The Study of Primate Brain Evolution: Where Do We Go From Here?

Harry J. Jerison

I am pleased to accept the title that Dean Falk and Kathleen Gibson assigned me for this concluding essay. And of course I thank them for arranging the meeting of the American Association of Physical Anthropologists in my honor. Most of all I must thank the contributors at that meeting and the others who have taken time to prepare the chapters in this book, which commemorates that meeting. In my judgment it would be inappropriate for me to comment on those excellent chapters, to argue with some of them or to agree with others. The chapters speak well for themselves, I will leave commentary to the journals, such as *Current Anthropology* or *Brain and Behavior Sciences*, that specialize in it. It has been a great pleasure to be involved with these activities.

I will depart from my assignment in three ways. First I must write about where I would go from here rather than prescribe for others. The chapters in this book present better prescriptions than I am competent to offer for the route our field as a whole can take. Second, I would like to write about where we have been, because my particular route is so much one involving the fossil evidence that I think it takes some explaining. Finally, I have to write about more than only primates, because my emphasis has been and continues to be on the evolution of the vertebrate brain, including the primates among the mammals.

Although I avoided specific citations of the chapters of this book, I was thinking about dolphin brains and the strange problems they pose for quantifiers and behaviorists when writing this essay. I had to discuss Preuss's chapter when reviewing my concerns with the whale brain and its evolution and the quantification of cortical thickness functions. I was able to maintain my resolve for the other contributors although some, of course, are mentioned by name.

I will emphasize themes that I have developed before, which I think need more work or correction, and indicate the way I would work on them now. I will be less ambitious about the details of mammalian and primate brain evolution than these deserve, covering mainly the quantitative analyses that come easiest for me and that I can handle. And I will discuss my current interest in the technology of computer graphics, which will improve the answers to old questions and, perhaps, suggest some new ones.

Personal and Other History

I call my discipline paleoneurology, following my mentor, Tilly Edinger. Tilly died when I began writing my "big book" (Jerison, 1973), which I dedicated to her. I have recently written a preface to Edinger's biography (Kohring & Kreft, in press) which I have added as an appendix to this chapter, as a footnote to the history of my discipline. In that preface I describe the circumstances of my meeting Tilly and my introduction to what she described as fossil brains (Edinger, 1929).

Almost from the beginning of my scientific life I sought to incorporate the fossil data into evolutionary schemes. I was especially impressed by Karl Lashley's famous presidential lecture to the American Society of Naturalists on the evolution of mind in which he mentioned brain-body analysis. Lashley, in turn, had probably discovered that analysis in informal meetings of a group of distinguished neurobiologists in Chicago in the nineteen-twenties and 'thirties. The group included Warren McCulloch (McCulloch, 1965) and Gerhard von Bonin (von Bonin, 1963), and I heard about these meetings from another of the participants, the pioneer neuropsychologist Ward Halstead (Halstead, 1947).

I reconstruct this relatively modern history as beginning with von Bonin's long-time interest as a neuroanatomist in brain evolution, and his penchant for quantitative analysis. He may have been inspired by early work published by Eugene Dubois (see Theunissen, 1989, especially chap. 5), but perhaps learning from Halstead, von Bonin performed an elementary statistical analysis to determine the regression of log brain weight on log body weight in mammals (von Bonin, 1937). He reported that 2/3 was the allometric exponent, the slope of the regression line for log-log data. In this way von Bonin introduced objective mathematical and statistical methods to studies of brain evolution.

Halstead told me years later that von Bonin had presented his results to the Chicago club, which

may have been where Lashley first heard of them, and this led to their being cited in Lashley's presidential lecture. I read the lecture's published version (Lashley, 1949), and discovered von Bonin's work, eventually verifying von Bonin's result in my first publication on brain evolution (Jerison, 1955). With that I began my commitment to my first "error" which I discuss later under the heading, "the allometric exponent."

In verifying von Bonin I did some scientific filtering of data, because I recognized that cetaceans, evolving in a gravitationally odd environment, had different constraints on the size of their bodies than land mammals, and that there must have been something equally odd about primates as a mammalian order of brain-size specialists. I did my regression analysis of what I thought of as typical mammal species, excluding cetaceans and primates from the sample that I used to calculate the slope of a "mammalian" line, the value of the allometric exponent. This filtering was of course a no-no for statistical purists who want to let all the data do the talking, but it strengthened my commitment to 2/3 rather than other candidates for the role of a "true" value.

Whatever the right thing to do is, the impressive results of allometric analysis of brain-body data, and of the role of encephalization that Lashley described as providing the only anatomical correlate of mind, led me to look at brain size as a kind of a statistic and to look for neural and behavioral parameters that it estimated. I wanted to learn why the simple measures of the size of the whole brain and of the body could be used in this way. After I began to work on the problem, I met Roland Bauchot who gave me a copy of his PhD thesis (Bauchot, 1963) on the volumes of thalamic nuclei. Tilly Edinger told me that she had published on fossil camel brains in a book edited by Bauchot's collaborator, Heinz Stephan (Hassler & Stephan, 1966). (I had been invited to the meeting that led to Stephan's book, but could not afford the flight to Germany.) Eventually I found the several compendia published by Stephan and his collaborators (e.g., Stephan, Frahm & Baron, 1981; cf. Stephan, Baron & Frahm, 1991) on the laboriously acquired data on the volumes of various components of the brains of insectivores, prosimians, and other primates. It was only later that I realized that Stephan was working in Tilly Edinger's father's laboratory at the brain research institute in Frankfurt, Germany, a laboratory that I mention in the appendix to this chapter.

Using Stephan's and Bauchot's data and those of their students, I was able to verify that the simple measure of brain size was worth studying and analyzing. These contribute to the quantification of brain size as a statistic with respect to the neural and informational parameters that it estimates. I was fascinated by the idea of developing the fossil evidence, which consists of an image of the external surface of the brain in mammals and birds. Accepting criticisms from anatomists such as von Bonin, I was suspicious of the use of gyral and sulcal patterns as correlates of behavior. Brain size was the most reliable measurement that was available, and it became my basic handle to interpret the data on fossil brains.

Numerology?

I can be correctly accused of enjoying numbers in a mindless way. I cannot describe my pleasure when I can attach numbers to a phenomenon, even when I know it is a pretty stupid way to spend one's time. After publishing my big book I actually tallied the dates of publication of my citations to check on my biases. I have the graph I drew somewhere, I hope lost, because otherwise I might inflict it on you. But it was nevertheless interesting as a study of the sociology of science. As I recall, like most authors I tended to be up-to-date, citing recent publications more often than older ones. I had more than 500 references, and since my book is now a standard source, I must apologize for being so conventional. In my defense I should note that I did try to cite the earliest rather than the latest publication that I found for a particular idea. I tried to honor the creator of a concept if I identified the author, rather than someone who had cited the publication as part of a review.

Later in this chapter I present some of my updated quantifications on the brain, graphs that I intend to illustrate what I think of as the most interesting results that I have run into. These graphs are my personal excuse for exercising my compulsion. It is not only fun, but the results are important.

My big book is now thirty years old. It should be extinct as a scientific monograph, which are usually given a half-life of about five years. But my book lives on, and as the first example of my

compulsion being acted out, let me illustrate the history of its rate of citation as determined from *Citation Index*. The citation rate has remained steady throughout the book's history, which surprised me. I like to think that people found my scientific results interesting.

