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JAMES ARTHUR LECTURE ON  
THE EVOLUTION OF THE HUMAN BRAIN  
1989

# BRAIN SIZE AND THE EVOLUTION OF MIND

HARRY J. JERISON

AMERICAN MUSEUM OF NATURAL HISTORY  
NEW YORK : 1991



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JAMES ARTHUR LECTURES ON  
THE EVOLUTION OF THE HUMAN BRAIN

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- Stephen J. Gould, *Chomsky Under the Spandrels of San Marco*; April 5, 1988
- \*Harry J. Jerison, *Brain Size and the Evolution of Mind*; October 10, 1989
- Paul H. Harvey, *Comparing Brains*; March 20, 1990

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\*Published versions of these lectures can be obtained from Publications, Dept. of Anthropology, The American Museum of Natural History, Central Park West at 79th St., New York, N.Y. 10024.

\*\*Out of print.

†Published version: *The Brain in Hominid Evolution*, New York: Columbia University Press, 1971.

JAMES ARTHUR  
1842-1930

Born in Ireland and brought up in Glasgow, Scotland, James Arthur came to New York in 1871. Trained in mechanics and gear-cutting, he pursued a career in the manufacture and repair of machinery, during the course of which he founded a number of successful businesses and received patents on a variety of mechanical devices. His mechanical interests evolved early into a lifelong passion for horology, the science of measuring time, and he both made some remarkable clocks and assembled an important collection of old and rare timepieces.

Early in this century James Arthur became associated with the American Museum of Natural History, and began to expand his interest in time to evolutionary time, and his interest in mechanisms to that most precise and delicate mechanism of them all, the human brain. The ultimate expression of his fascination with evolution and the brain was James Arthur's bequest to the American Museum permitting the establishment of the James Arthur Lectures on the Evolution of the Human Brain. The first James Arthur Lecture was delivered on March 15, 1932, two years after Mr. Arthur's death, and the series has since continued annually, without interruption.



James Anthony

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## INTRODUCTION

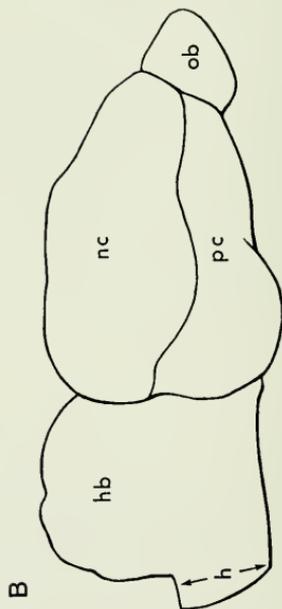
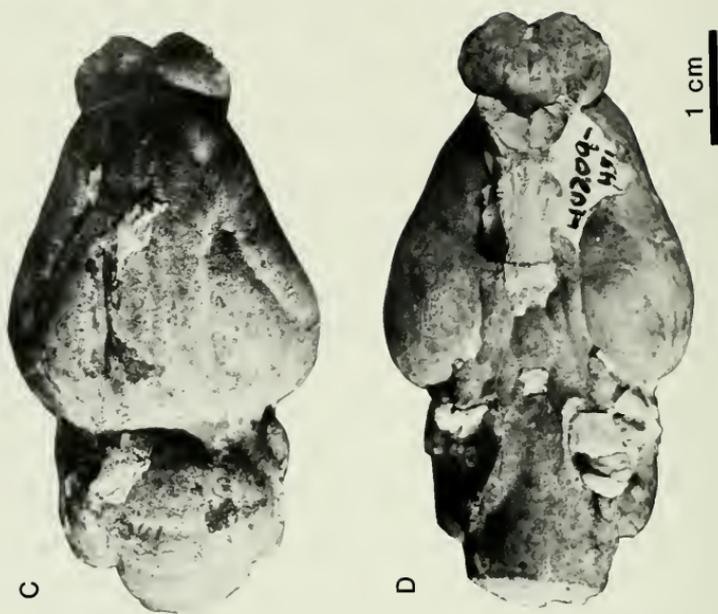
Brain size is important in biology and psychology for many reasons (Jerison, 1987). Tonight I discuss what it can tell us about the nature and evolution of mind. I introduce my analysis by showing data on fossil “brains,” and answering a few simple questions about the data. I want you to have a feel for my material, which is very solid and concrete.

We know a good deal about brain size in living and fossil animals. We also know how to analyze that information to provide a useful picture of a few features of the brain’s work. I will argue that some of the features that can be determined from brain size result in the creation of mind, and that the fossil record of the brain is, therefore, the most direct evidence on the evolution of mind. Let me show you an example of the fossil evidence and the way I use it.

The “brain” in figure 1 is from a fossil ungulate, *Bathygenys reevesi*, an even-toed hooved mammal from an extinct family of the order Artiodactyla. *Bathygenys* lived about 35 million years ago (mya) in the Big Bend area of Texas (Wilson, 1971), and looked something like a miniature sheep—about the size of a domestic cat.

In its external morphology, the brain of *Bathygenys* was similar to brains of living artiodactyls. Neocortical sulci and convolutions visible in the dorsal view (fig. 1C) and structures visible in the ventral view (fig. 1D) could easily be named by using the brain of the tiny living musk-deer, *Moschus moschiferus* (Brauer and Schober, 1970), as a model. In the lateral view (figs. 1A and 1B), we see a “rhinal fissure” separating neocortex from paleocortex. Olfactory bulbs, hindbrain, and the medulla region are also unmistakably identifiable in the fossil as being comparable to those in living species.

The similarities between *Bathygenys* and living species are obviously homologies and are evidence in favor of a uniformitarian (Simpson, 1970) interpretation of the brain of this 35 million year old fossil. Accordingly, we accept the assumption that *Bathygenys*’s brain was organized functionally as well as structurally in ways com-



parable to the brains of its living relatives. We reach the same kind of conclusion from the brains of most fossil mammals when we compare these with the brains of their living relatives.

My analysis of the brain is mainly on changes in its size during the course of evolution and the significance of those changes for the evolution of mind. The analysis begins with the volume of the brain, about 10 cubic centimeters in *Bathygenys*; since the specific gravity of brains is about 1.0, the brain of *Bathygenys* must have weighed about 10 grams, or a third of an ounce. That seems awfully small, but how much should it be expected to weigh? It makes little sense to talk about big brains or small brains unless we have some scale that tells us what is big and what is small.

I mentioned that *Bathygenys* was about the size of a cat, and that is a clue for the second step, which is to establish scales of “big” and “small.” From other data (Jerison, 1973) we know that cats are average mammals in relative brain size, as are most living ungulates. We can, therefore, determine whether *Bathygenys*'s brain was larger or smaller than average (for living species) by comparing it with a cat's brain. A typical cat's brain weighs about an ounce; thus, *Bathygenys* had a brain that was about  $\frac{1}{3}$  the size of that of an average living mammal of its body size. If we could find comparable evidence in other species, we might conclude that there was an evolutionary advance from a *Bathygenys* grade of relative brain size in the Oligocene to that of average living mammals at the present time.

My raw data and preliminary analysis are as simple as that. I compare many fossils of different geological age with one another, and I anchor my analysis in the data on living species. It inevitably becomes a bit more complicated, because we must determine an “expected” brain size for any animal, regardless of its body size. In the analysis that I just presented of *Bathygenys*, the living cat served as the source of information on expected brain size when body size

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Fig. 1. Natural endocast of *Bathygenys reevesi*, a Lower Oligocene oreodon (order Artiodactyla). **A:** Lateral view. **B:** Sketch of lateral view to indicate neocortex (nc), paleocortex (pc), hindbrain (hb), olfactory bulbs (ob), and medulla (h). **C:** Dorsal view. **D:** Ventral view. (Specimen UT 40209-431; courtesy of J. A. Wilson and the Department of Paleontology, University of Texas)

was “controlled.” But how does one know that a cat is an average living mammal with respect to the relation of brain size to body size? I discuss this and related questions later, under the heading of “Allometry and Encephalization,” where I review biometric issues.

I have been talking about brains, but you must have realized that the *Bathygenys* “brains” in figure 1 are really oddly shaped rocks. They are casts, “endocasts,” of the inside of the skull. In *Bathygenys* the casting was done by natural agents when the animal died. Its skull was somehow cleaned soon after death, presumably by bugs and microbes that eat soft tissue, and the cranial cavity was then completely filled by sand and debris that fossilized. The filling was shaped like the brain that it replaced, because a mammal’s brain is packed tightly in the cranial cavity and shapes the inner walls of the cavity to mirror a brain’s external surface. The inorganic packing material in *Bathygenys* became mineralized and fossilized into the endocast in the illustration. (Small bits of fossil bone remain attached to the endocast and are most clearly visible in fig. 1D.) “Artificial” endocasts can be made by filling the cranial cavity of a clean skull with latex molding compounds. Regardless of how they are made, endocasts in mammals are usually very similar in both size and shape to the brain and can be analyzed as if they were undissected brains. Under the uniformitarian hypothesis, we assume that this is true for fossil as well as living species.

These hard data, appropriately developed and analyzed, enable us to outline the history of mind as a topic in evolutionary biology. In view of the difficulty of nailing down the concept of mind (cf. Ryle, 1949; Fodor, 1983; Griffin, 1976; Williams, 1985, and many others), however, I have to present my view of the concept in enough detail to be sure that you know what I am talking about.

## ON MIND

I identify mind with knowing reality. Bertrand Russell (1912) discussed some of the main issues, and had Immanuel Kant been less categorical, his views on space, time, and objects might also have covered the ground for us. I will not attempt to develop a theoretical picture; that has become the province of a new discipline,

known broadly as the cognitive sciences ( Craik, 1943/1967; Johnson-Laird, 1983; Minsky, 1985; Rummelhart and McClelland, 1986, etc.). Rather, for my purpose it is sufficient to take a biological view of the “function” of mind, that is, of the way “knowledge of a real world” serves as an adaptive device.

The reality that we know is most obviously the external world of immediate (conscious) experience. There is also the reality of an internal world of mental images, memories, dreams, thoughts, plans, feelings, etc. Perhaps the most real of all objects in these worlds is the self—which is an “object” on the boundary between the internal and external world and part of both. There is, finally, the issue of consciousness as a feature of mind, but it will be easier to discuss that later, after discussing the brain’s work.

As a first approximation, most of our knowledge of the real world can be understood to result from adaptations that are usually categorized as sensing and perceiving. I begin the story of mind with these categories, because sensation and perception involve important and often unsuspected cognitive dimensions (Carterette and Friedman, 1974). Let us consider as an example a “simple” sensation: the experience of sensory thresholds. How strong must a sound or light be for it to be just audible or just visible? One of the surprising discoveries of sensory psychology is that to understand these thresholds one needs more than information about the strength of the sensory stimulus. Whether you can report that you hear or see weak signals turns out to be determined not only by the strength of the signal, but also by your knowledge of the “value” of a detection, of the “cost” of a wrong report, and of the frequency with which signals are likely to appear (Swets, 1964). These kinds of knowledge are usually thought of as higher order cognitive activities compared to merely sensing a signal. It is evidently appropriate to think of a *sensory-cognitive* dimension of mind, rather than pure sensations that are to be combined by “mental chemistry” to create mind (see Boring, 1942).

