Ratio of central nervous system to body metabolism in vertebrates: its constancy and functional basis

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We present and document an hypothesis that healthy adults of most vertebrate species use 2-8% of their basal metabolism for the central nervous system (CNS). This relationship is constant across all classes of vertebrates, as we found by examining data from 42 species, including 3 fish, 3 amphibia, 2 reptiles, 6 birds, and 28 mammals. To explain its constancy, we hypothesize that an optimal functional relationship between the energy requirements of an animal’s executor system (muscle metabolism) and its control system (CM metabolism) was established early in vertebrate evolution. Three types of exceptional cases are discussed in terms of the hypothesis: very large animals, domesticated animals, and primates.

We present detailed documentation for an hypothesis that we first pointed out several years ago: that the central nervous system of a mature healthy vertebrate attains a size at which it uses 24% the total basal body metabolism (11).

Although our thesis is a new one, concern with brain size is very ancient, from the time of Aristotle, who noted that “of all animals, man has the largest brain in proportion to his size,” the relationship between brain weight and body weight has been calculated for various
vertebrate species and related to the question of the comparative intelligence of these species. The early work of Perrault (1613-1688), Vicz-d'Azyr (1748-1794), and Cuvier (1769-1832) on this question has been reviewed by Cole (16) and Coleman (17). Considerable attention was devoted to it by Manouvrier and Dubois at the end of the 19th century, as summarized by Anthony (1). In recent years, the relationship of brain weight and body size and its significance for intelligence has been considered in detail by Jerison (44, 45).

The relationship of brain size to body weight across different vertebrates is not a simple function. It is an exponential function with an exponent close to 0.66 depending on the group of animals under consideration. Furthermore, it is necessary to construct at least two different equations, one for cold-blooded vertebrates and another for warm-blooded vertebrates, since values for the latter are somewhat more than 1 log decade greater than those of the former for animals of the same weight.

We noticed that the graphic representation of brain weight as a function of body weight was strikingly similar to the graphic representation of basal metabolism as a function of body weight. On logarithmic axes, cold-blooded and warm-blooded vertebrates lie along two separate lines with similar slopes (approx 0.66) and with y intercepts that differ by somewhat more than 1 decade, no matter whether the equations represent brain weight (45) or basal metabolism (36) as a function of body weight. The great similarity of the functions suggested that they might reflect a simple underlying relationship of size of the nervous system to basal metabolism.

The possibility of a relationship between brain size and body metabolism has been considered before. Benedict (8) briefly discussed the role of the brain in controlling metabolism and concluded that it cannot be demonstrated that brain size is the controlling factor in metabolism. Based on blood circulation and brain weights of “lower” animals, the German neurologist Kestner (48) concluded erroneously that about 40% of the oxygen consumption may be attributed to the brain. Finally,
Crile (19), on the basis of detailed measurements of the organs of many vertebrates, came to a conclusion similar in some respects to the one considered here.

We found a law, so fundamental that it embraces insects, fish, reptiles, birds, rodents, ungulates, and carnivores, but not higher apes and man. This law is expressed by the ratio between the weight of the brain of an animal and the number of calories produced by that animal in 24 hours. We found that 1 gram of brain is required to produce 12,115 small calories in 24 hours.

Our conclusion is similar to that of Crile, except that we consider the entire central nervous system, not just the brain, and we relate its metabolism, rather than its weight, to the total body metabolism. Because the spinal cord is an integral part of the central nervous system, it should not be neglected. Indeed, in many cold-blooded vertebrates, the spinal cord is as large or larger than the brain. And by emphasizing metabolism rather than weight of the central nervous system, we are able to emphasize functional aspects of the relationship. Unlike many earlier studies, we are not concerned with intelligence as related to brain size, or with maintaining a preconceived conclusion of human superiority. Instead, we believe that the relationship described here may reflect an optimal relationship for vertebrates in the amount of metabolic energy devoted to control (nervous) and executor (muscular) systems.