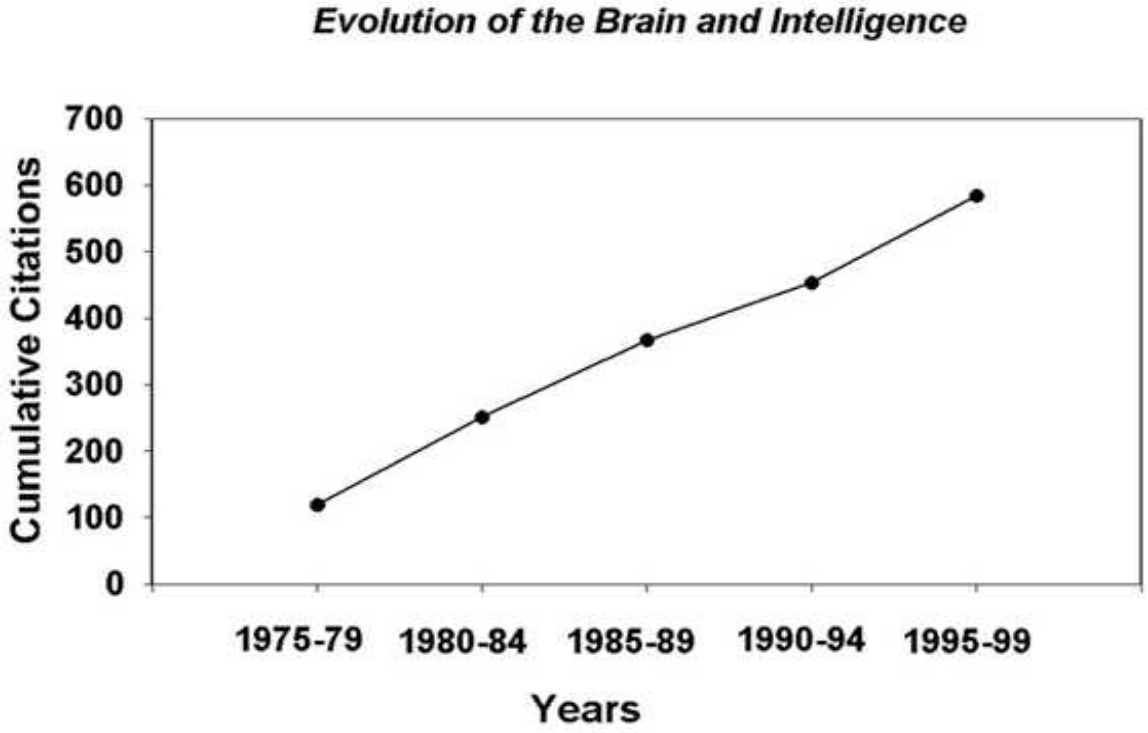

Figure 1. Cumulative rate of citation for Jerison (1973)

The book may have also had special value as a useful target for attack by correcting its "mistakes." Let me discuss these first, because their correction, rejection, or recognition as not mistaken at all are the first element in my describing where I would go from here.

There are, of course, real mistakes in the book, such as discussing the brainlessness of marsupials as a group in a paragraph intended to hoist only the didelphids on that petard. I was personally most offended by a mistake that I still cannot understand. Some of the graphs in the book were drawn by professional artists, but I made a half-log unit error in misplacing convex polygons in two graphs that I drew myself (Jerison, 1973, Figs. 7.4 and 8.4), exaggerating the difference between mammals and their ancestors. Advances in computer graphics make such errors rare. When I present graphs nowadays my numbers are on data sheets and my graphs are drawn automatically by a graphics program that never makes mistakes. (Well, hardly ever!) The graphs for this chapter were all drawn by my graphics program, not by me. The only possible mistakes are with the numbers, and I think most of mine are now gone from my data sheets.

Mistake 1. Brain reorganization other linguistic mistakes.

My biggest mistake was probably in describing differences among species in the organization of the brain as trivial. I do not apologize. My mistake was semantic. I wasn't thinking as a writer, alert to avoid misunderstandings. Look up "trivial" in your dictionary. You may sympathize with me if you know that my closest associations as a young man were with mathematicians, and when mathematicians call a "result" trivial they mean merely that it is obvious, a truism not worth discussing. That is more or less what I had in mind. The first usage is as "commonplace, ordinary." That is also OK. My drawing error in my graphs were of that type, and they served only to exaggerate an effect that was basically true. (Mammals are all relatively larger brained than reptiles or amphibians.) But a third dictionary definition of trivial is "of

little worth or importance," and I am afraid that this was the sense at which my usage has been taken. For that I apologize. Not only is reorganization worth recognizing, it is fundamental for understanding how brains of all vertebrate species differ from one another.

When I wrote further on reorganization in my big book I probably obscured my discussion by renaming it. I proposed a general principle of brain structure-function relations, which I termed "proper mass." I think of it as a principle applicable to all vertebrate brains, not limited to human evolution. The idea was that the mass of brain tissue devoted to a specialized function in a species was related to the importance of the activity supported by that brain tissue in the life of a member of a species. I was being semantically stupid in my choice of words, because even colleagues sympathetic to my general views mistook my usage as supporting Lashley's discredited idea of mass action.

The idea that the size of a neural system is usually related to its importance is obviously right, and I thought that it must have been named. I consulted with my old friend, Wally Welker, on the matter. Wally had published the clearest research result exemplifying proper mass (Welker, 1990; Welker & Campos, 1963) in the diverse adaptations of living procyonids. He described and illustrated the enlargement of sensorimotor neocortical representation of the paws of the raccoon as compared with the enlarged representation of the rhinarium in the neocortex of the coati mundi. Raccoons use their paws as hands, whereas coatis nose about to explore their environment. Wally could think of no word or phrase for the idea, which was as obvious to him as it was to me. Hence, "proper mass." The only textbook in which I have seen the designation accepted is Butler & Hodos (1996), but it is a valid organizing principle for understanding the diversity of brains as they evolved in vertebrates.

The unfortunate side of the unnecessary controversy, to which I may have contributed by my misuse of "reorganization," has been the emphasis on the specialized evolution of the human brain compared to other primates and other mammals, as if the structural reorganization of the human brain was unique in vertebrate history (Deacon, 1997). Of course the human brain is unique, perhaps because of the evolution of our language sense. But all species are unique, and the organization of their brains is unique. It is uniqueness that identifies a species. Reorganization as a phenomenon is a feature of evolution, which is part of what establishes the uniqueness of a species. It reflects changes that became fixed in the genetic material of various species as they evolved to enter their adaptive niches, and although we remain ignorant about the details of the genetic control of the diversity in brain structure, we can recognize it as one of the things to explain as we improve our understanding of the genetics of brain development.

Mistake 2. The allometric exponent.

In my first publication on brain-body relations (Jerison, 1955) I reported an allometric exponent of 0.73 for the entire mammalian sample on which I calculated the regression of log brain size on log body size. This value, or the commonly recognized one of 0.75 that we accept now (Martin, 1990) made no sense to me, whereas the value of 2/3 first proposed by Brandt (1867) and later rationalized by Snell (1891) made good sense. It reflected the brain's work in mapping information between surfaces and volumes, and it was easy to incorporate into a theory of encephalization (Jerison, 1977). Dubois' empirical value of 5/9 (see Jerison, 1973; Theunissen, 1989) made no sense either, and von Bonin's 0.66 found by regression analysis provided relief from the nonsense results with other values. I am distressed by the easy acceptance of 3/4 in the present literature, and am not optimistic that this brief statement will fix things, but I will try.

There are two problems. First, does it make sense to seek some correct value for the exponent in the genetic instructions that tell mammalian bodies and brains how to grow to their mature size? Second, if there is a theoretical true value of the exponent, how should we expect empirical estimates of that value to deviate from the true value. There is a third problem, which I am not competent to discuss, but which may be one of the paths to prescribe for the future of our field. This is to rethink the general issue of allometry in relation to recent developments in fractal geometry (West, Brown, & Enquist, 1997). Although exponents calculated by regression analysis may be interpretable in terms of fractal dimensions, I find only those in Bridgman's (1931) dimensional analysis easy to understand.

Allometry as theoretical biometrics was a theory of growth (Huxley, 1932). The idea was that if you knew the rates of growth of different body systems, their correlated changes should be related to one another in some specifiable way. The biometric problem is well described by Harvey & Pagel (1991). The aspect that intrigues me is that the growth pattern during development of an individual animal generates an equation that is equally useful for describing relationships among adults of different species. There is no question that the equation works, and it does describe brain-body relations. I am concerned with what this suggests about how the genetic system works and what it implies about how the brain works in mammals.

My prejudices will show. Although I have reported statistics as often as most people in our field, and I think I use them sensibly, my view has never been very respectful of statistical niceties. If a regression coefficient is reported, my first reaction is to ask about its referent: what does it describe? My second reaction is to ask whether there is any fundamental significance to its actual value.

In the case of brain-body allometry I have assumed that the fundamental referent for the exponent was some genetic constraint on overall growth of the body and brain in an animal. In mammals I assume that the constraint is related to the role of the brain in mapping information from sensory to neural surfaces, and that a rule evolved that prescribed the number of neural elements in different parts of the system. For brain-body allometry, I have assumed that the rule was related to the fact that sensory systems are distributed across what are approximately two dimensional bodily surfaces, such as the skin, the retina, the basilar membrane of the ear, and the olfactory epithelia, but that the size of the analytic systems (neocortex, etc.) involves volumes as well as surfaces, since their mass involves layers of nerve cell bodies distributed about white matter. The surface-volume relationship has always appealed to me intuitively, and for this reason a 2/3 exponent has seemed to me the *a priori* correct exponent to reflect the fundamental constraint on neural growth in a mammalian brain.