There is a stability about our experience of the external world, a “constancy” (Koffka, 1935), which is a major perceptual elaboration of sensory functions. For example, a coin remains a coin in our immediate experience whether it is seen head-on and is sensed as

circular, or whether it is rotated and sensed as elliptical. Processes of this kind, when simulated on computers, are called “pattern recognition,” and the simulation requires *much* more computer power than simulating the more usual candidates for examples of human intelligence, such as proving theorems in symbolic logic. Contrary to our intuition, perception may be harder than “pure thought,” if computers are reasonable models of the mind (Minsky, 1985).

We are misled, because we believe intuitively that things that are easy to do require little processing machinery. Perception, which is immediate and instinctive according to our intuition, would seem to require less brain tissue than complex thought. A more correct view, however, is that perception seems easy only because brains are built to do it, to handle information about the external world. Complex thought is hard, because, despite its size, the mammalian brain did not evolve as a specialized thinking machine. There are unlikely to be many fundamental neurobiological adaptations that are designed specifically for thinking hard about abstractions.

The amount of tissue that is actually devoted to a process in a living brain should be determined by how much tissue is needed to do it well, and how important it is to do it well. If a process is very important but requires a lot of neural machinery, then it might be worth a heavy investment in the machinery to do the job right. That is the correct way to think of the neural control of perception and of the brain’s role in perceptual activities. The activities are so important to mammals that brains have become significantly enlarged to support them.

I trust that you realize that I have now begun to discuss mind-brain relations and the evolution of mind. I have proposed that brains are specialized to process the sensory and perceptual information that provides knowledge of the external world, and I have invoked the idea of selection pressures (“activities so important to mammals”) and affirmed that there must have been a selective advantage, in a Darwinian sense, to have such knowledge. Furthermore, I have invoked the idea of evolutionary change with the words, “have become.”

But I am getting ahead of myself. To complete this statement on mind, I will review the words I use to define its dimensions and to

serve as my vocabulary for categorizing the brain's work. Since our concern is with the knowledge of reality, the basic word in the vocabulary is cognition, which means knowledge, and the basic idea is that a large fraction of the brain's mass is involved in cognition. Perception is a subset in the cognition category and might include mental images generated by language and memories, as well as those generated by sensory data. Memories and thoughts are also subsets, and I suppose that dreams and hallucinations might be sets within the set of mental images. Although we may distinguish these sets from one another, I am unsure about the extent to which they are biologically distinct, or the extent to which they are controlled by different brain structures.

In emphasizing perception I emphasize *experience* rather than behavior. But it is also possible to describe mind with purely behavioral categories. Among the categories that have been most important in discussions of the evolution of mind, I will discuss, briefly, learning, social behavior, and communication, all of which can be defined objectively, that is, with reference only to externally observable behavior.

These behavioristic categories are not independent of perception or of one another. Learning in natural settings is frequently social learning. Social interactions usually depend on perception and communication. Perceived "objects" in the external world are often other living creatures, which may be communicating with the perceiver. And animal communication is by definition a social interaction. Finally, although early ethological studies emphasized innate aspects of behavior, it is now a commonplace of animal behavior studies that some kind of learning (at least "imprinting") is critical for establishing almost all behavior (see Eisenberg and Kleiman, 1983).

The interdependencies transcend behavior. Mature nervous systems in vertebrates are produced by epigenetic systems based on the interaction between growing neural units and the environment in which they grow. A mammal, for example, cannot have a normal brain unless it develops in its normal environment (Hubel, 1988; Rauschecker and Marler, 1987; Udin and Fawcett, 1988; Wiesel, 1982). In an analysis of mind we must deal with complex interactions between nature and nurture, and it is simply foolish to emphasize

one at the expense of the other. It is equally foolish to assume that we can establish categories of mind that function independently of one another. We nevertheless need the categories to organize our thinking about mind.

*Categories in the Analysis of Mind: Learning*

Learning is probably the most frequently considered dimension for the evolution of mind. It usually appears in the older evolutionary literature as a statement about adaptability. For example:

The criterion of mind . . . to which I shall adhere throughout the present volume is as follows:—Does the organism learn to make new adjustments, or to modify old ones, in accordance with the results of its own experience? (Romanes, 1883/1895, pp. 20–21)

Learning was defined scientifically at the turn of the century, when it was studied in the physiological and psychological laboratory (Pavlov, 1904/1928; Thorndike, 1898), but it has proved to be a disappointing category for evolutionary analysis. The failure was stated most strongly by Macphail (1982) who reviewed the literature on laboratory studies and concluded that vertebrate species are remarkably similar in learning ability. (He considered these as studies of intelligence, and therefore asserted that nonhuman animals were remarkably similar in intelligence—a misleading statement, in my view, because of his narrow definition of intelligence. See Jerison, 1984.) In a series of rigorous experiments on comparative learning ability, Bitterman (1988) found (to his and everyone else’s surprise) that essentially all of the “higher order” learning abilities known from laboratory work with mammals were also demonstrable in honey bees. Although his results are interpretable as extending Macphail’s conclusion about learning to nonvertebrates, Bitterman prefers the view that they represent convergent evolution.

One problem with learning as a category is inherent in the strict behaviorism that has been the philosophy of its analysis in the psychological laboratory. The analysis is restricted to input and output—stimulus and response—and laboratory settings are designed to control these in the interest of rigor. So constrained, learning is

only marginally useful for an analysis of mind, because the acceptable phenomena for analysis are limited to a very small number of responses (usually two) that are recorded under a very small set (also usually two) of stimulus conditions. The input-output relations in different species can be assigned to the same "learning mechanisms," even if there are very different kinds of information processing inside the intervening black box that is the brain. Dramatic graphs have been published to show that, e.g., a "variable interval" reinforcement schedule produces behavior that is described by a characteristic performance curve, whether generated by a rat pressing a lever for food reinforcement or by a human pressing a lever for reinforcement by the appearance of a target signal (Skinner, 1957). However, it would be naive to conclude that all of the mental (or neural) processes associated with the behavior that underlies the performance curve are identical in rats and humans or that the curves give more than restricted evidence on the nature of mind.

Our present understanding of the nature of learning raises a more fundamental problem for using learning to understand the evolution of mind. The phenomena of learning are explained in terms of a limited set of paradigms: habituation, sensitization, and classical and instrumental conditioning. (Macphail discusses higher order phenomena, but these can be "reduced" to the simpler paradigms.) Although the procedures in these paradigms raise complex issues in the analysis of the behavior (Mackintosh, 1974; Rescorla, 1988), the basic mechanisms seem to be limited to changes in excitability at the synapse (Hebb, 1949; cf. Rauschecker, 1989) and should be identifiable in all organisms with synaptic nervous systems. In evolutionary perspective one must assume that the genetic programs for these fundamental mechanisms appeared early in metazoan evolution and have been retained in all later metazoan species. As basic characters in metazoans, learning mechanisms cannot be used in the analysis of the diversification of species in mental characteristics, except to identify these mechanisms as a common feature in all metazoans in which we assume that the character, "mind," is present. (Cladists might describe these fundamental mechanisms of learning as plesiomorphies, which provide no information for a phylogenetic analysis; see Cracraft and Eldredge, 1979.)

### *Categories in the Analysis of Mind: Social Behavior*

Social behavior as a source of evidence of mind can be subjected to a critique much like that just presented for learning. All multicellular animals are social to some extent. And although the analysis of their social behavior is a rich source of information on the varieties of adaptations (Allee, 1931; Wilson, 1975), social interactions are generated by many different mechanisms, most of which have little to do with mind. These mechanisms are different in different species and are useful for the analysis of phylogenetic relationships, but they may provide little or no information on how mind evolved.

I will illustrate this point with one "nonmind" mechanism among those that are treated in the study of instinct in the classic ethological literature (Lorenz 1935/1937; Tinbergen, 1951). Hailman (1967) analyzed pecking by gull chicks at the adult gull's bill, a "fixed action pattern" that is a necessary part of the social interaction between parent and offspring during feeding. He was able to demonstrate that some stimuli, quite unbeaklike to the human eye, were more efficient ("superstimuli") at releasing the pecking behavior in chicks than was the beak itself. The parent gull's beak is evidently not the "object" at which a chick pecks. Rather, the pecking is released by a configuration of stimulation that is approximated well by the parent's beak, but there are better approximations that can be made by other configurations. The chick is not "pecking at a beak." It is "pecking in response to a configuration." The beak is not an "object" in the chick's world. In this setting, the chick is an automaton, responding in a reflex way to a stimulus complex.

(Phenomena such as these force us to keep a distinction between sensation and perception in some form for the analysis of mind, because the sensory response to an external stimulus is not necessarily organized into a "percept" characterized by constancy effects.)

It is not clear how much of animal social behavior is controlled by nonobject signs in the environment, but ethological analysis suggests that such "sign-stimuli" that cannot be described as objects are typical governors of social behavior in nonhuman animals (Smith, 1977). Their role is usually underestimated in human social interactions, even though our social behavior also often depends signifi-

icantly on communication with nonmind “body language,” the sign-stimuli of human behavior.

Social behavior involves mind when it involves *knowledge*. To be relevant for mind, social behavior must be based on perceptions of other animals as objects that keep their identities under many transformations, and of signals as having meanings that are related to one’s knowledge of the external world. Cognitive factors in social behavior are usually perceptual factors, which enable animals to know (recognize) other animals and events in their social world.

To clarify the distinction between mindless and mind-relevant events, it may help to mention an interesting example of social behavior in which mind is almost certainly important. African green monkeys (vervets) have a repertoire of three different vocal warning signals, which they perfect (by learning and imprinting) during infancy and childhood, and they use these to warn members of the troop of the presence of their three major predators: eagles, leopards, and snakes. From carefully reviewed anecdotal as well as observational and experimental evidence it seems clear that although the signals are stereotyped, the information in these warning signals is of a picture of the external world rather than stimulus configurations that release fixed action patterns (Cheney and Seyfarth, 1985; Marler, 1983). These signals send messages that may have some of the features of natural human languages as communication systems.

### *Categories in the Analysis of Mind: Communication*

Like the example of vocal communication among vervets, most animal communication is typically with a fixed set of stereotyped signals. The signals are often morphological: rump patches in ungulates that are exposed by “tail flagging” to serve as alarm signals (Smith, 1977), hair crests in carnivores used as “intimidation structures” (Wemmer and Wilson, 1983), odors in territorial marking, trail marking, sexual signals and aggressive signals (see Eisenberg and Kleiman, 1983; Gorman and Trowbridge, 1989; Müller-Schwarze, 1983). Vocal signals are, of course, also morphological in that they are constrained by the design of sound-generating organs, although their correct production and use are frequently dependent

on some kind of learning. But whether learned or innate, in most species vocalizations are stereotyped and automatic signals that control social interactions, such as parent-infant relations, warning, threat, courtship, etc. (Gould, 1983).