METHODS

Data on the resting metabolism of the body and the central nervous system were sought in the existing literature. The search was carried out as systematically as possible through use of the Science Citation Index and bibliographies of relevant papers and books. Resting and basal metabolism of the body was found to be available for a large number of individuals of various weights and species (8, 13). Metabolism of the entire nervous system,
on the other hand, has not been determined directly; therefore all calculations of neural metabolism were made by multiplying metabolic rates of brain and spinal cord tissue by the corresponding tissue weight for each species. The obtained values for brain and spinal cord metabolism were then summed to yield the total resting metabolism of the central nervous system.

Brain weight data were found to be available for many vertebrate species. A number of investigators have documented the relationship between the size of the brain and the size of the body of individual vertebrates (12, 20).

Spinal cord weights were available for fewer vertebrates than were brain weights. Several investigators have collected spinal cord weight data for a number of vertebrate species. They include Latimer and co-workers (56-61) and Krompecher and Lipak (52). Direct data were available for the dolphin (79), whereas for the whale and alligator, spinal cord weights could be estimated from planimetric measurements and extrapolations from data in the literature (77, 89).

We determined the spinal cord weights of four cold-blooded vertebrates from our own specimens. The entire central nervous system was dissected from formaldehyde-fixed specimens of the dogfish, shark, perch, bullfrog, and goldfish after the entire specimen had been weighed. The brain and spinal cord were severed at their junction and the dura and spinal and cranial nerves were removed. The ratio of spinal cord to brain weight was computed. This ratio was subsequently applied to published brain weight data of other individuals of the same species, in order to estimate corresponding spinal cord weights.

In some species for which spinal cord weights were not available, we used spinal cord-to-brain weight ratios from other related species with similar body shape and size. The following extrapolations were made from one species to another: from frog to toad; from tree squirrel to ground squirrel; from guinea pig to opossum; from dog to fox; from brown bat to vampire bat; from macaque to baboon, from emu to ostrich; from human to chimpanzee; from
sheep to pig; and from horse to camel.

Direct measurements of in vivo rates of oxygen consumption of the whole brain were found in the literature for five species and have been plotted in Fig. 1. The data were obtained for the rat (68), cat (30), dog (32), rhesus monkey (84), and human (50). A regression equation was fitted to these data and took the form of

$$\log y = 0.86 - 0.13 \log x \quad (1)$$

where $y$ is brain metabolic rate in $cm^3 O_2 \cdot 100 g^{-1} \cdot min^{-1}$ and $x$ is brain weight in grams. The declining rates of metabolism in larger brains presumably reflect the lower packing densities of neuronal cell bodies, which is where most metabolism occurs (90).

![Graph showing brain metabolic rate as a function of brain weight](image)

FIG. 1. Brain metabolic rate as a function of brain weight in warm-blooded vertebrates, Data were obtained in vivo in rat (681, cat (301, dog (32), rhesus monkey (84), and human (50). Data are represented on logarithmic axes and are fitted with a linear regression equation of \( \log y = 0.86 - 0.13 \log x \) (y, brain metabolic rate in $cm^3 O_2 \cdot 100 g^{-1} \cdot min^{-1}$; x brain weight in grams.

Brain metabolism of cold-blooded animals could only be estimated indirectly, because there are no in vivo determinations in the literature. Therefore, we have used the $Q_{10}$ value for changes in nervous tissue metabolism.
as a function of temperature to calculate a function for nervous tissue at 20°C, the temperature used for most determinations of cold-blooded vertebrate metabolism. The value of $Q_{10}$ was set at 2.1, which is the mean of empirical calculations for brain tissue by a number of different authors using both warm-blooded and cold-blooded vertebrates (29, 67, 71, 88). Setting $Q_{10}$ equal to 2.1 and solving the following equation for the temperature coefficient of chemical reactions

$$\log Q_{10} = \frac{10 \log (k_1/k_2)}{t_2 - t_1} \quad (2)$$

with $t_2 = 37^\circ$C and $t_1 = 20^\circ$C, one obtains a ratio of $k_1/k_2$ equal to 3.5. This ratio is then used to convert Eq. 1 to a second equation for cold-blooded vertebrates in which each value is $1/3.5$ times the corresponding value for a warm-blooded vertebrate

$$\log y = 0.32 - 0.13 \log x \quad (3)$$

where $y$ is the brain metabolic rate in cm$^3$O$_2$·100 g$^{-1}$·min$^{-1}$ and $x$ is the brain weight in grams.

