determined by fitting a straight line to the log-log scatter plot of brain weight to body weight data; log k is the log E intercept of this line, and β is the slope. Although Eq. 1, the "allometric" size function (*2*), cannot be rationalized at the present time, it provides a satisfactory empirical description of brain and body weight relationships for the mammals as a class. Von Bonin (*3*) has found a correlation of .83 between log E and log P for 115 mammalian measurements and has determined the empirical values of the parameters as $k = .18$, and $\beta = .66$. Using an independent set of 163 measurements from Count's monograph (*4*), I have found a correlation of .92 between log E and log P, with $k = .16$, and $\beta = .67$. When the primates were removed from this computation, the correlation rose to .98. Count's data with fitted regression lines are presented in Fig. 1.

It has been assumed that β in Eq. 1 is a mammalian constant (*3, 5*). In terms of this assumption, k will be the parameter for a family of parallel lines with slope β, and these lines can be drawn through all the points in a log-log plot of brain and body weights. If it is also assumed that the evolution of the brain is described by the steplike displacement of the regression of log P on log E—that is, by increments in the value of k—the value of k for a given mammal can be used as an "index of cephalization"—a numerical statement about the level of evolution of that mammal's brain. This assumption is implicit in the work of Dubois (*5*) and his school and in the work of von Bonin (*3*). The index of cephalization k is, in fact, related to human estimates of intelligence of mammalian orders. Primates (excluding Prosimii) usually have values of k higher than representatives of other orders; ungulates and carnivores have intermediate values, and rodents generally have low values. Difficulties arise, however, when the index is used

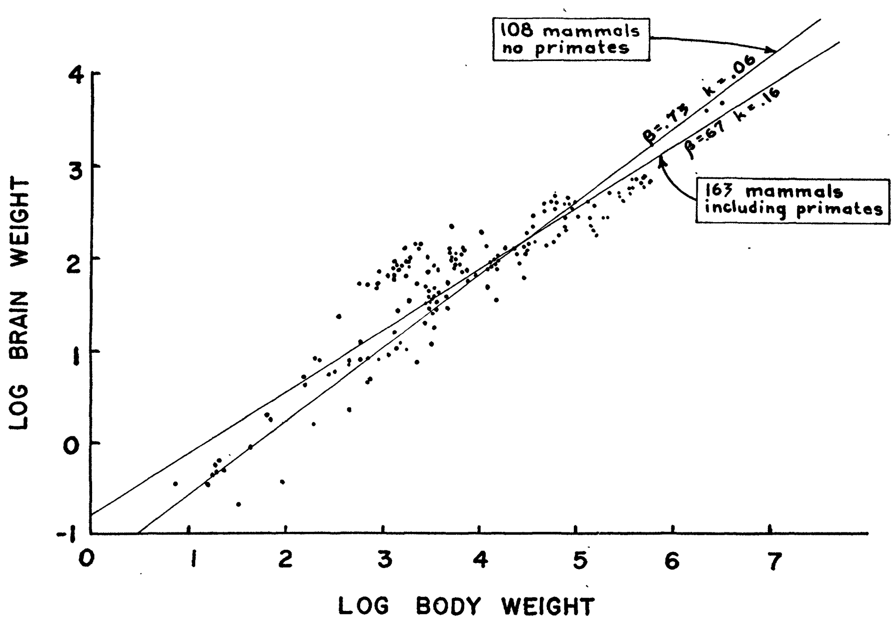

Fig. 1. Log brain weight (grams) as a function of log body weight (grams). The straight lines are graphic representations of Eq. 1 in logarithmic form. Data are from Count (*4*).

Table 1. Index of cephalization (k) and its variability in Anthropoidea. Equation 1 with $\beta = .66$ was used to compute k.

Group*	N	Mean k	σk
Man	50	.92	.16
Monkeys†	50	.41	.09
Great apes‡	35	.29	.07

* Groups are ordered in terms of mean k.
† Include *Ateles, Cynopithecus, Macaca, Papio,* and *Presbytis.*
‡ Include *Pongo, Pan,* and *Gorilla.*

within the order Primates. Analyzing data of various authors (*3–7*) for 50 human beings, 35 great apes, and 50 monkeys, the means and standard deviations of k indicated in Table 1 were obtained. Differences between means are all significant at the .001 level of confidence. The perplexing feature in Table 1 is the reversal of the expected order that should put great apes above monkeys in terms of relative brain development. One of the results of the following analysis accounts for this reversal.