Empirically, however, one finds a 3/4 exponent. This strikes me as a problem for theoretical analysis, not an issue about "true" exponents. It is especially valuable for guiding the tactics of theory building. The theoretical problem is, why are brains as big as they are, and why is their size related as it is to body size in vertebrates. I have published a bit of my answer for mammals in several places, and it is not inappropriate to repeat the argument now.

We must first differentiate between an empirical and theoretical exponent. The theoretical exponent can reflect fundamental relationships among information processing elements with respect to the transformation of information. The empirical value of the exponent should reflect structural relationships involved in the packing of the information-processing elements within organ systems such as brains and bodies. I presented the fundamental analysis in my generally ignored theory of encephalization (Jerison, 1977). To simplify the analysis I treated cortical thickness in mammals as a constant length (depth), although I knew that its measure was related approximately to the 1/6 power of brain size or the 1/9 power of body size. I had determined those from illustrations in Kappers, Huber & Crosby (1936). Here are a few more facts.

I took cortical thickness as constant because it very nearly is. Mouse neocortex averages about 0.5 mm in thickness, whereas human neocortex averages about 2 or 3 mm in thickness. Not much of an increase. I have never published data on the issue, since I could find none and would have to collect them myself, Schüz and I are currently working on the problem, relying on digitized brain data that are available. Taking some measurements from charts published by Rockel, Hiorns, & Powel (1980) and trying to be statistically correct by avoiding anything to bias the measures, I assembled the data for Figure 2. It is clear that neocortical thickness is not constant among species. Its relationship to brain size across species appears to be relatively orderly.

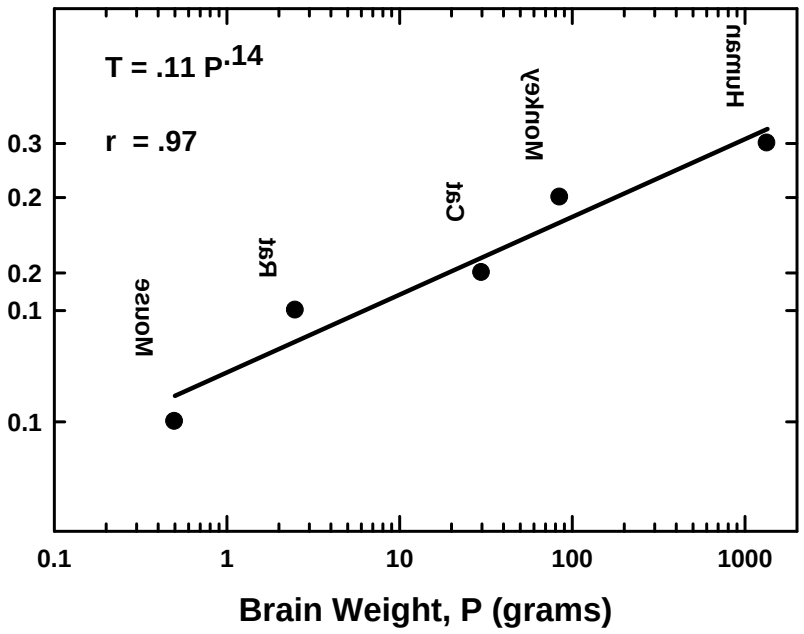

Figure 2. Cortical thickness as a function of brain size in five species of mammals. Measured from graph on motor cortex in Rockel et al., 1980.

Since there is a substantive issue about the value of an empirical allometric exponent, let me free-associate about the correction required for my 1977 theory of encephalization. The theory was based on the idea that an equation relating brain size (a three-dimensional volume) to body size (another three-dimensional volume) had to be dimensionally balanced in Bridgman's (1931) sense. After a bit of analysis I presented my concluding theoretical statement:

$$E = 0.1\ m\ P^{2/3} + A \qquad (1)$$

The units are in the centimeter-gram-second system. E and P are brain and body size (grams or milliliters), m is a dimensionless constant, and to balance the equation, I pointed out that the multiplier 0.1 was a depth in centimeters, i.e., 1 millimeter. The two sides of the equation are then balanced. One point, of course, is that the exponent 2/3 reduces the dimensionality of the body to that of a two-dimensional sheet of 0-thickness. I wrote that the depth of 0.1 cm could represent the depth of neocortex, which is of that order of magnitude in living mammals. A was an added amount of brain tissue, a three-dimensional term in grams or milliliters, and represented the amount of encephalization in a species.

The "mistake" in Eq. 1 is in having neocortical depth as constant. To be represented by the actual depth of the neocortex, we need the kind of information presented in Figure 2, and we have to remember that the right hand side of the equation has to be exactly three dimensional for the equation to be balanced.

You can do the numbers yourselves. The data of Figure 2 are needed only to clarify the dimensionality of the multiplier, and we should also remember that Figure 2 is only an ad hoc representation of a "true" relationship. To make things a bit easier, we can begin by replacing the 0.14 exponent with 1/6 (= 0.167), implying a relationship to the depth dimension (the square root of the depth as the dimension that is the cube root of the volume, whatever that suggests). The physical source of the right-hand side of the equation is body size, hence the suggestion from Figure 2 has to be converted into something that affects the dimensionality of the measure of body size. A reasonable way to handle that is to consider brain size as a theoretical function of the 2/3 power of body size, i.e., that it is proportional to the area of a map of the information spread over a kind of body surface. The multiplier would then have a dimension of $(P^{2/3})(P^{1/6})$, or$(P^{1/9})$. (Dimensional analysis would replace P with L^3, to indicate that the

operations are on the dimensions.) The expected empirical exponent if one measured body size in a regression analysis of brain-body relations is therefore (2/3)+(1/9), or 0.78. In other words, if the dimensional approach is correct we should expect a regression analysis to show brain size as approximately a function of the 0.78, or 3/4 power of body size whereas the fundamental allometric relationship for the system would be still be given by terms involving the 2/3 exponent to convert volumes to surfaces.

$$E = m\,(P^{1/9})P^{2/3} + A \qquad (2)$$

The term, $(P^{1/9})$, represents a dimensional transformation of the depth term, m is no longer dimensionless; its dimension would bring the dimensionality of the right side of the equation to 3. The term A remains a three-dimensional term, the residual encephalization. For the "average" mammal it has a value of 0 and disappears in the regression equation.

I am doing no more than pointing out the direction I would take to try to resolve this problem, and mine is not a pretty solution. To require a fractional dimension for the multiplier is the sort of thing that fractal geometry might handle but not the Bridgman physics that I prefer. The approach reported by West and colleagues (1997) may be relevant.

Although it is incomplete, my statement supports theorizing about brain size with the idea that the brain works as a mapping machine. For the theory, the map is two-dimensional. However, the empirical map to which the theory refers is a sheet of cells (neurons) with some thickness. When the extent of the mapping is determined from a measure of body size, as it is in allometric analysis, one of the issues is to understand departures from theoretical expectations about a mapping system. From this cursory review it seems to me that the appearance of a 3/4 exponent in empirical regression studies is pretty much what one would anticipate if the fundamental activity is a mapping but that the physical map that is generated by the brain, though thin, does have a thickness, and that thickness is related to brain size. The thickness relationship must be determined empirically, as in the analysis I offer in Figure 2. It is this that affects the dimensional relationships that can be inferred from regression equations and allometric exponents.

Uniformities and diversity

In recent years, my favorite graph has been Figure 3, which is based on data from Brodmann (1913), Elias & Schwartz (1971), Ridgway (1981) and Ridgway & Brownson (1984). I use it to argue that brain size is a statistic that estimates the total neural information processing capacity in a mammalian species. The argument can be developed in several ways, but the simplest is based on the Rockel, Hiorns & Powell (1980) report that excepting the visual cortex of anthropoid primates, the number of neurons under a measured area of cortical surface is constant among species. The report was based on only 5 species. A more relevant datum is from Schüz & Demnianenko (1995) who counted the number of synapses in neocortex of hedgehog and squirrel monkey. Consistent with an old speculation of mine (Jerison, 1973, p. 70), they found that the number of synapses per unit neocortical volume was constant in the two brains. As a first approximation, cortical volume is estimated from brain size independent of species (Jerison, 1991b), from which one can infer that the number of neocortical synapses in a mammalian brain is estimated by brain size. All of these measurements are worth reexamination and refinement, and given my enjoyment of Figure 3, I especially appreciated the critical review of the anatomical issues in Preuss's chapter, which can temper my enthusiasm. On the other hand I would hope that anatomists concerned with these issues show more concern with the uniformities in their data when they compare species. One expects them to emphasize the diversities.