It is almost a principle in ethological analysis that simple signals by one animal can release complex behavior in another (Maynard Smith, 1978). The gull's beak as a sign-stimulus is relatively simple to analyze, especially when it is recognized that its effectiveness is due to fairly simple stimulus properties and not to its character as an object in the chick's world. The chain of responses that follows is more complex, consisting of the chick's pecking and eventual feeding. In adult vervets, the alarm call is acoustically stereotyped and in that sense fairly simple. The response it elicits in other monkeys is complex, involving evasive movements of running, climbing, jumping, etc., with the paths determined by the immediate environment and the information (a choice among just three alternatives) provided by the call.

In thinking about the evolution of communication as a category of behavior, we recognize that selection should be for accuracy and simplicity. The signals should be uniform and unequivocal, consistent with the simple messages that are usually transmitted, hence the value of morphological signals. The important requirement is that there should be minimal uncertainty about the significance of signals. Neural control of such a signaling system could be fairly simple, requiring a relatively small investment in neural machinery.

As a category of mind, communication and the neural adaptations associated with it is one that students of human evolution are inclined to emphasize, because of the importance of language as a human adaptation for communication and the uniqueness of language as a human trait. The requirements for reliability in animal communication systems, however, are not met by human language, which is notoriously subject to misunderstanding. Partly for this reason it seems likely that human language had different biological roots from those typical for animal communication. I will argue that brain functions in language can be understood only if the human language system began to evolve in the earliest hominids as a cognitive system in response to selection pressures for improved knowl-

edge of the external world, rather than as a system devised for improved communication with other individuals. I will argue that only later (though not much later) in hominid evolution did language begin to evolve into the tool for communication that it is now. As in some of my other propositions about mind, this argument depends on features of brain organization and functions, which I consider in later sections, as well as the peculiarities of language when compared to typical animal communication.

### *The Function of Mind*

Having rejected behavioristic dimensions of mind, let me treat our topic in the conventional functional terms of evolutionary biology by asking how “mind” functions as an animal adaptation. The alternative to mind is a Cartesian reflex machine. Why have mind—a knower of reality? The answer is relatively easy. With the exception of a few sessile species, most animals move about and need information about the external world to guide their movements. “Mind” is one of the adaptations that evolved to handle such information.

In species in which the behavior repertoire is small and the environment predictable, action and reaction, stimulus and response can be tied to one another directly, by reflex mechanisms, to ensure appropriate behavior. Many vertebrate behaviors are of this type: tight bonds between stimulus and response. Frogs and salamanders catching passing insects with flicks of the tongue are classic examples (Ewert, 1974; Lettvin et al., 1959; Roth, 1987). The response is elicited by any small dark object moving at appropriate speed in the animal’s visual field. In nature, most small dark moving objects are things like flies, and the tongue-flicking is an effective “mindless” way to insure a balanced diet.

Mind evolved to handle stimulus-response contingencies where reflex control would fail. This could occur when the information in signal and response was too great to be handled by a purely reflex system. The problem was how to handle very large amounts of biological information. To analyze it we need answers to some specific questions: What are the units of information for the organism? How is information partitioned, categorized, or organized? And

when is there too much information to handle with reflex mechanisms? Although there are elegant analyses, especially of the first two questions (e.g., Miller, 1956; Simon, 1974), an information overload cannot be analyzed without considering the biological limitations of the organ that processes the information, namely, the brain. The complete answer requires a review of the mind-brain problem, but we can indicate a few preliminaries.

Like all large information processing systems, the mind must be organized hierarchically. Information is processed in stages, which correspond to the hierarchical organization of the brain. Biologically, information from the external world is first transformed from physical energy into sense cell activity, and then it is processed and transmitted through a cascade of structures in the nervous system. From the perspective of mind as I have been discussing it, the later stages of processing transform the information from patterns of neural data into a representation of an external world.

The later stages are perceptual and cognitive, and their special feature is that information is organized into chunks (Simon, 1974) or packets, which can represent objects, space, time, etc., that are invariant under many transformations. It is beyond the scope of my discussion to treat the information and its transformations in more detail; there is an impressive literature on exactly that (e.g., Longuet-Higgins and Sutherland, 1980), and possible mechanisms for generating the invariances for visual perception have been described with unusual precision (Marr, 1982).

Although I discuss consciousness in more detail later, I can note that the packets would also organize the contents of *conscious* experience. There is an aura of mystery about consciousness, and I want to conclude my statement on mind by questioning the appropriateness of that aura. How would one suppose that an animal's information processing machinery would be organized to manage the job of living and moving about in the external world? If its possible movements are restricted and the relevant features of its world are few, then an animal might function successfully as a reflex machine that responds to stimuli without organizing them into a representation of an external world. But if the animal's life is more complex, a pictorial rendering of an external world is as natural as

any. Consciousness need be no more than the fact that a picture is constructed. There might be various levels of organization, or complexity, of the representation, but why the mystery? Consciousness can be thought of as an aspect of the organization of information from the external world to cope effectively with the problem of behaving in it. It would be created by the machinery that handles the information, namely the brain, and it would result in easier information processing. The only odd feature is that we must then recognize that the *experienced* real world is a construction by the brain.

### THE MIND-BRAIN PROBLEM

If “mind” refers to our knowledge of reality, then the mind-brain problem is: How do brains handle information about the real world, and how does the brain’s processing of neural information correspond to “knowing reality”? Neural information in the brain is measured as weak, usually brief, electrical, magnetic, or chemical signals associated with activity of a nerve cell. Some of the activity originates in stimuli from sensory cells that respond to events in the external environment, but most of the neural activity in the brain results from activation by other neurons. There is a mind-brain problem, because none of the activity of single neurons, not even that generated by sensory cells, is directly related to the real world as we know it. The activity of individual neurons can be recognized as related to events in the real world only if outside observers (usually neuroscientists), who monitor the machines that record the activity of neurons in experiments, can correlate that activity with environmental events. A neuroscientist monitoring the activity of a single nerve cell could not even ascribe that activity to a specific kind of stimulus, such as a sight or a sound, without information about environmental correlates of the activity.

With that limitation in mind, there is nevertheless quite a bit known about how the work of the brain is related to the work of the mind. Although I will obviously oversimplify, let me outline some of the more interesting things that we have known for some

time, about how information in the brain is organized into maps of the external world.

### *Mapping in the Brain*

There are two important ways to think about mapping. First, there is mapping as the work of neuroscientists when recording the results of certain experiments on the brain. The second is to recognize mapping as a feature of the organization of the brain as an information processing system: The brain is to a very significant extent a mapping machine. These are distinct though closely related usages of "mapping," and recognizing the distinction may help us appreciate some of the features of the mind-brain problem.

The activity of particular neurons in particular regions of the brain can be correlated with particular environmental stimulation, and we can draw a series of maps to record and describe the correlations. The initial map is an undistorted picture of the external environment, and the next maps are projections of the initial map onto various surfaces, beginning with a picture of the external world on a sense organ such as the retina of the eye. Later maps that we draw show the projection proceeding inward to successive regions of the brain and indicate the extent to which the information from the environmental map remains coherent. These maps reflect the information processing going on in the brain and thus suggest the second usage of the idea of mapping.

When we prepare these maps, perhaps the most interesting result is that although the maps drawn on brain areas appear distorted relative to the environmental map, they are distorted in orderly ways. Among the most familiar of the maps are those of the somatosensory system, which are drawn as distortions of a skinned animal or person, with unusual expansion and contraction of some regions. The human picture is a homunculus distorted by having very large thumb, lip, and tongue areas. The same sort of map in other mammals can be prepared more carefully to show more detail. The "animalculus" may seem even odder than the homunculus, because it turns out to be at least twins or triplets, that is, as several copies of the body map (fig. 2).

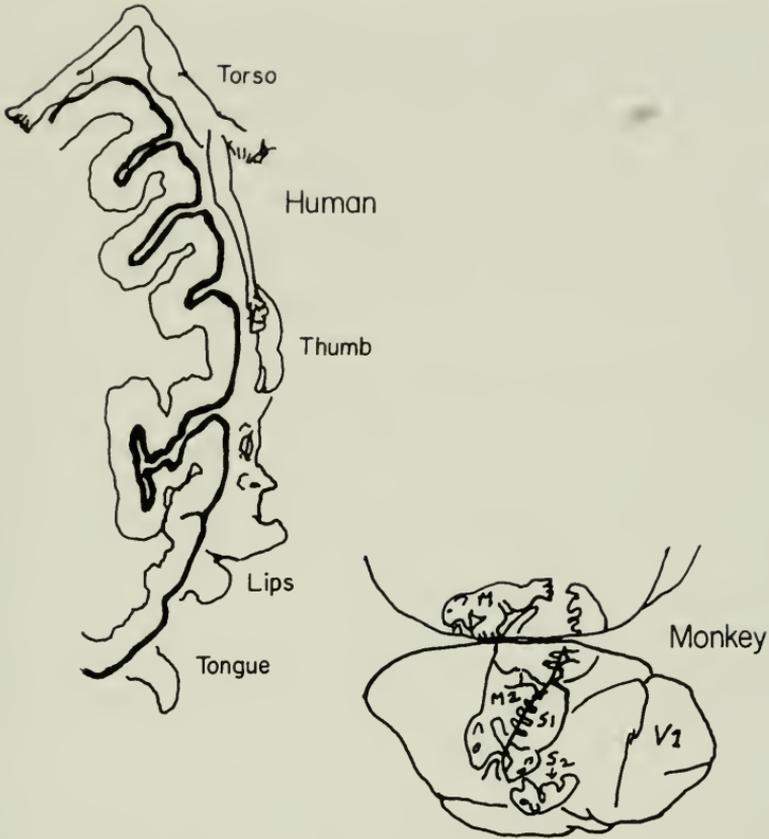


Fig. 2. Maps in the brain. The human map (left) is shown adjacent to a slice of neocortex at approximately *S* in fig. 8, below, where neocortex is about 2 or 3 mm thick. The monkey maps are of two motor and two sensory areas, and are partly on the lateral and partly on the medial surface, shown here on the left hemisphere. (Based on Woolsey, 1958)

The mappings on the brain from the retina of the eye are the most completely studied and best understood (Hubel, 1988), and perhaps for this reason we recognize how unusual a mapping can be. First, these maps, usually called projections, are split between the two halves of the brain, and the details of this split suggest that it is involved in a transformation of data from binocular disparity into a record of the depth of visual space. (The other two dimensions of visual space are encoded by the spatial array of cells in the retina, the locations of which are reasonably well conserved in the spatial

arrangement of neurons at more central neural processing stations.) Splittings occur subcortically and cortically, with major subcortical way stations in the thalamus and the midbrain. There are, furthermore, other splittings of the information from the retina, on color, shape, etc., which are channeled to different layers and regions of the neocortex. There are perhaps a dozen copies of various parts of the map of the retina spread through the visual cortex and the area immediately adjacent to it. In addition, there are major projections of the visual field to other parts of the brain, especially in the temporal lobe.

Other information processing systems in the brain are also very complex. The auditory system has multiple projections through nuclei and tracts in the medulla, midbrain, and thalamus, terminating at several centers in the auditory cortex. Cortical maps project to the cerebellum, and there are recursive systems sending the information back. And all of these maps are connected to one another via assembly points in the hippocampus ("old cortex") and in the prefrontal region of the neocortex (Goldman-Rakic, 1988). I have emphasized sensory and perceptual maps, but motor systems are also mapped systems and support the active manipulation of the environment, which can be crucial for the normal development of the brain as a sensing system (Held, 1965).