Let us, first, examine the assumption that k is a function of level of cerebral evolution. This implies that a group of mammals at the same level of cerebral evolution—that is, of equal intelligence—should have equal values of k. Thus, if we plot k against log P for the primates in Table 1, we should obtain sets of points arrayed about three parallel horizontal lines representing $k = .92$, $k = .41$, and $k = .29$, and within each group the correlation between k and log P should be zero. The actual results of such a plot are given in Fig. 2. (The curves in Fig. 2 will be considered later.) It is immediately obvious that the arrays of points indicate an inverse relationship between k and log P and that the baboons must be differentiated from other monkeys. These suggestions were verified by computing product-moment correlation coefficients for the four arrays of points. The correlations between k and log P are as follows: for man, $r = -.83$; for the great apes, $r = -.82$; for the baboons, $r = -.88$, and for the other monkeys, $r = -.92$. The appropriate description of the subgroups of primates is clearly in terms of a functional relationship between k and log P rather than in terms of mean values of k.

To write a function that is descriptive of the data in Fig. 2, the following assumptions were made. (i) The allometric size relationship between brain weight and body weight stated in Eq. 1 is a primitive relationship that holds true for all mammals including primates. (ii) β is a mammalian constant, and $\beta = .66$. (iii) The evolution of the mammals, characterized by increasing intelligence, involved the differentiation of additional cerebral tissue. The amount of this tissue is correlated with the evolution of intelligence and is unrelated to the body weight, except as the body weight, itself, may be correlated with the evolution of intelligence.

Thus the total weight of the brain, E, may be regarded as composed of two parts, E_v, which varies with the body weight allometrically, and E_c, which is constant for a group achieving a given level of cerebral evolution. In formal terms:

$$E = E_v + E_c \quad (2)$$

and

$$E_v = k'P^{\beta} \quad (3)$$

where log k' represents the log E intercept (see Fig. 1) for primitive mammals—that is, mammals with $E_c = 0$. Equation 1 can then be rewritten as

$$k = \frac{E_c}{P^{\beta}} + k' \quad (4)$$

An appropriate technique for estimating k' enables us to draw a family of curves with E_c as a parameter. The value of k for the opossum, our best contemporary approximation of a primitive mammal (*8*), was used as an estimate of k'; thus $k' = .05$. Equation 4 was then fitted to the data of Fig. 2 by choosing k and log P coordinates in the midst of a cluster of points for each group and computing the corresponding values of E_c. The values of E_c are given on each curve in Fig. 2.

Two results of this approach are of immediate interest. First of all, the problem of the relationships among the mean values of k for the primates disappears. These values, from the present point of view, depend solely on the body weights evolved by con-

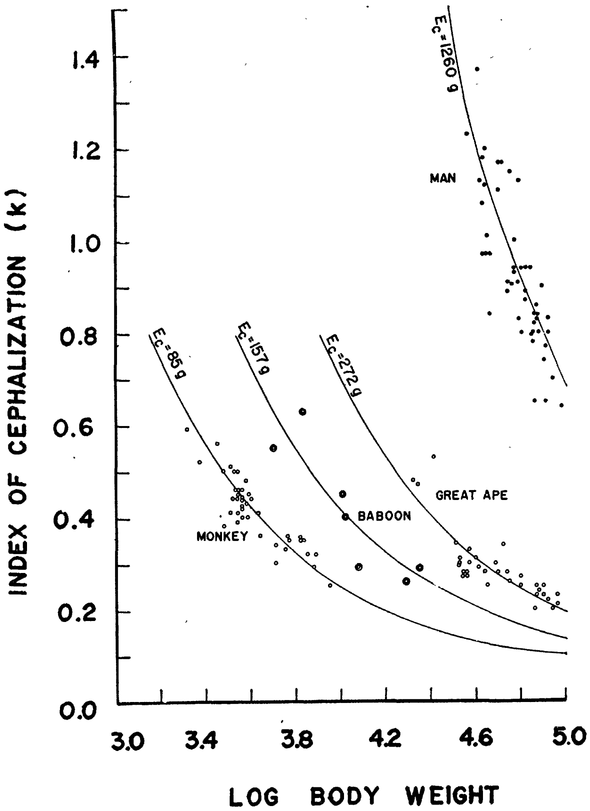

Fig. 2. Relationship between index of cephalization (k) and log body weight of primates in Table 1. Fitted functions are Eq. 4 with E_c as the parameter.