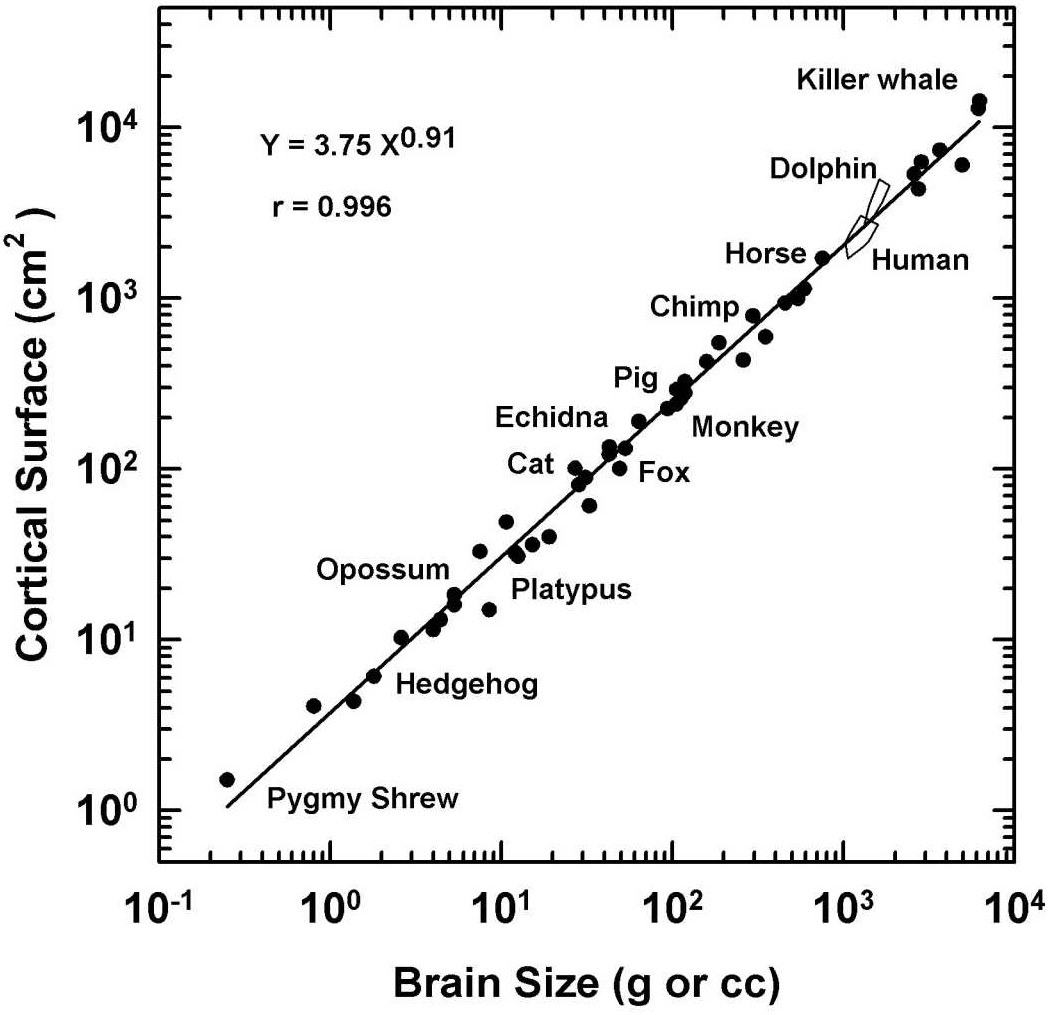

Figure 3. Cortical surface area as a function of brain size in fifty species of mammals, including orders Monotremata, Marsupialia, Artiodactyla, Carnivora (including pinnipeds), Cetacea, Perissodactyla, Primates, and Xenarthra. Minimum convex polygons enclose individual human (N=20) and dolphin (*Tursiops truncatus*, N=13) data and indicate within-species variability. (From Jerison, 1991b, by permission.)

We are unlikely to find a more diverse sample of species than in Figure 3, but the measurement of cortical surface area has been chancy in the past. With the advent of computer graphics applied to imaging the brain, the measurements can be redone, and the data for these are presently available in computerized databases (e.g., at http://www.neurophys.wisc.edu/brain/, on the internet as this volume goes to press). The uncertainty about Figure 3 is the apparent irrelevance of gyrencephaly. Smooth and convoluted brains are included, and a single equation fits all of the species.

It is helpful to debate problems of uniformity versus diversity as Preuss raised them in his chapter, but I think that it is really a matter of style and emphasis. There is no real conflict. There are uniform features in neural organization and important differences as well. The danger in overemphasizing one or the other is that we can miss important issues. My impression has been that anatomists tend to emphasize diversity whereas evolutionists look for uniformities. The uniformities serve as benchmarks of a sort, to which diversity is referred.

As a historical aside, I think that Karl Lashley's reputation as a neurobiologist suffered from his report with George Clark (Lashley & Clark, 1946) in which he challenged the ability of anatomists to use cytoarchitectonic data as available then for the parcellization of cortical functional areas. It challenged the

validity of classical cytoarchitectonic studies. I think that there was almost universal disapproval of the conclusion of Lashley and Clark among anatomists and fairly general approval among physiologists and psychologists working with the same material. But I also think that some of the rejection of Lashley's concept of mass action was related to the sense that he and Clark had gone too far in their criticisms, and that, in fact, cytoarchitectonics provide valid criteria.

On dolphin cytoarchitectonics, it is hard to imagine a mammal operating without a Layer 4 in its neocortex, but to my knowledge there is no debate that this layer is effectively absent in the cetacean brain, as Preuss reports. But there must be thalamic relays in the dolphin neocortex that are involved with neurons in layer 4 in land mammals, so the question may simply be to discover where the neurons are hiding in the dolphin's brain.

To complete this aside, I would add that Lashley's mass action, which was thought of as opposed to a strict localization-of-function view of the brain, may be more correct than the views of localizationists, at least as the problem is presently understood. It is very likely a question of which functions are being looked at. More than a half century ago Lashley himself provided some of the foundation for our understanding of localized visual function, although we now understand the issues much more adequately (Zeki, 1993). But broad cognitive functions may indeed be controlled by so broadly distributed a system that a kind of mass action would be the best description, and the functions would be difficult to localize. This may have been true for Lashley's rats running in their mazes, in which the performance deficit following brain lesions was correlated with the size of the lesion rather than its locus in the brain. One thinks of the brain's cognitive control systems as working as distributed systems in which the activity may be spread through broad regions (Goldman-Rakic, 1988). There is, nevertheless, a continuing search for foci of activity, which is a localization of a sort.

The issue is not dead. It arose in a paper by Duncan and his associates (Duncan et al., 2000), which I saw as I began work on this essay. They reported the localization of intelligence (at least the *g* factor) in the human brain as focal frontal lobe activation in human subjects when performing high-*g* tasks. Controversy is not dead either as one can read in the critique in an unusual review of the paper by Sternberg (2000), one of the leading students of studies of human intelligence.

I should present an additional caveat. The work by Duncan and his colleagues involved the measurements of PET (Positron Emission Tomography) scans in people during mental work and looking at the pattern of activation. They found "localization" in the frontal lobes. The issue can be, what does one mean by localization? The size of the activated areas was of the order of several square centimeters, which would include perhaps 100 million neurons in the activated region of each frontal lobe. That is hardly a precisely localized control. Their point was that the control was not scattered throughout the brain. But who would expect scattered activation in this kind of study? It is quite comparable to recognizing visual system activation focused in visual cortex, or activity in motor cortex associated with voluntary movement. We should not think it necessary to contrast a localization view with a distributed-system view. Both are probably correct, depending on what one is looking for.