Spinal cord metabolic rates were found for only three species. Rosenberg (82) found that the spinal cord metabolic rate was 90% that of the brain in the European frog. McIlwain (66) found that guinea pig spinal cord slices respired at a rate 40% that of cerebral cortex slices. Hertz and Clausen (37) reported that slices of calf spinal cord respired at a rate 18% that of cerebral cortex slices. The latter two figures must be adjusted because cortex respiration is 40% greater than whole-brain respiration (23, 25, 66). Therefore, one may assume that guinea pig spinal cord metabolic rate is 56% that of whole brain and that the metabolic rate of calf spinal cord is 25% that of whole brain. These data, along with data from the frog, are plotted in Fig. 2 as a function of spinal cord weight.
and fitted with a regression equation

\[
\log y - \log x = -0.25 - 0.16 \log SW \tag{4}
\]

in which \( y \) represents spinal cord metabolic rate in \( \text{cm}^3 \text{O}_2 \cdot 100 \text{ g}^{-1} \cdot \text{min}^{-1} \), \( x \) represents brain metabolic rate in the same terms, and \( SW \) represents the spinal cord weight in grams.

**FIG. 2**, Spinal cord metabolic rate as a percentage of brain metabolic rate (upper line) and volume of gray matter at cervical level as percentage of total spinal cord volume (lower line). Metabolic data are from published measurements of European frog (82), guinea pig (65), and calf (37). Equation of line fitted to these data takes form \( \log \left( \frac{y}{x} \right) = -0.25 - 0.16 \log SW \). Data on spinal cord gray matter are from published measurements for mouse, *Mus musculus* (39), turtle, *Testudo* sp. (39), polecat, *Putorius* sp. (39), agouti rodent, *Dasyprocta agouti* (39), cebus monkey, *Cebus* sp. (39), and human (55). Slope of regression line for these data on logarithmic axes is -0.17, ▲, % value: spinal cord metabolic rate divided by brain metabolic rate. ●, 5% value: gray matter volume divided by total spinal cord volume.

Although basal metabolism data were available in the literature for all species under consideration, in some cases it was necessary to extrapolate from data in the literature to match the size of an individual for which brain and spinal cord weights were available. This was necessary because both basal metabolism and brain-to-body weight ratios are a function of the size of the individual animals. In those cases in which the body weights of animals for which the two sets of data were
available differed by less than 10%, no adjustment was made. In case of differences greater than 10%, the metabolic rate was adjusted according to the following equation

$$\log BM_2 - \log BM_1 = 0.75 (\log BW_2 - \log BW_1)$$  \hspace{1cm} (5)

where BM is body metabolism and BW is body weight (8)

The spinal cord metabolism of the elephant was treated as a special case. No data were available on the size of the spinal cord of a mature elephant. However, judging from the data on other large mammals, one could assume that the overall metabolism of the spinal cord is no more than 10% of the brain metabolism. For example, in the camel it is 9%, in cattle 10%, and in the horse 9%. Therefore, we used a figure of 9% of brain metabolism as an estimate for metabolism of the elephant spinal cord.

When data were available from many individuals of a species, we chose data from mature, healthy individuals as reported in the literature. A second consideration was made in choosing which values to use. Insofar as possible, we used animals of the same body weight for both the body metabolism data and the brain and spinal cord data.