temporary representatives of any given group. If the great apes, for example, had developed the body-weight characteristics of baboons, their predicted range of k would be from .40 to 1.00. Second, and perhaps more important, within the range of values of log P for each of the groups in Fig. 2, Eq. 4 approximates the slopes of the regression lines that could be fitted to the data. Thus, a single rational function has been written, which, when applied to these primates, replaced four empirical equations otherwise necessary to describe the data. It is of some interest that Eq. 4 was written before human data were analyzed, and, as can be seen in Fig. 2, it predicted with some success the slope of the regression of log P on k for man.

Assumption iii, which is fundamental to this analysis, is, of course, a simplification. However, because of the success of Eq. 4 in accounting for our data, it seems reasonable to examine the possibility that this assumption is approximately correct. To do this, it would be necessary to determine precise relationships between number of neurons and brain weight, neuron weight and brain weight, neuron weight and body weight, and similar relationships between weights of other cellular constituents of the brain and the total brain and body weight. But even without such information to lend precision to the present analysis, the suggestion that a large portion of the primate brain weight is independent of the body weight may be important. It indicates, for example, that a specific anatomical correlate for intelligence may be found by pursuing quantitative anatomical studies of the relative development of parts of the brain in monkey, ape, and man as a function of the body weight. Rensch's recent work (*9*) appears especially important in this context.

A more difficult aspect of the third assumption involves the definition and measurement of intelligence in animals. This is largely an unsolved problem, but the present approach suggests that in seeking a solution it would be appropriate to compare species in terms of their values of E_c. In the monkeys, for example, we would expect no differences between *Macaca mulatta* and *M. nemestrinus,* but these forms should be differentiable from the baboons. This analysis can, thus, be considered as contributing to an important problem in comparative psychology, namely, the development of criterions for selecting species for comparisons.

In summary, the general relationship between brain weight and body weight enables us to estimate the expected brain weight for any given body weight. Deviations from the expected brain weight in the primates can be accounted for by assuming a special evolution of the brain in the direction of the development of additional cerebral tissue, the weight of which is independent of the body weight. This approach results in a solution of problems arising from inconsistencies in the "index of cephalization" of primates and suggests directions for further research on the evolution of the brain and intelligence.

References and Notes

1. I wish to thank Virginia L. Senders and Stanley M. Garn for their criticisms and suggestions and Shelley Ehrlich for checking the computations. This research was done independently of my activity as an Air Force Psychologist.
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6. G. v. Bonin and P. Bailey, *The Neocortex of* Macaca mulatta (Univ. of Illinois Press, Urbana, 1947).
7. G. Crile and D. P. Quiring, *Ohio J. Sci.* **40**, 219 (1940).
8. The choice of the opossum as a representative primitive mammal appears to be especially appropriate for studies on the evolution of the brain, for the endocranial casts of this mammal have been found by Tilly Edinger (*Evolution of the Horse Brain,* Waverly, Baltimore, 1948) to resemble those of the Eocene Equid, *Hyracotherium* (= *Eohippus*).
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Enrico Fermi

IF the earmark of genius is ability to reach the summits of creative thought by personal, unsupported effort, Enrico Fermi ranks extremely high among the scientists of our time. He was born in Rome on 26 September 1901. In his childhood he began to manifest an extraordinary interest in mathematics and physics, although there was nothing in the family environment—his father was a railway official—to induce an overpowering desire for these forms of abstract knowledge. During his high-school years Fermi absorbed and thoroughly mastered the contents of an odd assortment of books on higher mathematics, mechanics, and classical theoretical physics, including the theory of relativity.

In 1918 Fermi entered the University of Pisa, where he had little to learn from his teachers, since in most fields his knowledge already equaled or excelled theirs. Thus, he could devote himself fully to the study of the quantum theory, which had developed during and immediately after World War I, chiefly through the work of Planck, Bohr, and Sommerfeld, and which was virtually unknown to Italian physicists. At 21 he received the Ph.D. degree by, strangely enough, presenting an experimental dissertation on x-rays, even though he had already written several important theoretical papers ranging from classical mechanics to statistical mechanics and general relativity.

Fermi then visited the universities of Leiden and Göttingen and met several members of that brilliant