Perhaps even more important for the analysis of the evolution of the brain, in particular for an understanding of unique features in human brain evolution, is that one can make PET scans and fMRI (functional magnetic resonance imagery) scans in animals as well as humans. Such research is new and not easy to do. Animals have to be well trained to sit through the restraints required for scanning while performing appropriate mental work. The University of Georgia Language Research Center (represented here by Professors Gibson and Rumbaugh), famous for their work on language-like behavior in bonobos (*Pan satyrus*), has reported preliminary results of such work (Rilling et al., 1999) in which they mapped PET (positron emission tomography) scan data onto pictured brains of chimpanzees and humans working on experimental language-related problems. Although the areas lit up in the two species were somewhat different, the total amount of activity appeared to be similar in the two species and it clearly reflected the brain's role in conscious experience in the subjects of the study. The tentative conclusions reported thus far suggests that the language of the chimpanzee is organized neurally in different ways from human language.

To return to the manifest diversity of neural organization and the anomalous histology of the

cetacean brain, I recognize that this remains an unresolved puzzle. There was no dolphin brain in the Rockel et al. report on which Figure 2 is based, and there is no question that had a datum been available it would have been an unusual outlier. But in a large enough sample of species it would have had little effect on the overall analysis of the utility of brain size as a statistic that estimated mammalian neural information processing capacity. When appropriate, I have cited Garey & Leuba (1986) on dolphins, since they reported that dolphins had about 60 percent as many neurons per unit cortical surface area compared to the land mammal species in Rockel et al.

Just as we can be surprised but not overwhelmed by how much more extensive the surface area of the dolphin brain is than that of the human brain, we are equally surprised by its thin population of neurons. One can note from Figure 3 that although dolphins have much thinner cortices, their cortex is half again as extensive as the human cerebral cortex. (We can also learn how to think about log-units from the graph, since the dolphin polygon is only slightly displaced from the regression line.) These opposite trends, which are examples of the diversity in quantitative measures of mammalian brains, pretty much balance one another. When these are combined they support the simple measure of brain size to characterize the overall information-processing capacity of both the human and the dolphin brain as being about the same.

Does this mean that dolphins are as smart as we are? I suppose that depends on what one means by smart. But it is a nonsense question. It should be obvious that all species use their processing capacity in species-typical ways. The analytic problem is to determine what it is that dolphins do that encumbers so much processing capacity. The approach points one to selecting species for behavioral studies, and for seeking examples of behavior that are likely to require a lot of neural information-processing capacity. It was the unusual encephalization of dolphins that led me to speculations about the ways the very large amounts of processing capacity might be used to support unusual cognitive processes (Jerison, 1986). We continue to receive reports about the unusual capacities of cetaceans,and their use of auditory information, sometimes in more complex ways than we humans can (Janik, 2000; Tyack, 2000).

The uniformities that we find, such as that represented by Figure 3, tell us what we can expect, but the diversities point us to exceptions. A major diversity within the mammals, for example, is with respect to encephalization. Anthropoid primates as a group are about twice as encephalized as other mammals, that is, they have about two or three times as much brain for a given body size. A 50 kg wolf (*Canis lupus*) has about a 150 g brain; a chimpanzee weighing about the same may have a 400 g brain. A kangaroo with the same body weight may have a 60 g brain.

Fossil Brains

Having taken so much space to discuss dolphin brains, it is time to introduce the fossil record of the brain for an unusual speculation that I would like to offer. We know that dolphins have big brains, and in my big book I was able to report that the cetacean brain has always been big as mammal brains go (Jerison, 1973, Ch. 15). There is a problem with their watery environment and the lack of selection pressures to keep their bodies small, hence we are not surprised by the body size of very large whales. That was my original reason for excluding them from my first search for a "true" allometric equation. There is a singular fact about the evolutionary history of cetaceans that may be related to their having evolved very large brains. I want to present that, as a teaser about how clues may appear in the fossil record. It is not convincing, just suggestive. There is a lot more from the record of fossil brains, which I will not trouble you with here.

The present consensus is that cetaceans are most closely related to living artiodactyls, and that their ancestors were early Eocene archaic ungulates. We have data on a member of the ancestral group, the middle Eocene *Mesonyx obtucidens*, which lived about 50 million years ago and was a contemporary and close relative of the earliest whales. We have illustrations of its brain (Radinsky, 1976), which was surprisingly modern in appearance. In body configuration it was not at all like any living ungulate or any marine mammals for that matter; it might have passed for a small bear or wolf (see Savage & Long, 1986). Most unusual was the extent to which it was neocorticalized, more than any of its contemporaries except, perhaps, the early primates.

Figure 4 is one of the graphs that I have published before on the fossil evidence of the evolution of the neocortex (Jerison, 1991a), modified for this chapter by identifying data contributed by *Mesonyx* and by a creodont *Pterodon dasyuroides*, a late Eocene species of about 40 million years ago. The mesonychids, though technically ungulates, may have filled a niche for carnivorous mammals, prior to the appearance of large carnivores (Carroll, 1987), and the first carnivores in that niche were the creodonts, such as *Pterodon*. Neither was a "true" carnivore of the mammalian order Carnivora. Radinsky (1978) considered the *Mesonyx* and *Pterodon* as approximately equally encephalized (EQ = 0.5, approximately), which is about half as much as living true carnivores of the order Carnivora. With the exception of the primates, middle Eocene mammals were less encephalized than *Mesonyx*; typical values of EQ were about 0.3.

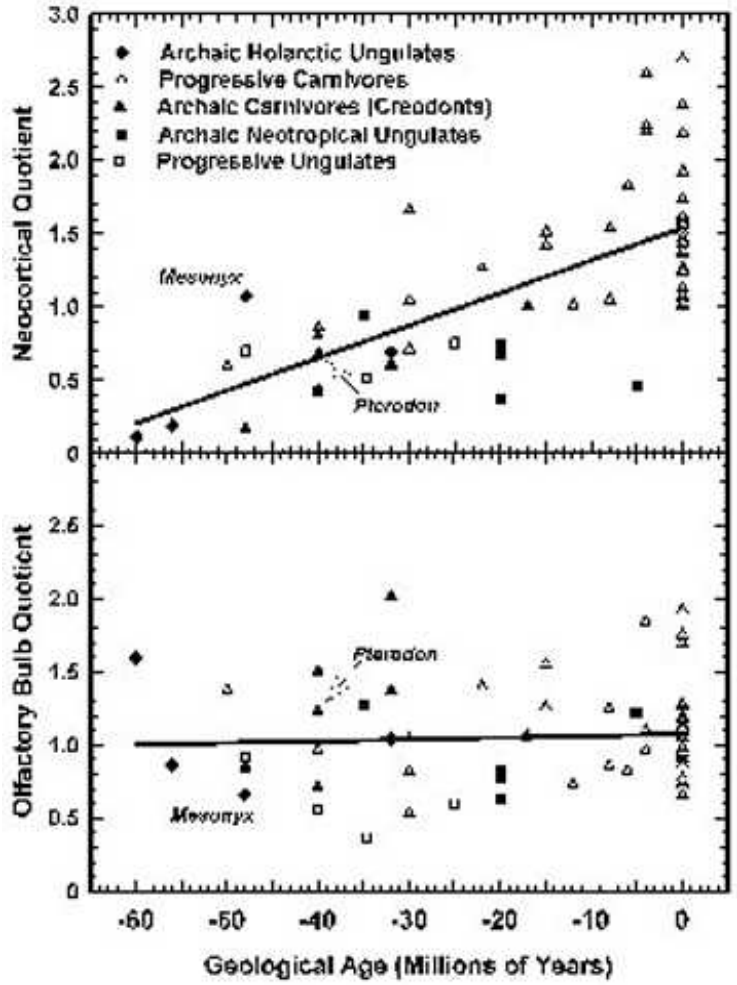

Figure 4. Top: Change in relative neocortical surface area (neocortical quotient) as a function of geological age. "Progressive" change noted here (positive slope of regression line) indicates increased neocorticalization over time. Each point is a species. Bottom: Absence of change in relative surface area of the olfactory bulbs as a function of geological age. (From Jerison, 1991b, by permission.)

Figure 4 graphs data derived from two-dimensional lateral projections of the brains of 35 fossil and 24 living species of carnivores and ungulates. The sample covers the last 60 million years of mammalian history. A lateral projection of the brain of a species in this sample shows a clear rhinal fissure, and neocortex is forebrain dorsal to that fissure. In the same projection one has a view of the olfactory bulbs, and I could analyze the evolution of the peripheral olfactory apparatus in the same way as that of neocortex.