DISCUSSION OF METHODS

The temptation to apply statistical procedures to the data must be tempered by the fact that one cannot make a “random sample” of vertebrate species. We must work with the data available, and such data tend to come to a great extent from domesticated animals, laboratory animals, and higher primates. Data for other vertebrates are available for only a few species. Instead of trying to obtain a random sample, we have tried to obtain data from all the vertebrate classes and from animals that lie at the extremes of the various parameters under consideration. Thus, we have obtained data for fish, amphibia, reptiles, birds, and mammals. Among fish we have a weight range from a 9-g goldfish to a 4,200-g shark, and
among mammals we have animals ranging from the shrew and mouse to the elephant and whale. As weight and taxonomic differences would be expected to increase the variance of our data, one may claim that our procedure is a conservative one. If anything, we should end up with more variance than would be expected if it were possible to do a random sampling procedure, and, therefore, our ability to generalize to the vertebrates as a whole should be, if anything, enhanced.

We are also unable to obtain a random sample of data from individuals within each species. Instead, we have limited our data to healthy adults and have, whenever data must be combined from several individuals, used data from individuals of similar body weight. This procedure would be expected to reduce the variance in the data obtained. There are changes in the various relevant parameters over the course of ontogeny that are quite complex and variable from species to species. The human infant, on the one hand, uses a very high proportion of total metabolism for the central nervous system as evidenced by the fact that the brain-to-body weight ratio is much higher than that of an adult (18), and the metabolic rate of the brain is greater as well (49). The rat or dog pup, on the other hand, does not use a significantly greater proportion of metabolism for the central nervous system (CNS) than does an adult; although the brain-to-body weight ratio is greater for an infant, the metabolic rate of brain tissue is correspondingly lower (38, 83). Comparable data are not available for other vertebrate infants. In old age, the metabolic rate of brain tissue (and consequently, the ratio of CNS to body metabolism) decreases slightly in both humans (49) and rats (64). Similarly, health could be a factor in the data, since an emaciated animal might have a lowered body metabolism, but still require the normal brain metabolism. Therefore, to eliminate these sources of variance as much as possible from the data, we have limited our sample to healthy adults.

There are good theoretical reasons to exclude data of very young, very old, and unhealthy individuals from our sample. The metabolic activity of a very young bird or
mammal should not be considered without regard to the metabolism of the parents and siblings. In a sense, from an evolutionary perspective, the family unit might be considered as the appropriate unit of analysis; in some cases the parents may “sacrifice” a considerable proportion of their own body metabolism in order to make possible the development of the offspring. For example, it may be the prolonged feeding of the human infant by the mother that makes possible the fact that it can devote such a large proportion of its metabolism to the developing brain. Very old and emaciated animals may be eliminated in order to concentrate on metabolic ratios of those types of individuals (i.e., healthy but not very old individuals) that have most likely made the major contribution to the evolution of the species, i.e., contributed to the gene pool that determines the relationships under consideration.

The reliability of data on brain and body weights and resting metabolism is well established in most cases. Figures that show the relationship between brain and body weight and between resting metabolism and body weight for healthy adults of various species usually have remarkably low variance (8, 18). There are two species, however, in which the resting metabolic rates may be called into question: the shrew and the whale. Although one source on whale metabolism suggests that the body metabolic rate of the finback whale is half that of a dolphin (42) another reference suggests that is may be considerably less, perhaps only 1/5 or 1/7 the metabolism of the dolphin (46). The latter figure is more consonant with predictions from other mammalian data (41) and will be used here. In the shrew, there is the problem that the animal is never really at rest (70), and therefore the quoted values or “resting metabolism” may be more the equivalent of an active metabolic rate in other species.

The reliability of data on spinal cord weights is probably less than that of brain weight. Because of the scarcity of data in the literature, we have been forced to make some extrapolations across species, in two cases (whale and alligator) make estimates from planimetry,
and in one case (elephant) make an overall estimate for spinal cord metabolism without regard to its weight. However, since spinal metabolism in most of these animals accounts for 10% or less of the metabolism of the CNS, one may assume that errors deriving from such extrapolations would not have a very great effect on the final data; i.e., a 30% error in spinal cord weight would change the overall ratio of CNS to body metabolism by only 3%.