This very brief overview of the mapping that is recorded from the brain only begins to suggest its complexity. But in the face of the complexity, it remains correct to generalize about these results as demonstrating a cascade of coherent mappings in the brain of information about the external world.

I began this section by stating that mapping was a way of describing information processing in a brain, but that it was also a fundamental feature of the organization of the brain. This may be obvious from the use of maps to describe what the brain does, but I am concerned that we might miss the significance of our ability to do this. The maps are not mere artifacts that we create in order to understand a complex system. They certainly help at that level, but they can be drawn only because the anatomical system is in fact coherent. There really is a biological wiring system in place, whereby the information transmitted over the "wires" results in a set of mappings that repeat

and analyze sensory and motor maps of the external world. Our artificial “model” of the system—a set of drawings—reflects the neurobiological phenomenon of projection of information from one domain onto another according to fixed rules. These organic maps in the tissues of the brain are aspects of its workings.

In his theory of mind, Kenneth Craik (1943/1967) developed the idea that thinking consists of making models that work in ways comparable to what is being explained (cf. Bower and Morrow, 1990). Similarly, describing the brain’s work as mapping enables us to think about it in terms of a model of how we make a map. We make a map on a piece of paper by drawing lines and points that correspond to features of the external world. Our view of the brain is that it is wired to do this kind of mapping automatically. The brain’s mapping begins with maps of the external world painted onto sensory surfaces, such as the retina of the eye, which are made up of sense cells and closely associated nerve cells. The maps are then projected along nerve fibers, sometimes organized as tracts, which form the “hardwired” system for projecting the maps. Although the fiber pathways may become jumbled, one of the beauties of the system is that it becomes reorganized and again coherent at each of the major “surfaces” at which analysis takes place. In the case of the visual system, for example, fiber tracts often lose their orderly mapped patterns, but order returns at the superior colliculi (mid-brain), the lateral geniculate bodies (thalamus), and in the various maps in the visual cortex.

A map is more than a metaphor for what is going on in the brain. It describes a major feature of the structure of the brain. The cascade of maps in the brain is involved in successive analyses of the data, each analysis extracting or adding features to the information.

A crucial aspect of the brain as a mapping machine is quantitative. How much brain tissue is involved in this work? The mappings occur at sense organs and more centrally at many subcortical and cortical levels in the brain. There is insufficient quantitative analysis of most of the subcortical systems, although mapping almost certainly accounts for a good part of their mass, either as fiber systems transmitting mapped information or as “surfaces” in which the maps can be recorded. There are good data on the neocortex, however,

indicating that most of it is involved in mapping (Jones and Powell, 1970; Diamond, 1979). Since the cortex alone accounts for about 40 percent of the size of the mammalian brain, this means that much of the brain in mammals is devoted to processing information about the external (real) world.

From considerations like these about mapping I have concluded, first, that the elaborate analysis of information about the external world in the brain can be the basis for what we describe as “knowing reality.” The enormous investment in neural machinery in the analysis can be the explanation for some “peculiar” features of our external world, such as its stability in the face of the changing patterns of stimulation at sensory surfaces and the ability to extract precise, deterministic, information from statistical or probabilistic features of neural activity. These stable features of the reality that we know are clearly generated by the work of the brain, and this is part of my meaning in stating that our experienced reality is a construction of the brain.

My second conclusion involves two other features of this activity, which are related to the role of gross brain size as a measure for the analysis of mind. The first of these features concerns the categories of mental activity to which the massive mapping system should be assigned. This is clearly the perceptual-cognitive category, rather than learning, social behavior, or communication. (Perceptual-cognitive dimensions of the latter categories would, of course, be controlled by the mapping system.) The second feature is that the mappings are distributed through much of the brain, and although localization is extremely precise, the maps interact with one another and involve almost all of the mass of the brain. The brain works as a very large “distributed” system involving components present throughout most of the brain (Mountcastle, 1978; Goldman-Rakic, 1988). To sum up, for the mind-brain problem, the analysis suggests that much of the mass of the brain, at least in mammals, is related to perceptual-cognitive adaptations, i.e., for knowing reality.

### *Consciousness: External Reality*

I have used the word “consciousness” several times and discuss some of the issues related to it at the conclusion of the lecture. I

need a few paragraphs here to explain my usage and to show how it fits in with our ideas on mapping and on the brain's work. I distinguish consciousness-as-awareness from self-consciousness, the knowledge that we are knowers. Awareness is the pictorial representation of the real world that we know without special reflection. I believe that awareness in this sense is both more complex and more fundamental a phenomenon than is self-consciousness, which can be analyzed as a type of awareness. My definition of mind as "knowing" reality might suggest that consciousness is necessary for mind. But this is not true. There is excellent scientific evidence of knowledge without awareness, which can be understood only in terms of unconscious processes.

An especially dramatic example is "blindsight" (Weiskrantz, 1986). Patients with partial "cortical blindness" due to lesions in the visual cortex can correctly point to objects that they insist they cannot see—objects that fall in the "blind" region of the visual field affected by their lesion. Their loss of awareness is not accompanied by loss of all information about the location of objects in that region in space. In other words, they "know" features of the external world without being "aware" of them. And the world that they know is mapped like that of the sighted, within the dimensions of time and space rather than by reflex mechanisms.

There is more direct evidence of the mapping of awareness of the external world from the electrical stimulation of the exposed human brain during neurosurgery. Such stimulation can produce a variety of conscious experiences that are determined by the region in the brain that is stimulated and which are often localized in distinct regions of an external world (Ojemann, 1983; Penfield and Roberts, 1959).

Evidence for a "seat of awareness" for *self-consciousness* in the brain is well established and well known in neurology. It is not so much a seat as a nonmapped region, and it also has some paradoxical features, including an odd divisibility. The evidence is clearest in split-brain patients in whom the corpus callosum is cut and who seem to "know" two separate worlds with each half of the brain (Bogen, 1986; Levy, 1988; Sperry et al., 1979), as if there were two minds in one brain. Their worlds refer to different selves, with the

self of the language hemisphere clearly being the self that the patient can talk about, and the self of the other hemisphere identified (by the speaking patient, of course) as a kind of stranger (Dimond, 1979).

### *A Resolution of the Mind-Brain Problem*

The persistent mind-brain problem is, first, how the translation takes place from neurally coded maps into a pictorial world that is experienced as reality. This is the problem of understanding the neural basis of perceptual-cognitive dimensions of mind. I believe that we have an adequate, if not complete, solution of this first problem in the evidence on mapping. But there remains a problem of describing exactly what is mapped, which depends on an analysis of mind that can be related with precision to the brain's work.

We might have the brain generating Kantian categories of mind, for example, and there is no reason to reject this on the basis of current evidence. We do not normally talk of "space," "time," or "object" areas in the brain, but the categories used by neuroscientists could easily be related to Kantian categories. Our direct experience of space corresponds to its projection on the retina on which the visual field is mapped. It is also reflected in the maps projected repeatedly to and from other parts of the brain. The shape and color of objects in the visual field are also mapped at the level of the retina, and part of the depth dimension of visual space is represented as binocular disparity, analyzed at a cortical level. There is no correspondingly direct representation of time in the brain, but a time dimension is involved in the analysis of many signals, especially in the auditory system. There is thus nothing in the structure or function of the brain that eliminates the possibility that part of its work involves the creation of categories comparable to (but not necessarily the same as) those created by Kant. The only problem is with the precise description and understanding of the categories.

Kant's categories are an outstanding achievement of armchair analysis of the nature of mind, but natural categories are almost certainly different. The most important difference is that at least some of the categories that may seem fundamental are species-specific, or "suborder-specific" for us as anthropoid primates. We are

simply too odd a species to be able to use our unaided intuition as a guide to mind in other animals. The metaphor of the mind's eye is a primate's metaphor, which reflects one of the unique features of a primate's world. We say, "I see" to mean that we understand. Were we not primates we might more likely have said, "I smell" (as a transitive verb, of course).

We are odd in at least three ways, two of which we share with other anthropoids (monkeys, apes, and humans) and the third of which is unique. First, while almost all mammals can see, as anthropoids we humans use vision in ways unusual for other mammals. Where ours is a world of colors, most nonanthropoid species live in visual worlds that we would think of as painted in shades of gray. Although color vision is more common in mammals than has been realized (Jacobs, 1981), information from color is not as salient in controlling action in most species as it is in anthropoids. Our second oddity as anthropoids is our insensitivity to the rich world of odors that guides behavior in other land mammals. As anthropoid primates, we might be described as smell blind analogously to the way other mammals are color blind. We receive and use important information when we rely on odors, but our world of odors is not nearly as informative as that of, e.g., cats or dogs or rats, or almost any nonprimate land mammal (Brown and Macdonald, 1985). Our "receivers" for smells, the olfactory bulbs, are a fraction of the size that we would expect them to be at our body size, were we normal mammals (see fig. 12, below).

Our third and uniquely human oddity is that we know the external world through a unique species-typical "sense" that we call language. This is so odd an adaptation that I can discuss its nature and evolution only after presenting more of my analysis of neurobiological and evolutionary issues. It is probably the most important of the species-typical adaptations that affect our armchair choices of "categories."

Our intuitions do not always mislead us about the realities of other animals. There is plenty of evidence that perceptual categories, such as faces or sounds, are known by other species in ways similar to ours. Pigeons are as good as, or better than, people at finding familiar human figures, even well-disguised ones, as individuals in

a crowd (Herrnstein, 1985). It is hard to imagine such a perceptual skill without the availability to the pigeon of a representation of reality that works as well as the human mental image of a person in a crowd. Similarly, although our intuitions are inadequate for us to conjure up a comparable image generated from olfactory information, species that are not smell blind, such as wolves, may know their world with object-specific olfactory images that are as useful as our visual images (Gorman and Trowbridge, 1989; Peters and Mech, 1975; Rasa, 1973; Roeder, 1983).

Regardless of its details, a resolution of the mind/brain problem includes the conclusion that the real world *as known to an animal*, including the human animal, is a construction of its brain and, therefore, that the mind is a construction of the brain. An enormous amount of information has to be processed to generate this construction, and this processing capacity evolved as the brain evolved to larger sizes.

## BRAIN SIZE AND PROCESSING CAPACITY

Among the many important facts about brains, I emphasize that much of the brain's enormous capacity to process information is organized in the form of mappings of the external world. In this section I provide quantitative estimates of these features. I show how and why the information processing capacity of a mammalian brain can be estimated from gross brain size, and consider questions of the uniformity of the organization of the brain. The answers enable us to evaluate the utility of brain size as an overall measure of the brain's functional capacity. They provide the basis for steps from a quantitative analysis of the evolution of brain size to statements about the evolution of processing capacity and other brain activity related to "higher mental processes."