The analysis was comparable to that of encephalization, determining an expected size of either the

neocortex or the olfactory bulbs from the regression of these measures against body size, estimated from the height of the foramen magnum. These enabled me to calculate the neocortical and olfactory bulb quotients graphed in Figure 4. Additional details on the procedure are in Jerison (1990).

The main inferences from Figure 4 are about neocorticalization. Secondary inferences are methodological, that the method was good enough to distinguish between the neocortical system, which was evolving progressively during the Cenozoic era, and the peripheral olfactory system, which was at a steady state during those 60 million years. Presenting data on the evolution of the olfactory bulbs, based on the same data set, is essentially evidence on the adequacy of the method, namely that it could distinguish between evolutionary progress and evolutionary stasis. This graph is presently the only quantitative evidence from the fossil record that neocortex increased in relative size when the mammals evolved, i.e., that neocorticalization was a fact of mammalian evolution.

A less certain, though statistically significant, conclusion from the graph is that progressive species as defined by extinction data may have enjoyed their selective advantage because of the enlarged neocortex. The regression line has more progressive species above the regression line and fewer archaic species above the line than would be expected by chance.

I am accustomed to data on brain morphometrics that are as orderly as the surface-volume relationship shown in Figure 3. Typical correlations are greater than 0.98. The product-moment correlation coefficient for the neocortex vs. age relationship in Figure 4 is 0.69, significantly different from 0 (N = 59), but there seemed to me to be quite a bit of scatter about the regression line. This may reflect a true diversity within this sample, but I suspect that some of the scatter is simply a failure of the two-dimensional projection to assess an effect that is, in fact, three-dimensional. In the next section I describe my current work on 3-D imagery, which includes the reanalysis of the same endocasts, the same fossil brains. It should be possible then to measure the actual exposed surface area of the neocortex.

There is more to be inferred from Figure 4. As an early Eocene mammal, *Mesonyx* was obviously unusual in brain development. This is evident in the appearance of the brain (see Radinsky, 1976). A measurable criterion is its size, and this fossil brain was significantly larger than that of its contemporaries, with significantly more neocortex.

As major groups of animals competing for the available niches of their time, the mesonychids (*Mesonyx* and its relatives) were ungulates within a carnivore's niche. As a group they were probably replaced by a carnivorous order, the Creodonta, and the earliest true carnivores (order Carnivora) which were smaller in body size at that time. Did the brain have a role in the replacement? Figure 4 says no, at least for the mesonychid-to-creodont transition. The representatives of the two orders in Figure 4 were similar both in brain size and body size. The *Mesonyx* brain was about 80 ml and that of Pterodon about 60 ml. They weighed about 38 and 27 kg, respectively (Radinsky, 1978).

Interestingly, Figure 4 is affirmative on the transition that eventually occurred between the creodonts and true carnivores, the transition indicated as from archaic to progressive carnivores. The second transition is difficult to ascertain from inspection of the endocast, and as experienced a student as Len Radinsky argued against the suggestion that brain size could have been an element in the success of the true carnivores. The quantitative data of Figure 4, however, favor a role for encephalization. In the graph the progressive species are distinguished from the archaic species. Although the numbers are low, by conventional statistical criteria the probability that it was a random thing for the archaic species to fall below the regression line while the progressive carnivores were above it, is less than 5 per cent. In short, statisticians might say that the difference was significant beyond the 0.05 level. (If a species is a member of an order that is entirely extinct it is defined as archaic, whereas members of surviving orders are progressive. It is a matter of survival not modernity.)

Now for the conjecture. It is a bit of a stretch, but if the determinants of brain size in the mesonychids were similar to those of the earliest whales, then they may have been operative in both groups. Cetacean encephalization may have a history as ancient as that of the primates. The earliest true primates, relatives of living tarsiers, were the most encephalized mammals of their time (Jerison, 1979), and there may be some genetic features that evolved in the earliest anthropoids, retained through the rest of anthropoid evolution, that support instructions for relative brain enlargement. The Eocene primates, the

Eocene mesonychids and the earliest whales, were contemporaries. Although it is not presently possible to generalize in the same way about cetaceans, or about the mesonychids, the extent of their encephalization relative to other mammals of their time is relatively easy to establish. and it would provide an additional element for our knowledge of the history of encephalization.
[*Note added in 2007. This speculation about a mesonychid connection was completely wrong. The present consensus is that cetaceans were connected to artiodactyls and mesonychids were not in the picture. The unique brain enlargement in cetaceans remains unexplained.*]

Measurement and High and Low Technology

I don't want to outstay my welcome, but I have two more items to present about where we go from here. Some are based on my own research and others on my ability to speculate. You can appreciate the first, my plans for 3-D imaging, by inspecting Figure 4. I was surprised when I made the measurements that two-dimensional projections of the extent of neocortex compared to other parts of the brain would yield as clear a picture as they do. The projection, after all, is a profile of the brain. It cannot show curvature. The analysis worked adequately for neocortex, because in the species in which I made the measurements none of the neocortex was hidden except that buried in the folds of the convolutions. And those hidden ones will never be seen in fossils, because we are dealing with rocks not with brains. Fossil brains are endocasts, not brains, and they merely mirror what is molded by the cranial cavity.

If we can make 3-D images, however, the data would not be distorted by the fact that brains that differ in overall size may also differ in the extent to which the external surface is visible in a lateral view. When I first analyzed the data I tried to include measurements on "paleocortex" or "old brain," that is, cortex below the rhinal fissure. It was immediately evident that much of this part of the brain is not visible in a 2-D projection; it is on the ventral surface of the endocast, and it curves around differently in different brains. From the time that I recognized that data on surface area measures would be useful I sought a way to make the measurements. With the advent of computer imaging methodology the problem has been solved and has become simple if one can scan the endocast.

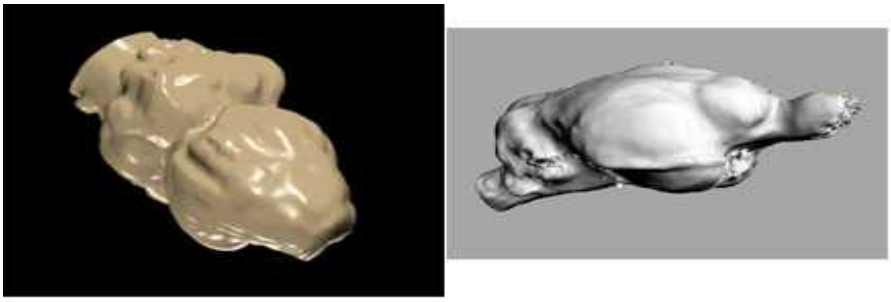

Figure 5. 3-D scan of the fossil "brain" (endocranial cast) of *Pterodon dasyuroides*. [*2007 change: virtual endocast of Adapis parisiensis (Eocene prosimian) at the right was made with my current apparatus, Model 15 from Cyberware: http://cyberware.com. Pterodon* about 60ml, *Adapis* about 10 ml, 4.5 cm long.]

Figure 5 is one of the first scans that I made, of *Pterodon*, the creodont mentioned earlier. The particular endocast with which I worked had olfactory bulbs missing, but you will see the information that is available from one of these "virtual" fossil brains. I leave it to you to identify significant fissures, and I have resisted the temptation to point to the rhinal fissure . . . My present plan is to generate a graph like Figure 4 but with data based on virtual endocasts. The procedure could also eliminate much of the uncertainty with respect to body size.

A major benefit of the computerized procedure is that one will be able to make the measurements on more species, in particular on primate brains. [*see Jerison (2006, 2007) in the online CV.*] We have excellent endocasts for the earliest of these, the lower Eocene *Tetonius*. The fossil brain was relatively

large, almost as encephalized as average living mammals and about half as encephalized as its living tarsier-like prosimians. Until the advent of computer imaging, it has been impossible to include it or any other primate in the analysis presented in Figure 4, because the rhinal fissure is obscured by the curvature of the temporal lobe. With a virtual endocast one can "paint" the entire neocortical surface that can be read from the endocast in three dimensions, and in that way perform the analysis in a wider range of species. Carnivores and ungulates were selected for the sample, because only in these species could I gather enough data to answer the questions about neocortical evolution.