The greatest problem in data reliability concerns the estimates of brain and spinal cord metabolism. The two functions that we have plotted in Figs. 1 and 2 are derived from the only direct data that are available, and these data are not as numerous as one would like. However, there are considerable indirect data that support these functions. We have relied upon in vivo measurements, but there are also many in vitro measurements that can be compared. As a general rule, in vivo measurements of tissue metabolism are twice as great as the equivalent in vitro measurements of sliced tissue (i.e., tissue with the cell structure still intact) according to McIlwain (66) and in vitro measurements from sliced tissue are 2.2 times greater than measurements from homogenized tissue with the cells broken down (25, 71). Also, one can make comparisons between metabolic rates of whole brain and isolated cerebral cortex in mammals on the basis of the fact that cortex metabolism is 40% greater than whole-brain metabolism (23, 25, 66).

The function for brain metabolism in warm-blooded vertebrates is supported by both in vitro measurements and by in vivo cortical measurements. The function for metabolism of cortex in vivo can be calculated from data supplied for the rat (23) rhesus monkey (9), and human (66). A regression equation fitted to these data is

$$\log y = 1.04 - 0.13 \log x \quad (6)$$

where $y$ is brain metabolic rate in cm$^3$ O$_2$ · 100 g$^{-1}$ · min$^{-1}$ and $x$ is brain weight in grams. Reducing this equation by a factor of 1/1.4 in order to make it equivalent to
whole brain rather than cortex, as noted above, one obtains the equation

\[ \log y = 0.89 - 0.13 \log x \]  \hspace{1cm} (7)

and this question can be taken as confirmation of \textit{Eq. 1}. Similarly, one can obtain a function from the in vitro determinations of slices of cortical tissue from the mouse, rat, cat, and cow, as obtained by Eliot and Henderson (25). A regression equation fitted to their data is the following

\[ \log y = 0.76 - 0.15 \log x \]  \hspace{1cm} (8)

where \( y \) and \( x \) represent the same parameters as in previous equations. To convert this to an equivalent whole-brain in vivo measure, one must multiply by a factor of two (whole brain-to-slice metabolic ratio) and then reduce it by a factor of \( l/1.4 \) (whole brain-to-cortex metabolic ratio). When this is done, one obtains the following equation which also corresponds well to \textit{Eq. 1}

\[ \log y = 0.91 - 0.15 \log x \]  \hspace{1cm} (9)

The function for brain metabolism in cold-blooded vertebrates is also supported by data from in vitro measurements. Data for homogenized brain tissue in vitro has been obtained for the bass (29), bullfrog (74), turtle (63), salmon (71), and goldfish (27) at approximately 20°C. The obtained data are as follows, expressed in \( \text{cm}^3 \, \text{O}_2 \cdot \text{100} \, \text{g}^{-1} \cdot \text{min}^{-1} \) and multiplied by 4.4 to convert from homogenized to in vivo equivalents. They may be compared to expected values predicted by \textit{Eq. 3} derived from the \( Q_{10} \) equation. Bass, obtained value 1.8 and predicted 2.1; bullfrog, obtained value 1.5 and predicted 2.4; salmon, obtained value 2.6 and predicted 2.7; turtle, obtained value 1.8 and predicted 2.5; and goldfish, obtained value 2.2 and predicted 2.8.

Independent and theoretical support for the form of \textit{Eq. 4} for spinal metabolic rate may be obtained from a
consideration of the proportion of the spinal cord that is made up of gray matter. Because gray matter has a much higher metabolic rate than white matter (24) one can explain the lower proportional metabolism of large spinal cords in terms of their lower gray matter content. We have calculated a function for the proportion of spinal cord made up of gray matter as a function of spinal cord weight in a variety of vertebrates, using data from Hovy (39) and Lassek and Rasmussen (55). The resulting function has approximately the same slope as that of \( \text{Eq. 4} \)

\[
\log y = 0.52 - 0.17 \log SW \quad (10)
\]

where \( y \) is the percent of the spinal cord consisting of gray matter and \( SW \) is the spinal cord weight in grams.