Even a mouse's brain is an enormous information processing system. Schüz and Palm (1989) have recently shown that there are about 10 million ( $10^7$ ) neocortical neurons and an additional 30 million neurons in other brain structures (mainly in the cerebellum) in the mouse. Their truly astonishing figure is on the number of connections among neurons. There are more than 80 billion

(80,000,000,000 =  $8 \times 10^{10}$ ) synapses in the neocortex! This in a brain that weighs half a gram: a fiftieth of an ounce. If things were simply proportional when comparing brains, the human brain, which typically weighs about 3 pounds (1.4 kg), would have a total of about 100 billion ( $10^{11}$ ) neurons and about a quadrillion ( $10^{15}$ ) neocortical synapses.

### *Quantitative Implications of Neocortical Organization: Mapping*

The brain's business is packaging, organizing, and managing the flow of information that is related directly or indirectly to events in the external world. Much of the information is organized into maps such as those summarized in figure 2, and the quantitative question is: how much of the brain is actually involved in mapping, or, as I would have it, in perception and cognition? According to the work mentioned earlier, essentially all of the neocortex is mapped brain. In figure 3 there is more detailed evidence from the brains of tree shrews and bushbabies.

In presenting the data of figure 3, Diamond (1979) suggested that it may be a general rule in mammalian brains that neocortical extent is accounted for almost entirely by projection systems. He argued, further, that the categories "association" and "projection" are not really appropriate for describing structure-function relations in the brain, and I accept his position. But the categories may be too deeply embedded in our view of both brain and mind to be discarded (they are relics of the "mental chemistry" psychology of the 19th century). It is not difficult to retain the words to describe functional, but not structural, categories. It would be correct to consider association systems as intercalated within and among projection systems; the two would then be mapped as overlays rather than as separated areas. The intimate connections between these systems suggest that neocortical function, in general, should be thought of as related to analyzing information about the real world, although there are, perhaps, different levels of analysis provided by the intertwined "projection" maps and the "association" maps.

I am not proposing a view of how the brain's analysis is organized with respect to projection and association. My concern is with what

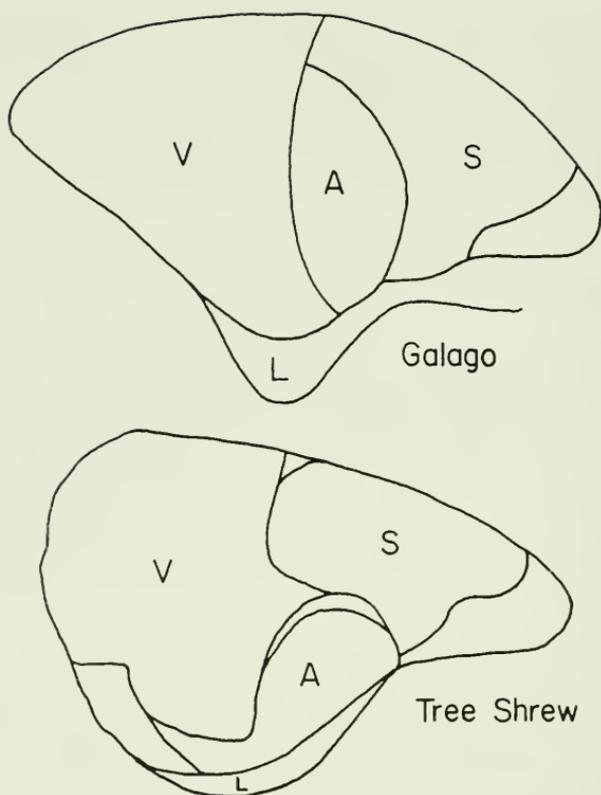


Fig. 3. Sketches of the lateral surface of the neocortex of the right hemisphere in the bushbaby (*Galago senegalensis*) and the left hemisphere's in the tree shrew (*Tupaia glis*), traced from Diamond (1979). V, S, and A refer to projection fields of the visual, somatic (sensory and motor), and auditory systems. Regions without letters had not been assigned to projection systems at the time of Diamond's review. "Old cortex" (L = limbic) is also labeled, though it is not considered in this context. Note that essentially all of the neocortex is mapped brain in these two species.

is being analyzed, which is information from the real world. In addition, I want to emphasize the extraordinary size of neocortex, as a specialized "organ" for perception and cognition, which implies that the amount of processing capacity required to analyze this information is very great.

This conclusion has important implications for our inferences about the enlargement of the brain in mammalian evolution beyond that associated with body size. This increase in *relative* brain size,

which is called encephalization, was driven by the expansion of the neocortex, according to the evidence from fossil endocasts (Jerison, 1990; Radinsky, 1979). The evolution of encephalization may, therefore, be interpreted as having provided neural machinery for more elaborate analysis of information about the external, or real, world. This is the logic behind the idea that mind, i.e., the capacity for "knowing reality," evolved as species became more encephalized. To extend the argument, I point the arrow for causal inference both ways, to suggest that whenever an evolutionary trend toward encephalization can be detected, the most likely explanation for the trend is that there was selection for improved (or at least different) ways of knowing reality.

#### *Quantitative Implications of Neocortical Organization: Packing Units*

The neuron and the synapse are often thought of as morphological units of information processing in the brain. A popular third candidate is the module, which in the neocortex consists of a column of tissue in the brain that covers the full depth of neocortex, perhaps 0.5 mm in the mouse or 3 mm in man. A columnar module may be about 0.5 mm in diameter in all species (Hubel, 1988; Mountcastle, 1978; Szentagothai, 1978; this uniformity is only approximate). Columnar organization occurs elsewhere in the brain as well (Scheibel and Scheibel, 1970), but it is in the neocortex that it has been studied most thoroughly and is the model for a modular unit that is involved in the brain's analysis of information (Eccles, 1979). If we take the column as the unit, then the processing capacity of the brain would be proportional to the number of columns, and the number of columns in a brain would be proportional to the surface area. Differences among species in surface area would estimate differences in processing capacity.

If we take the number of neurons as our measure, we are also led to the cortical surface area as a measure of processing capacity. Rockel, Hiorns and Powell (1980) reported that the number of neurons under a given area of neocortex in the brains of very different mammalian species was remarkably constant at somewhat under

150,000/mm<sup>2</sup>. (This implies almost 30,000 neurons in a typical column.) The total neocortical surface area would therefore estimate the total number of neurons in the neocortex and total neocortical processing capacity. The number of synapses is usually estimated as proportional to the number of neurons; hence these too would be proportional to surface area. The key to a morphological estimate of processing capacity is clearly a measure of surface area.

I have no data on neocortical surface alone, but there are published data on the total cortical surface area in many species of mammals. The areas probably include hippocampus, piriform lobes, and other "old cortex" structures in addition to the neocortex. From a broad information processing perspective, the entire cortex is the major part of the great information processing system that is the mammalian brain, and "old cortex" structures are important components of that system. The "archicortical" hippocampus, for example, appears to be a crucial part of the system for handling certain kinds of memory and of mapping the external environment (O'Keefe and Nadel, 1978; Olton, 1985; Squire, 1987). In any case, my data on surface area are on total cortical surface, not just neocortex, but it is not unreasonable to consider that surface as representing the sum of the areas of the maps in the brain.

Could we make an educated guess about the area of the cortex (the sum of the maps) if we knew only the total size of the brain? Could we determine it in fossil brains? A quantitative question deserves a quantitative answer, and it is presented in figure 4. Our guess would be well educated.

Figure 4 presents data on cortical surface area correlated with brain weight in a very diverse sample of mammalian species. There are encephalized species such as the killer whale, elephant, monkeys, a chimpanzee, and sets of humans and cetaceans, but there are also several supposedly primitive species, including egg-laying monotremes (platypus and spiny anteater), marsupials (opossum and wallaby), and primitive placentals (pygmy shrew and armadillo) to name a few examples.

Technical details about this graph and its equation are reviewed later, in a section on uniformities in the organization of the brain. In a few words, the graph tells you that if you know the brain size

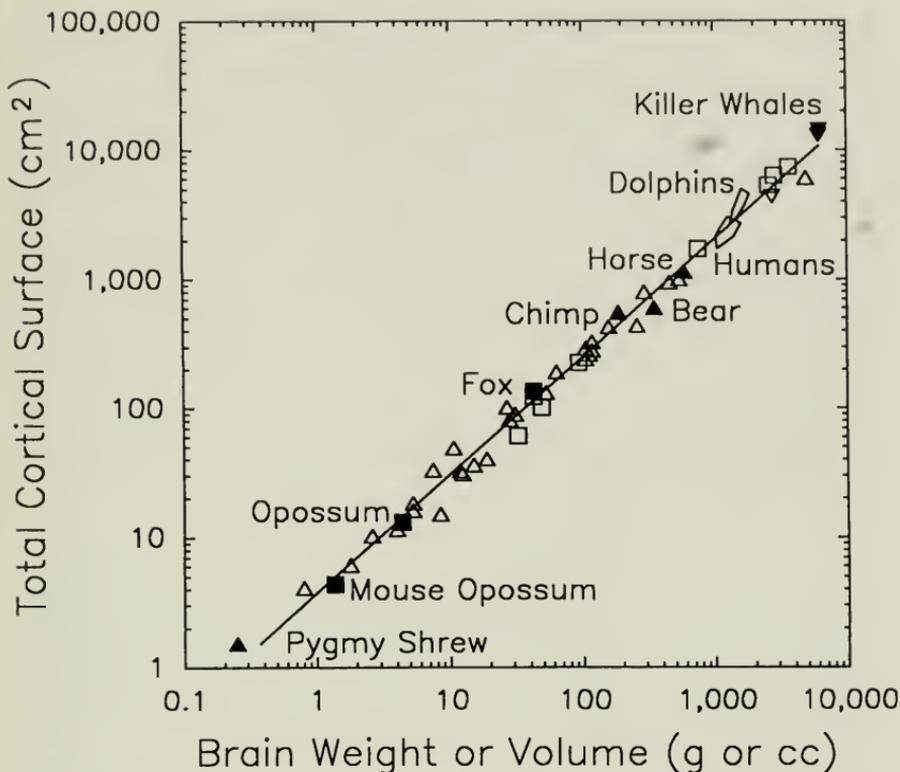


Fig. 4. The relationship between cortical surface and gross brain size “between-species” in mammals. Each point represents a species. In addition, two labeled minimum convex polygons enclose all of the presently available individual data for “humans” (N = 23) and “dolphins” (*Tursiops truncatus*, N = 13), and probably typify the magnitude of within-species variability. ( $\Delta$ ) Data from Brodmann (1913); ( $\square$ ) from Elias and Schwartz (1971); ( $\nabla$ ) from Ridgway (1981) and from Ridgway and Brownstein (1984). Species named on the graph are also identified by the filled data points. Regression (least-squares fit, assuming errors only in Y):  $Y = 3.75 X^{0.91}$ ,  $r = 0.996$ ,  $N = 50$  species.

of an unfamiliar species, you needn't worry about whether it is primitive or progressive when you estimate the extent of the surface area of its cortex. Your estimate is unlikely to err by more than 1 or 2 percent. Taken together with the relationship between surface area and processing capacity, the message in figure 4 is, therefore, that brain size is a good estimator of total information processing capacity.