If there is enough information to reconstruct a "virtual" body, then its volume is equally easy to measure. This would be an improvement over the procedure based on the size of the foramen magnum as a surrogate for body size. (I should add that the size of the medulla is an excellent surrogate; the difficulty with the foramen magnum is that it includes the great cistern, the size of which is proportional to brain size and is correlated with encephalization. I have guessed that this enlargement of the foramen magnum reflects the utility of providing sacks of blood that can cushion the medulla from shocks incurred by the movement of larger brains within the cranial cavity as an animal runs or leaps.) The procedure of creating virtual equivalents of the body and its parts using 3-D imagery and computer graphics is an enormous contribution to the study of vertebrate morphology and biomechanics. Within a few years procedures for working in this way should be routine.

The low technology is the familiar technology: weighing whole brains, measuring the area of sections through the brain and so forth. It continues to be the way much of our gross data has been generated. For comparative studies of brain size that included the analysis of the parts of the brain, we have all been indebted to Heinz Stephan and his research group at the Max Planck Institute for Brain Research. These laborious methods can be replaced or supplemented by computerized approaches to measuring area and volume, including the measures taken from histological sections of brains from living species. For many of these it will be sufficient to use digitized images of histological slides prepared classically. The main outstanding problem with these is uncertainty about shrinkage and distortion introduced by the histological procedures.

The great contributions of analyses of brain-body relations may be in the way outliers in the analysis can be identified. I have recently reviewed my data on these, updating old graphs and adding data and correcting errors. The graph of the present situation in living vertebrates in Figure 6 includes all presently available data (Jerison, 2001). I don't think a contribution from me would be complete without such a summary. It is less neat than some I have published before, mainly because I have added more groups than I usually show: electric fish, cartilaginous fish, and jawless fish. Usually one summarizes such data with regression lines, but in my view the polygons are more valid devices. The method is to draw convex polygons about the points belonging to a group of interest. To the extent that the polygons are distinct one distinguishes the groups from one another, and from Figure 6 we can see the extent to which one is justified in discussing "lower" versus "higher" vertebrates. The sharks and electric fish confound the picture, but the distinction is generally easy to maintain.

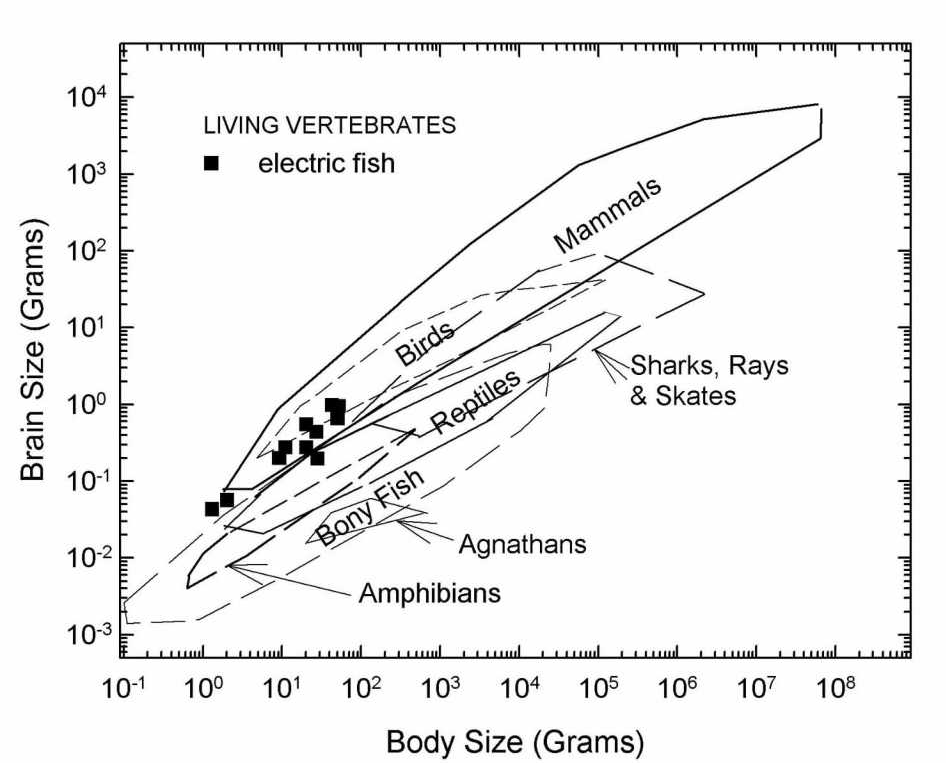

Figure 6. Brain-body relations in 2,018 living vertebrate species enclosed in minimum convex polygons. The samples are 647 mammals, 180 birds, 1,027 bony fish, 41 amphibians, 59 reptiles, 59 cartilaginous fish (sharks, rays, and skates), and 5 agnathans, or jawless fish. Electric fish are Mormyriformes, unpublished data, courtesy of Professor Andy Bass of Cornell University. Most of the other bony fish data are unpublished except as in this graph, data courtesy of Professor Roland Bauchot of the University of Paris VII. Note that birds and mammals overlap one another as "higher vertebrates," and reptiles amphibians and fish overlap one another as "lower vertebrates." Electric fish, however, are in the "higher vertebrate" range of encephalization, and chondrichthyans (sharks, rays and skates) overlap the lower and higher vertebrate ranges.

The role of graphs like Figure 6 is to provide a map of brain-body space, of brain-size opportunities that are presently realized by vertebrates. One can add fossils to the graph, and doing that indicates that the present situation remains representative of the diversity of brain size within the vertebrates. A graph made before the Mesozoic era would have shown no birds or mammals and the range of body sizes would have been smaller, but all species would have fallen within appropriate polygons. There would have been no outliers. The most unusual specimen may have been a Carboniferous era shark, about 300 million years old, which would have been graphed in the chondrichthyan polygon, in the mammalian region. It was the first "experiment" with encephalization in the vertebrates.

Graphs made during the Mesozoic, after the appearance of birds and mammals would have contributed points to the avian and mammalian polygons, although all would have been near the lower borders but above the other polygons. There is an exception. Some of the late Mesozoic dinosaurs, in particular the ostrich-dinosaurs (struthiomimids) were more encephalized than any living reptiles and fell in the lower part of the avian polygon. The main effect of adding dinosaurs to the data set is to expand the reptilian polygon to be more similar in body-size range to that of the living mammals. The "mammal-like reptiles" (amniotes ancestral to the mammals, including synapsids and therapsids) were reptilian in encephalization. Their data fall within the reptilian polygon.

Finally most living electric fish (Mormyriformes) are large brained, falling within the living mammal polygon. Their brains are enlarged because of an expanded cerebellum rather than forebrain. Cenozoic graphs would show the mammals gradually filling the polygons by expanding upward with more encephalized species appearing. By about 20 million years ago it probably would look much as it does

today, because the cetaceans would have been diverse enough, and encephalized enough to provide species for the upper border of the mammalian polygon. Early hominids would be with living pongids, upper class, as it were, but not the largest brained animals of their time. Only within the last million years did hominids expand to approximately their present grade of encephalization and they definitely achieved it only with the advent of *Homo sapiens* and the neandertals, less than a half-million years ago.

Figure 6 is a chart for future research. It points to species about which we need to know more, in particular about their activities in which there could have been selection for increased information-processing capacity. We can guess that this might explain the expanded brain in electric fish, though we might be hard put to explain why handling information from electric organs should be more greedy a task relative to brain control than, say, the handling of visual information by frogs or any of the many unusual adaptations in fish revealed by ethological research.

We should be impressed by the data on cartilaginous fish. It is one of the benefits of the analysis that it points one to comparisons that might not otherwise be considered. One does not know how to measure or define animal intelligence behaviorally, but from their encephalization, it is clear that sharks and their relatives deserve much closer scrutiny by ethologists and comparative psychologists than they have received. There are additional comparisons that should be made. The approach would single out parrots as birds to study, because they are among the most encephalized of living birds, justifying Pepperberg's (1994) efforts. The only other living avian group that is in their range are the corvids, and the common crow is surely worth a close look. Among the cartilaginous fish, the most encephalized appears to be the manta ray (*Manta birostris*), and we know almost nothing about the normal behavior of this gentle giant, but other shark species are also unusually encephalized (Northcutt, 1989). My approach does not, and, as I indicate later, cannot in principle, explain the details of the behavior of a species, but it is clearly useful in helping us choose the species to study.

It is a challenge to ethologists and comparative psychologists to analyze the utility of the neural extra processing performed by that system. The analogy might be to the enlarged inferior colliculi in bats specialized for echolocation, since these structures are especially implicated in the analysis. Of course, the forebrain in these bats is not unusually enlarged, but it is specialized for auditory analysis (Grinnell (1995).