RESULTS (click here for Table 1)

The ratios of central nervous system (CNS) metabolism to resting body metabolism for 42 vertebrate species are presented in Table 1. The data on weights, metabolic rates, and calculated metabolism of the body, brain, and spinal cord are also shown for each species in Table 1 so that the reader can follow the derivation of each ratio. Sources for the empirical data and methods of calculation for estimated data are indicated in notes to Table 1. As explained in METHODS, each set of data represents the values for a single healthy mature individual of that species.

Most of the vertebrates use from 2.7 to 7.7% of their total resting metabolism for the CNS, with a mean of 5.3%. There are several exceptions, however. The mouse uses 8.5% of its total body metabolism for its CNS and all primates studied use over 10%. Other species use less than 2.7% of their metabolism for the CNS, including domesticated livestock (horse, cow, chicken, and pig) with values from 1.6 to 2.0% and the shrew at 1.5%. Very large animals also have low ratios; in addition to the domesticated horse and cow, the ostrich has a metabolic ratio of 0.7%, and the extraordinarily large elephant and
finback whale have ratios of 2.0 and 0.5%, respectively.

There is a close correlation between total body metabolism and calculated CNS metabolism among all of the 42 species in our sample. A linear regression equation expressing CNS metabolism as a function of total body metabolism for these data takes the form

$$\log y = 1.27 + 0.91 \log x$$  \hspace{1cm} (11)

where \( y \) is CNS metabolism and \( x \) is total body resting metabolism as they have been given in Table 1. The correlation coefficient for this equation is 0.97 and the standard error of estimate (corrected) is 0.32, which indicates that the relationship is a close one. The data are shown in Fig. 3, along with the regression line for the equation shown above.

A more conservative conclusion can be drawn from the animals in which there have been direct measurement of brain metabolism. Data from those animals are shown in an insert of Fig. 3. From these data two other regression equations can be drawn, depending on whether or not the human data are included. With human data, the regression equation is

$$\log y = -1.43 + 1.2 \log x$$  \hspace{1cm} (12)

Excluding the human data (since by all accounts the human data cannot be taken as representative of the vertebrates as a whole), one obtains a regression equation with a slope that is close to unity

$$\log y = -1.16 + 0.99 \log x$$  \hspace{1cm} (13)

There is not much difference between cold-blooded and warm-blooded vertebrates in the proportion of metabolism used for the central nervous system. The mean metabolic ratio of CNS to body metabolism for the eight cold-blooded vertebrates shown in Table 1 is \(4.8 \pm 0.6\%\) (mean \(\pm\) SE). The mean metabolic ratio for the 34 warm blooded vertebrates is \(5.5 \pm 0.7\%\) (mean \(\pm\) SE).
DISCUSSION

The main hypothesis, that vertebrates use 2-8% of their resting metabolism for the CNS, applies with remarkable consistency across all vertebrate taxa and to species of greatly different body size. The simplicity and consistency of this relationship is much greater than the relationship of brain size to body size that has been noted by previous investigators. Unlike the latter, the new finding does not require separate equations for cold-blooded and warm-blooded vertebrates. Also, unlike earlier findings, the present findings may be explained with an equation that is more or less linear rather than with complex logarithmic equations.

Several taxa of warm-blooded vertebrates appear to be exceptions to the rule that 2-8% of the resting metabolism is used for the central nervous system. These include primates, domesticated livestock, the whale, the elephant, the ostrich, and the shrew. The shrew, as indicated in METHODS, may be only an apparent exception due to technical problems of measuring its metabolic rate. Very large animals such as the whale, ostrich, elephant, and alligator may have attained a size at which the basic relationship breaks down. After all, most physical laws break down at the extremes. In fact, if animals with body weight over 100,000 g are excluded from the data, the slope of the resulting regression equation is exactly unity, i.e., the relationship is linear.

The apparent fact that domesticated livestock use a lower percent of their resting metabolism for the central nervous system may reflect the purposes of the selection by humans during the process of domestication. The horse, cow, pig, sheep, and chicken may have been deliberately selected for an increase in body size and for no increase, or if anything, a decrease in CNS size. Corroboration of this hypothesis is found in the fact that the brain-to-body weight ratio of domesticated pigs is 30% lower than that of their feral counterparts (53), and a similar relationship holds between domesticated and wild sheep (15). By contrast, dogs and cats that have presumably not been selected for increased body size or reduced intelligence have metabolic ratios similar to
those of nondomesticated vertebrates.