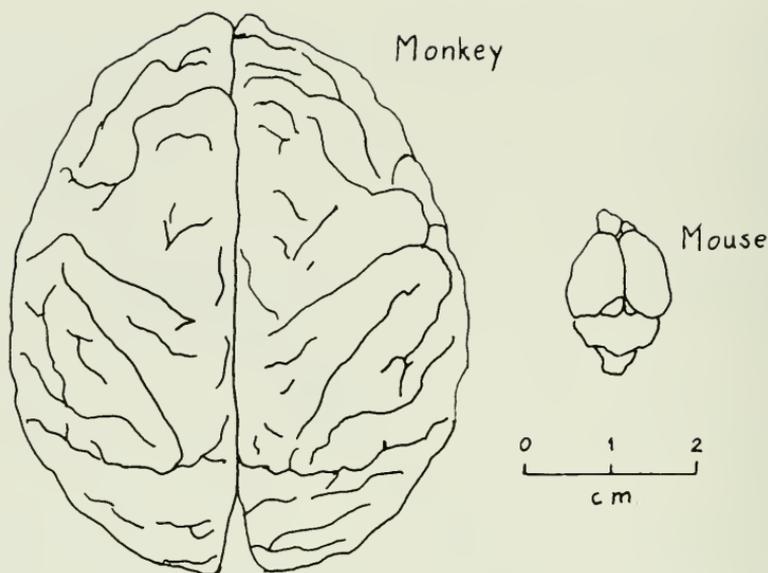


Fig. 5. Tracings from photographs of rhesus monkey and mouse brains (dorsal views) used for electron microscopic data on the corpus callosum. Only neocortex is visible in monkey; parts of the brain in the mouse may be identified by referring to fig. 1B. Both brains are oriented vertically, anterior end up. The mouse structures, anterior to posterior, are olfactory bulbs, cerebral hemispheres (forebrain), colliculi (visible as small exposed structures), cerebellum, and medulla.

#### *Neocortical Organization: Fiber Diameter in the Corpus Callosum*

One of the bases for quantifying the information processing capacity of brains according to estimates of the number of neurons that are packed into them is the idea that the cell bodies of neurons are approximately equal in size in different species, and that the number of neurons, independently of their size, can be used to estimate processing capacity. During the summer of 1989 I had a chance to test the hypothesis of uniform cell size in collaborative work with Dr. Almut Schüz of the Max-Planck-Institute of Biological Cybernetics at Tübingen and would like to share the result with you. It is preliminary but convincing. We compared species with impressively different brain sizes: a rhesus monkey and a mouse (fig. 5). The monkey's brain is about 200 times as big as the mouse's: 100 g vs. 0.5 g.

To test the hypothesis most severely, we decided to compare the

diameter of nerve fibers in the corpus callosum in the two species. The corpus callosum is the enormous fiber tract that connects the two hemispheres of the brain, and thicker fibers conduct nerve impulses more rapidly than thinner fibers. Contrary to the uniformity hypothesis, fiber diameters in the corpus callosum might be expected to vary with brain size, because such an adaptation would enable different species to use similar circuitry for at least some sensory and motor coordination. If fiber diameter were correlated with brain size, it would be possible to conserve the same circuitry in species that differ in brain size. To illustrate, if conduction velocity were constant, a message from a neuron in the left motor cortex in a monkey might take 5 msec to reach the right motor cortex, a distance of about 5 cm. A comparable message in the mouse, traversing only, say, 1 cm, would require only 1 msec. If monkeys had larger fibers, they might also be able to transmit the signal in 1 msec. We know that the circuitry is, in fact, similar in different species and that there appear to be no special problems related to conduction velocity. The question is, how were such problems avoided? Was size uniformity sacrificed, or have other mechanisms evolved? Comparing fiber diameter in the corpus callosum of a large brain (as in the monkey) and a small brain (as in the mouse) is, therefore, a good way to examine the hypothesis that uniformity was conserved.

Our preliminary results are in figure 6, which is a montage of electron photomicrographs, two each from mouse and monkey. They suggest that fibers are fairly similar in diameter. If you cover the labels you might still guess which is from monkey and which is from mouse, but I hope that you are impressed by the similarity of the sections. The 200-fold difference in brain size would translate into 35-fold difference in area or a 6-fold difference in diameter, so we would expect the average fiber diameters to be 6 times as great in monkey as in mouse if there were a simple (linear) proportionality with respect to brain size. It is obvious that the differences here, such as they are, are much smaller.

For a quantitative analysis, we measured the cross-sectional areas of the myelinated fibers in both species in sections like those in figure 6. The results were surprising and instructive. They are summarized in figure 7.

Monkey

Mouse

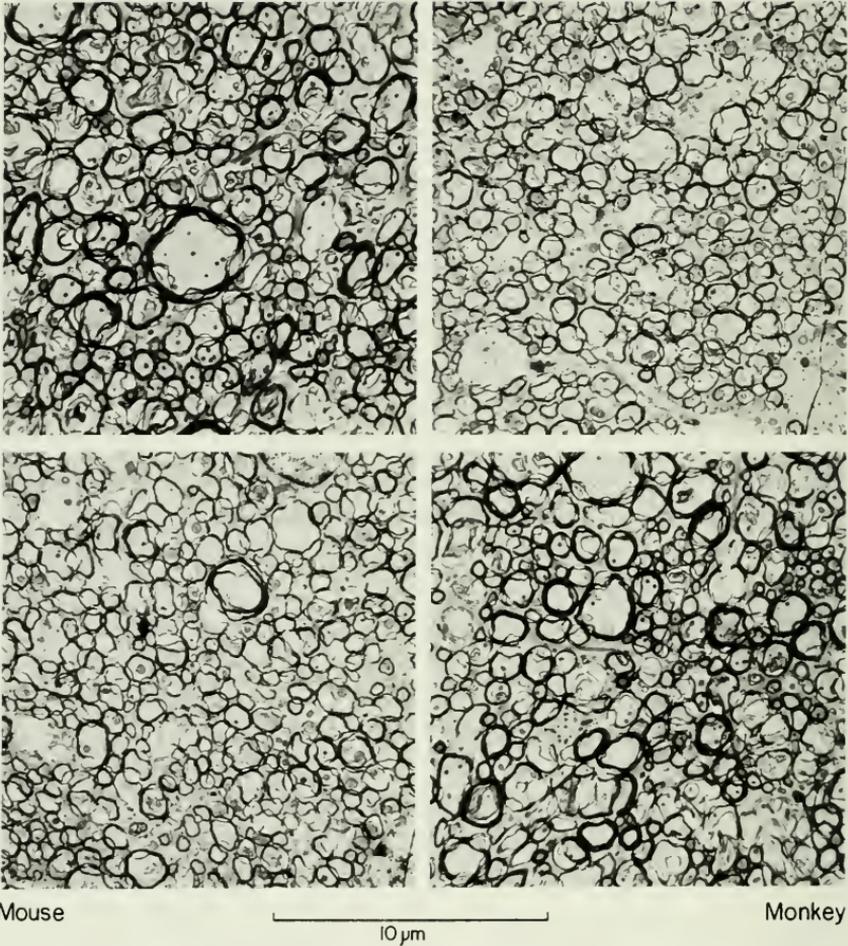


Fig. 6. Electron photomicrographs of cross sections of the corpus callosum in monkey and mouse. (Courtesy Dr. Almut Schüz)

The lower graph is a frequency distribution of the number of fibers that we counted at 0.1 micron-square steps of cross-sectional area in the two species. The modal regions of the distributions for mouse and monkey are surprisingly similar. This is even clearer in the upper graph, in which the relative instead of absolute frequencies of fibers of different cross-sectional areas are compared.

The overall result suggests that only a fraction of the myelinated

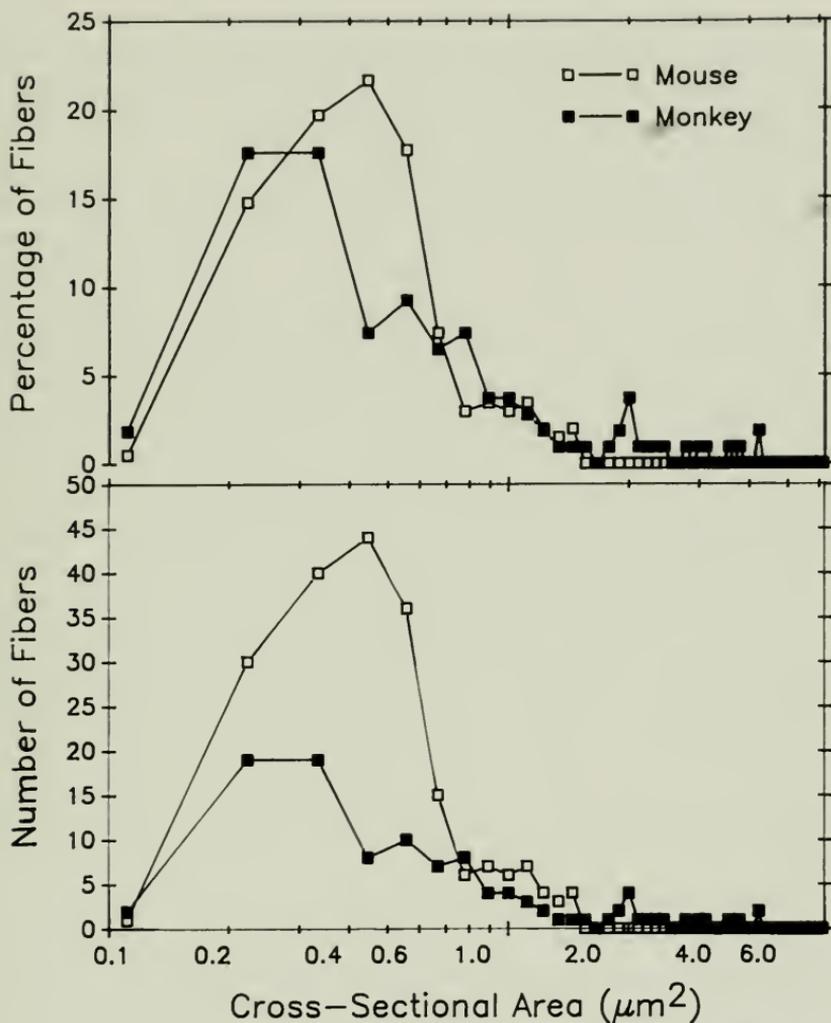


Fig. 7. Relative frequency (upper graph) and absolute frequencies (lower graph) of myelinated fibers of the indicated diameters in the corpus callosum of monkey and mouse. Counts from a total of four sections, comparable to but not the same as those shown in fig. 6.

fibers have to have higher conduction velocities to compensate for the effect of difference in transmission distance between the brains. There may also be important differences in the number of unmyelinated fibers, with many more in mouse than in monkey, and this may be another adaptation for handling the conduction velocity

problem. For my present purpose, however, it is sufficient to examine the data on myelinated fibers. Despite the major “pressure” for increased conduction velocity in monkey corpus callosum relative to that in mouse, the majority of callosal fibers were comparable in cross-sectional area in the two species.

Cell size evidently tends to be constant across species, and since brains are packed efficiently, the amount of neural material per unit volume of the brain should tend to be uniform in different brains. The amount of information that is handled should be proportional to the amount of processing machinery, and larger brains should, therefore, normally have more information processing capacity than smaller brains. The conclusion is the same as that from the surface-volume relationship described in figure 4: Brain size is likely to be a good “statistic” for estimating processing capacity in a species.