Neurogenetics?

The ignorance that I can bring to molecular biology and neurogenetics is great enough that I can speculate with ease. A major issue, which my laboratory work has never addressed though my speculations have, is what kind of genetic programs will effect the kinds of brain evolution that is evident from the fossil record. I have, of course, been impressed as we all must be by the discovery of common genetic systems in humans and fruitflies for differentiating the head region of an embryo (see Deacon, 1997, for a review). It is one of the finest biological uniformities that one can cite. An equally difficult problem that I can only state but to the solution of which I have nothing to suggest is the translation of genetic programs into phenotypic structures and functions. I can imagine part of a neural network to be prescribed in the genetic code, but I cannot imagine that enough code can be squeezed on to the chromosomes to prescribe a full network. Here is one example that I gave, to show how to convert a chimpanzee into a person.

> It may be helpful to consider the way the genetic information might be encoded. A possible genetic blueprint of a species might include code for the following instruction to regulate growth in a primordial nerve cell: "perform 32 cell divisions and then stop." If that instruction were followed and no cells died, 4,294,967,296 nerve cells would be produced. Imagine now a major (but small) mutation, which changed "32" to "34." This small change would yield 17,179,869,184 nerve cells. Were these fated to be neocortical neurons the mutation would be about right to distinguish the number of neurons in the brain of a chimpanzee from that in a human (Pakkenberg & Gundersen, 1997). In this example, the code may seem overly simple, but it is that kind of code that can be written, and it is a code that would have a very great morphometric effect. Instructions that are

> significantly more complex may be beyond the capacity of genes to encode information. (Jerison, 2000, p. 218)

In this example there is nothing about localized functions, or the creation of specialized systems such as the language system of the brain. I have shared the example with a few geneticists, and I have one testimonial that it is not a crazy way to ask the questions. I sent the paragraph as an e-mail to M. V. Olson (cf. Olson, 1999) who replied that he had not published a complete statement of his analysis to describe how the necessary counting of the sort that I asked about could be done. He added the following: "I agree entirely that it is likely that "simple" genetic changes of the type hypothesized will account for the really major differences between chimps and humans. My molecular point has been that such changes are likely to involve loss of regulation rather more subtle genetic innovations. We know that the regulatory systems that govern development are full of nearly redundant and nearly dispensable features. Hence, one could get the effect envisioned just by dropping one of the regulatory subsystems that limits the number of cell divisions in a particular chimp cell lineage" (Olson, personal communication).

Conclusions

Scattered through this essay I have made a number of suggestions about ways for the future. One obvious requirement is for more and better data, suitably prepared for analysis. We need data on species currently under-represented in our broad analysis of vertebrate brain evolution. We are too reliant on Stephan's work and those of his colleagues for background on the diversity of mammalian brains, and the new data are insufficiently quantifies to be added to his set. One of the delightful features of Barbara Finlay's contributions has been the way the set has been expanded.

It is a fairly obvious prescription to announce that "more research is needed" even if we slip into the passive voice to make this banal statement seem more profound. Yet that is clearly what we need. The substantive chapters in this book have pointed the way, and we need only follow.

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Appendix

Tilly Edinger (1897-1967) was affiliated with the Senckenberg Museum of Natural History in Frankfurt, Germany, until 1938. She had published her PhD thesis, in which she named endocranial casts of fossils as "fossil brains" (Edinger, 1929) during her tenure at the Senckenberg. Her father, Ludwig Edinger (1855-1918) founded what is now the Max Planck Institute for Brain Research in Frankfurt. Tilly fled to the United States at about the time of Kristalnacht when Nazi hoodlums smashed windows of Jewish shops and vandalized Jewish property as part of an organized anti-Semitic campaign by Hitler's Germany. Through the efforts of leading American paleontologists, Alfred Romer and George Gaylord Simpson, she was appointed a research associate at Harvard's Museum of Comparative Zoology. I was asked to prepare this preface, which is on pp. 5-6 of her biography: Kohring,R. & Kreft, G. (Eds.). [(*2003)*. *Tilly Edinger - Leben und Werke einer juedischen Wissenschaftlerin*.- Senckenberg-Buch Nr. 76. Senckenberganlage 25, Frankfurt/Main

"PREFACE

When I dedicated my book on brain evolution (Jerison, 1973) to Tilly Edinger, I tried to convey my special intellectual debt to her in the following words:

> "Among the individuals whose help and support I would like to acknowledge, I must name, first, Tilly Edinger, to whom this book is dedicated. Her frequent letters, sharing with me, an experimental psychologist, the advances and retreats of vertebrate paleontology as it was concerned with the evolution of the brain, were major contributions to my education and important introductions to the data of this book. When she died shortly before I began writing, my anticipated pleasure in the work diminished because I could no longer look forward to her reactions. These, I am sure, would have combined pleasure in having data about endocasts used in unusual ways with bewilderment at some of the details of that use - as she put it to me, she never could understand logarithms and other magic." (Jerison, 1973, p. xiii)

It is a great pleasure to be able to discuss our friendship in a more personal way in this introduction to her biography.

I first met Tilly in the red-bound Memoir 25 of the *Publications of the Geological Society of America*, her first major English publication, which has the unusual title, *Evolution of the Horse Brain*. That was in 1953 when I found the book on the shelves of the library of Antioch College, in Yellow Springs, Ohio, in the USA. The book was a revelation. I was amazed to learn that the evolutionary evidence that she presented could be read directly from the fossil record. Can I be blamed for seeking to learn more and to get to know her? I wrote her, and a few years later we met in person at the Museum of Comparative Zoology at Harvard.

Although she has been described as the daughter of a rich German Jewish family, there was no evidence of that background in the small flat In Cambridge, Massachusetts where I brought a bottle of inexpensive white wine for the light dinner that we shared at our first meeting. She often remarked on that gift later, a successful beginning for our friendship. Tilly was a gentle and kind friend, who tried very hard to appreciate the quantitative arguments that I developed to analyze the fossil brains.

To appreciate her kindness to me, one should keep in mind her deep hatred for Othniel Marsh, which I never fully understood. In many publications (e.g., Edinger, 1961) Tilly took great pains to expose what she considered the fraudulence of Marsh's claims. She was convinced that he invented the images of bird brains (*Hesperornis* and *Ichthyornis*) that he published, and that he had never prepared the specimens. I could vouch for two criticisms of Marsh, which Tilly enjoyed. First was his fantastic picture

of the cerebellum of *Coryphodon* and second, his enlarged olfactory bulbs in one uintathere endocast that made the cast look like an enlarged rodent brain. Both of these were preparation errors. Whoever made the preparations had removed "matrix" from the cranial cavity that was, in fact, fossilized bone. Another of Marsh's "errors," as Tilly saw it, was his advocacy for an evolutionary teleology that saw brain-enlargement as one of the imperatives of vertebrate evolution. It was, therefore, certainly wrenching and difficult for her to accept my own demonstrations of something close to substantiation for some of those views in my quantitative analyses, in particular of mammalian and avian brain evolution.

What I showed was that there were many instances of measurable encephalization within the lineages of birds and mammals, although I hope I successfully avoided the teleology and aristogenesis often offered then as explanations. My explanations, which Tilly could accept, was that there was some selective benefit for encephalization in some environmental niches, and that species evolving in such niches would have responded by selection for encephalization. She could appreciate this qualitative statement, though its quantitative justification puzzled her. On one occasion I remember looking at data on rodent evolution with her, in which she questioned my statements, showing me measurements of squirrel brains and bodies that seemed to be outlandish outliers compared to brain/body data in rodents and other mammals. I "taught" her by taking out a piece of log-log graph paper on which I plotted the points. These fell very close to a general mammalian regression line. It was then that she commented to me on logarithms and other magic.

Although like Tilly I am Jewish, and my wife, Irene, is a survivor of the Nazi holocaust, I remember no reference to Judaism in conversations with Tilly. It would hardly have been appropriate. Our relationship was entirely as scientists, and mine was as an admirer of her dedicated work on the fossil evidence for the evolution of the brain. When I learned more of her personal history, her major scientific and economic losses upon her exile to the United States, and when I realized that she was the daughter of the great neurologist, Ludwig Edinger, it only added to the deep respect and love that I felt for her. Her tragic death was evidently directly related to her deafness. I was told that because she could not hear a truck's approach, she had walked into its path near the steps of the Museum of Comparative Zoology."