Primates devote a relatively high proportion of their body metabolism to the CNS. It would appear from data on brain-to-body weight ratios that this shift began to occur early in primate evolution (78). The greatest increase occurred in the last 1,000,000 yr during the evolution of Homo erectus and early H. sapiens (72). Crile (19) noted this fact and suggested an explanation that is consistent with the present thesis: he postulated that when an animal’s thinking capacity could control “energy outside themselves, whether it is the energy of a club, of fire, or of another animal, the brains of such animals will be larger than the brains of animals that execute energy entirely within themselves.”

FIG. 3. Central nervous system metabolism as a function of body metabolism. Data are taken from Table 1, columns G and J, and regression Eq. 11. Insert, data are shown for those animals in which direct measurements of CNS metabolism are available. Regression lines are shown for data without (solid line) and with (dotted line) inclusion of human CNS metabolism, Eqs. 12 and 13, respectively.
The constancy of the metabolic ratio for the CNS and total body metabolism may reflect a general relationship between control and executor systems in the animal kingdom. We may hypothesize that there is an optimal proportion of metabolism used for control systems (the CNS) and executor systems (the muscular systems) such that control systems use 5-10% of the energy used by the executor systems.

To test the hypothesis that there is an optimal control-to-executor energy ratio, we need to obtain data that are not yet available in the scientific literature. First, we need direct data on CNS metabolism from more species to confirm the relationships hypothesized in the present paper. Second, we need data on metabolism for normally active organisms over long time periods, rather than the available data that represent resting animals for short time periods. If such data are obtained, we may find that the relationship is similar to the one hypothesized for resting animals; thus species of fish that are continually active have total body metabolic rates that are twice those of species that are inactive (34), and, similarly, active species of fish have brain metabolic rates (as measured in vitro) that are double the comparable rates in sedentary species (91). In warm-blooded animals the data are less complete, but we know that very active humans may have metabolic rates that are double those of inactive people of comparable size [see Table 48 in Fulton (28)], and brain metabolism also increases as a function of short-term activity (87). Third, we need data on long-term metabolism of the muscular system rather than total body metabolism. Presumably, the muscular system uses most of the total body metabolism as opposed to digestion, nonmuscular heat production, tissue repair, etc., except perhaps during the high growth rates of the young animal and the pregnancy and lactation of the mammalian mother. However, total muscular metabolism must be less than total body metabolism, and for that reason we have suggested that the control/executor metabolic ratio is not 2-8% but more on the order of 5-
This theory can explain why there was such a great increase in relative brain size during the evolution of warm-blooded vertebrates, a fact that previous theories have not been able to explain very well. The evolution of warm-blooded vertebrates was marked by a great increase in energy metabolism that had to be matched by a proportional increase in food intake and, therefore, an increase in the amount of work done to obtain food. It has been estimated that at an environmental temperature of 16°C, a field mouse of 20 g will require nearly 60 times as much food to meet resting metabolic requirements as a common frog of the same weight (3). The converse is also true: warm-blooded vertebrates that reduce their body temperatures to 20°C during hibernation have values for resting body metabolism during hibernation on the order of the cold-blooded values (36).

We know, from the present data, that in the course of evolution the warm-blooded vertebrates increased not only their overall metabolism in comparison to cold-blooded vertebrates, but their CNS metabolism as well, and that each was increased in the same proportion. The equivalent proportional increases can be explained by the theory proposed here; since it is proposed that there is an optimal relationship between metabolism of the control and executor systems, any increase of muscle metabolism should be matched by a similar proportional increase of CNS metabolism.

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REFERENCES
33. HALL, F. G. The respiratory exchange in turtles. J. Metab. Res. 6:393-401, 1924.
84. SCHMIDT, C. F., S. S. KETY, AND H. H. PENNES. The gaseous metabolism of the brain of the monkey. Am. J. Physiol. 143: 33-52, 1945,