The constancy in amount of neural material can be contrasted with the packing density of neurons, which is known to *decrease* proportionally to the cube-root of brain size. In comparisons between mouse, human, elephant, and whale, for example, neuron density is of the order of 100,000 neurons per cubic millimeter of motor neocortex of the mouse, whereas in the three larger brained species it is of the order of 10,000 per cubic millimeter. I have used this relationship to analyze the meaning of brain size (e.g., Jerison, 1973, 1985b) and should reconcile this finding with the idea of uniformity. There is no real contradiction, just a bit of confusion about what a neuron is.

Neuron density is determined by counting neurons that are prepared for microscopy by staining the cell bodies and not the axo-dendritic arborization. In larger brains, the cell bodies are further apart, and this is what the neuron density analysis is about. But if we consider the arborization as well as the cell body of a neuron, the total amount of neural material per unit volume is about the same in all brains, and this is what “packing efficiency” is about. [The average size of neurons is, thus, larger in larger brains, if we include both cell body and arborization; the real constancy appears to be in the number of synapses per unit brain volume. In this connection we should remember that although synapses occur on cell bodies, most of them occur along the arborization (Schüz, 1988).]

When I first analyzed this issue, I recognized that there was an inverse relationship between data on “neuron density” and the “length of the dendrite tree.” In a slightly convoluted way, I reached the correct conclusion that the amount of information processed *per unit cortical volume* was constant across species (Jerison, 1973: 70), which means that processing capacity would be proportional to brain size across species.

### *Remarks on the Corpus Callosum Fibers*

While the comparability of data on mouse and monkey was, of course, gratifying support for my basic hypothesis of uniformity, a closer look at the data is also rewarding. I have used the phrase, “as a first approximation,” several times, and my general view is that a correct *evolutionary* analysis of mind is probably limited mainly to first approximations. I see mind in terms of “knowing reality,” but recognize that the knowledge is likely to take different forms in different species. The “first approximation” would be to the most general features of knowledge, and could refer to between-species aspects of mind, whereas finer analysis would lead to detailed statements that would be needed for an understanding of within-species, or species-typical, adaptations.

For our data on the corpus callosum, the first approximation is in the comparisons involving the major parts of the curves in figure 7, the regions about the mode. Here it is clear that the distributions of fiber cross-sectional areas are remarkably similar, and this argues for a major generating force, or constraint, that works in the same way in very different species, independently of brain size or specialization. The tails of the distributions, however, are clearly different in important ways, which are evident in the data as shown in figure 6, and in the difference between the upper and lower curve in figure 7.

The modal regions of the distributions (areas less than  $1300 \mu\text{m}^2$ ) are fairly symmetrical about the mode and appear to be approximately log-normal distributions. This is clearly the case for the mouse fibers. A large fraction of the monkey fibers are also represented by the modal distribution, but 15 percent of the monkey fibers were in

the long tail. If one were to prepare a processing model involving the timing of nerve impulses, the correction for faster conduction in the monkey brain would, clearly, involve the activity of that 15 percent. That 15 percent is also the reason for the much smaller absolute frequencies in the modal part of the monkey distribution as compared with the mouse distribution. A total of only 108 monkey fibers were counted on these sections, whereas 203 mouse fibers were counted. The tail of the monkey distribution, that is, the upper 15 percent of the fibers, accounted for more than half of the area of these sections, and that is why there are fewer monkey than mouse fibers in our data set.

A still closer approximation to a complete description of the operating characteristics of the corpus callosum would almost certainly include information transmitted by nonmyelinated fibers, and although these were not considered in this analysis, Dr. Schüz and I are acutely aware of the fact that there were surprisingly few such fibers in the monkey, whereas more than half of all of the fibers in the mouse were in this category. We did not analyze the difference, mainly because we are not certain that it was not an artifact; it is possible that differences between the way that the mouse and monkey material was prepared for microscopy affected the identifiability of nonmyelinated fibers differently from the myelinated fibers in monkeys.

## BRAIN ORGANIZATION

The issue that I address now is the extent to which the brain is put together and works the same way in different species. It is important for our discussion, because at some levels of organization, brains of different species are, of course, different, and yet it is the uniformities among brains that enable us to evaluate the evolution of brain size as related to the evolution of mind.

It is not uncommon to hear competent neuroscientists remark that, "Brain size is trivial; it is the organization of the brain that is important." A correct statement is that both size and organization are important in the brain's work, and size is especially important for our understanding of the evolution of mind. Although I will try

not to drown you with data as I present the evidence on the importance of brain size, I am convinced that nothing but data in heavy doses can overcome our prejudices against simplicity (Deacon, 1990), when we try to think straight about the extraordinarily complex system that is the brain. Some things about the brain are in fact fairly simple.

We have seen that brain size estimates the total processing capacity for mammalian brains, and it is this fact that is crucial for our understanding of the evolution of mind. However, processing capacity is allocated to different functions, more or less in proportion to the importance of the functions in the life of a species, a principle that I have called “proper mass” (Jerison, 1973: 15–16). For example, species using auditory information have expanded auditory centers; we as primates are visual specialists and have expanded visual centers, and so on. In spite of such specializations, which occur in some form in all species, the broad outlines of the evolution of mind can best be appreciated from the uniformities, that is, the extent to which brains are organized in the same way, at least as first approximations. The evolution of mind is then seen as a general phenomenon, related to processing capacity, and the evolution of specializations of mind can be understood as specialized adaptations.

My purpose in this section is to describe some of the uniformities of brain organization, while also indicating a few major diversities related to the specializations of different groups of mammals. My evidence on organization is primarily on how the brains of living species of mammals are similar and different in the absolute and relative sizes of their larger parts. I restrict it in this way, in order to be able to apply the evidence on living brains to the data on fossil endocasts. The application is to judgments about the “mind” of an animal such as *Bathygenys*, which might be based on evidence of its brain as shown in figure 1.

Structural organization can be represented by *allometric* (“quantitative comparison of structures”) analyses of the relationships among the parts of the brain. The question in such analyses can be very simple: if one knows the size of one structure, how well can one estimate the size of other structures in a species? For most of the brain, the answer is “quite well.” You have seen one example

in figure 4, above, in which 99 percent of the variance in cortical surface area was determined by brain size in 50 very different mammalian species. We could use the results shown in figure 4 to estimate the surface area of the cortex of any mammal. In *Bathygenys*, for example, the brain weighed about 10 g, and we can, therefore, estimate the area of its cortical surface as approximately 30.7 cm<sup>2</sup> (see eq. 1, below).

It has been appreciated for many years that at the species level brain size is determined primarily by body size, but that species are also different in *encephalization* beyond the expectations from body size. It is natural to ask whether more encephalized brains are organized very differently from less encephalized brains. The answer seems to be that it usually makes no measurable difference whether a brain achieves its gross size because of allometry or because of encephalization for the gross measures used in most allometric analyses. There are differences among major taxonomic groups, however, some of which will be evident in the detailed analyses that follow.

#### *Uniformities in the Brain: Surface-Volume Relations*

One of the most impressive and most important of the structural uniformities in the mammalian brain was displayed in figure 4, above, and it is a good point of departure for a discussion of uniformities and diversity. This graph showed that as a very good first approximation, the area of the cortical surface in mammals is determined by gross brain size. The correlation coefficient of 0.996 means that more than 99.2 percent of the variance in cortical surface is "explained" by brain size. When we look more closely at the data, however, we are rewarded with the surprising discovery that the one percent of "unexplained" variance involves significant deviations from uniformity and is not attributable to "error" in the statistician's sense. The most interesting example is for human data, because it destroys an old myth about our marvelous brains.

The equation shown in figure 4 was calculated as a regression of  $y$  on  $x$ , which is the proper equation to use to estimate cortical surface in a specimen in which brain weight or volume has been determined. To three significant figures, the equation is:

$$S = 3.749 E^{0.913} \quad (1)$$

Equation 1 enables us to assert that the human brain is less convoluted than one would expect for a mammalian brain of its size. In the analysis that leads to this conclusion, we first determine the relationship between cortical surface and convolutedness, and then we determine our place among the mammals with respect to expectations about convolutedness.

The relationship between surface area and convolutedness is based on the fact that the exponent in Eq. 1 is greater than  $2/3$ , which implies an orderly change in the shape of the cortex as a function of brain size. If there were no change in shape, the exponent would be  $2/3$ .<sup>1</sup>

The obtained exponent of 0.913 has a standard error of 0.0116; its 99 percent confidence limits are between 0.88 and 0.94—clearly greater than  $2/3$ . (The probability that the obtained exponent was sampled from a population with a true value of  $2/3$  is of the order of  $10^{-51}$ , or about one divided by the square root of a googol—my first encounter with the latter number outside of dictionaries and mathematical entertainments.) The change in the shape of the brain “between-species” as the brain becomes larger is toward more surface in larger brains, a change produced by the appearance of folds, or convolutions, in the surface. The first conclusion from figure 4 is, therefore, that as brains become larger they become more convoluted. The high correlation between surface and volume (log units) indicates that the relationship is very strong and that most of the differences among species in convolutedness are accounted for by the differences in brain size.

A brain would be more convoluted than expected if its surface area were more than that predicted by Eq. 1. We can, therefore, determine whether human brains are unusually convoluted by finding whether they exceed the prediction. My data are on 23 human brains from Brodmann (1913) and Elias and Schwartz (1971). Of these, four had more surface and 19 had less surface than one would

<sup>1</sup>For example, the surface-volume measures for all cubes are related by the exact equation,  $S = 6 V^{2/3}$ , and all spheres—whether the size of a golf ball or of the sun—by the equation  $S = 4.84 V^{2/3}$ .

expect from eq. 1. The expected division is, of course, 11.5 above and 11.5 below. A chi-squared test of the obtained versus the expected frequency yields chi-square = 9.78,  $df = 1$ ,  $p = 0.002$ . Thus, there is about 1 chance in 500 that my sample of human brains was from a population that was as convoluted as expected in the sample of mammal brains in figure 4. Not only are our brains not average in convolutedness, they are below par for mammals. But we are close to where we would be expected to be, given the size of our brains, so we needn't go into mourning.

We hardly need a statistical analysis of the dolphin brains described by Ridgway and Bronson (1984). This sample of 13 *Tursiops truncatus* brains is enclosed in the convex polygon labeled "dolphins" on figure 4. All 13 brains had more cortical surface than predicted by Eq. 1. They are clearly more convoluted than expected: chi-square = 13,  $df = 1$ ,  $p = 0.0003$ . The contrast between the human and dolphin brains in convolutedness is obvious and visible to the naked eye (fig. 8).

These departures from uniformity in brain organization are further clarified by more microscopic analysis. The human brain appears to be a normal primate brain with respect to most features of its organization. The number of neurons under a given area of neocortex is like that of other primates (Rockel et al., 1980), and we shall see shortly that it is a normal primate brain with respect to the sizes of other brain structures relative to the whole brain. Dolphin brains (and, very likely, other cetacean brains) are not like those of land mammals in this respect. The neocortex is thinner, its layers are less clearly defined, and it has only about 2/3 the number of neurons per unit surface area compared to that of land mammals (Garey and Leuba, 1966). Greater convolutedness in delphinids is more than made up for by the less dense packing of their neuronal material.

To conclude, the amount of surface area, and associated convolutedness of the brain in mammals seems to be determined primarily by brain size. (There are other important factors that cause the relationship, which are discussed by Rakic, 1988, and by Welker, 1990; the relationship in figure 4 may be thought of as describing the net effect of the causal factors.) If the neuron is the unit of processing, the processing capacity of a brain is, thus, estimated by

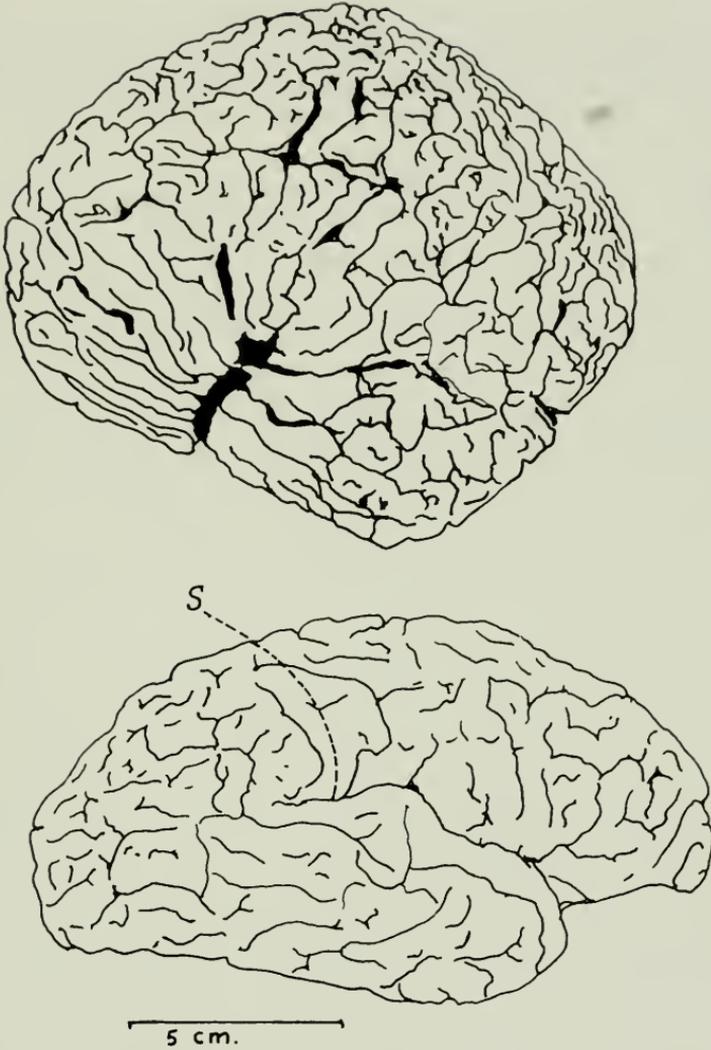


Fig. 8. Tracings of the fissural patterns in lateral aspects of neocortex in man and dolphin. Upper sketch, dolphin (*Tursiops truncatus*) left hemisphere. Lower sketch, human right hemisphere. (From a photograph by Dr. Sam H. Ridgway)

brain size, and this is the outstanding uniformity of organization revealed in this analysis. But even though almost all of the variance in surface area is accounted for by brain size, some of the small residual differences among species are significant. The most surprising of these, perhaps, is that the human brain is less convoluted

than average for mammals. Unless we agree to give up our place at the top of the tree as the wisest of creatures, this should be enough to quash forever the old canard that convolutedness is related to intelligence in animals.

### *Uniformity and Diversity: Forebrain and Cerebellum*

While preparing these notes for publication, I was browsing through a popular but important critique of computational analyses of mind by the physicist, Roger Penrose, and found the following statement about “real brains and model brains” (Penrose, 1989: 375):

The part [of the brain] that human beings feel that they should be proudest of is the cerebrum—for that is not only the largest part of the human brain, but it is also larger, in its proportion of the brain as a whole in *man* than in other animals. (The *cerebellum* is also larger in man than in most other animals.)

I think that this statement is pretty close to conventional wisdom about the human brain, and although it evidently passed the scrutiny of Penrose’s expert consultants in neurobiology, it is misleading where it isn’t wrong. The questions are of the kind that I am reviewing—about clues from the organization of the brain for our understanding of man’s place in nature, and I am pleased to correct Penrose. Is the “cerebrum” the largest part of the human brain? Is it disproportionately large relative to our brain as a whole? And how about the human cerebellum? It is easy to check quantitative relationships like these, and this is the issue that I address in this section.

First, an overview. The cerebrum, which could refer either to the cerebral cortex or to the entire forebrain, is indeed the largest part of the human brain, but it may be important to add that its size follows a single rule for all anthropoids as a proportion of the total brain size. Cerebral cortex accounts for about 40 percent, and forebrain accounts for about 75 percent of the brain’s volume in all anthropoid primates. There is nothing special to be proud of about the human brain in this respect. Our cerebrum is large but not disproportionately large. We are properly proportioned primates.

Like the cerebral cortex, the human cerebellum is also about the size one would expect given the total size of our brain (actually slightly too small relative to other orders, but right for anthropoids).

It accounts for about 10 percent of the brain, and this seems to be the case not only for primates but for all mammals. There is nothing special about the relative size of the human cerebellum. Of course, the human cerebral cortex, cerebellum, and forebrain are among the largest known, but they are very large because the whole human brain is very large, exceeded in size only by the brains of elephants and cetaceans. If we know the size of the whole brain, we can estimate with fair accuracy the size of the cerebellum in any mammalian species.

Now, the data. Stephan and his colleagues (Stephan et al., 1981) have published extensive data on the volume of the brain and many of its parts in 76 species of mammals, and I have reanalyzed and, in some instances, reinterpreted the data from the perspective of organization and reorganization of the brain. The data are on 26 species from the order Insectivora (shrews, moles, and hedgehogs), two Macroscelididae (elephant shrews), three Scandentia (tree shrews), and 45 Primates, of which 18 are from the suborder Prosimii (lemurlike species) and 27 from the suborder Anthropeidea; I have followed Carroll (1988) on nomenclature. I have separated the data on tree shrews in the graphs, but I followed Stephan et al. in treating the elephant shrews as insectivores (omitting them does not affect the results). The tree shrews, which Stephan had included among the primates, are evidently more like prosimians than like insectivores in the absolute and relative sizes of the brain and its parts.

In all of the analyses that I present here, I use either total brain weight or total body weight as the independent variable, since these can be estimated in fossil animals. I am concerned primarily with the pattern of relations of the parts of the brain to those independent variables.

Let us consider, first, the measures mentioned by Penrose. If the cerebrum is interpreted as forebrain it would include all of the cerebral cortex (neocortex, paleocortex, and archicortex, including hippocampus), the basal ganglia, and the diencephalon (thalamus, epithalamus, and hypothalamus). I exclude the olfactory bulbs by analogy with the exclusion of the retina of the eye (also brain tissue, embryologically) as an elaborate sense organ, though many authors would include these as well. The relationship between the volume

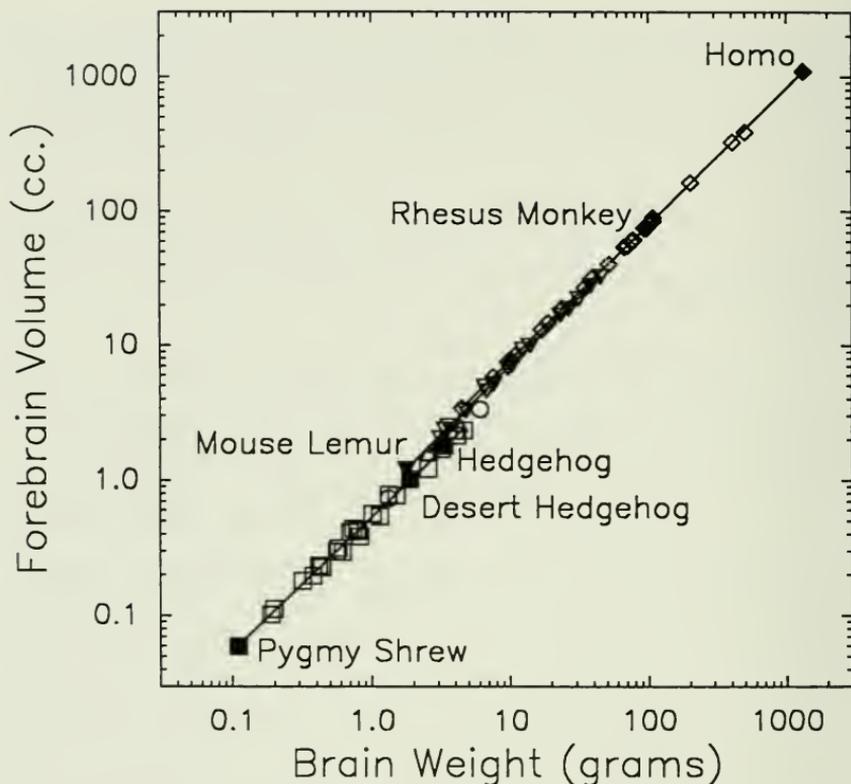


Fig. 9. Forebrain volume as a function of brain size in 76 species of mammals. ( $\square$ ), Insectivores; ( $\Delta$ ), tree shrews; ( $\circ$ ), elephant shrews; ( $\nabla$ ), prosimians; ( $\diamond$ ), anthropoids. Regression equations (assuming errors only in Y) and correlation coefficients: entire sample:  $Y = 0.56 X^{1.07}$ ,  $r = 0.999$ ; insectivores:  $Y = 0.53 X^{0.99}$ ,  $r = 0.998$ ; prosimians:  $Y = 0.66 X^{1.02}$ ,  $r = 0.999$ ; anthropoids:  $Y = 0.74 X^{1.01}$ ,  $r = 1.000$  ( $= 0.9999$ ). Species named on the graph are also identified by the filled data points. Data from Stephan et al. (1981).

of the forebrain, excluding olfactory bulbs, and that of the whole brain in 76 mammalian species is illustrated in figure 9.

Despite the very high correlation for the entire sample ( $r = 0.999$ , log data), the slope (exponent) of 1.07 is misleading. It implies that larger-brained species had disproportionately large forebrains because of a single rule about brain size, independent of taxonomic group. In fact, the slopes for each order or suborder were all approximately 1.0, indicating that within each group the forebrain was an approximately constant fraction of the whole brain. The coeffi-

cients tell us what that fraction is. For the higher primates (anthropoids) it is 0.74288 (rounded to 0.74 in the legend of the graph), and this is the basis for my statement earlier that forebrain is about 75 percent of the anthropoid brain.

The point representing human data lies on the line, indicating no positive deviation for us. We are "normal." To illustrate with the actual data, the human forebrain volume reported by Stephan et al. was 1094 cc. The volume estimated from the regression equation for higher primates (exponent = 1.01448; brain weight reported by Stephan et al. = 1330 g) is 1096 cc.

There are statistical lessons for us, comparable to our discovery that even a correlation of 1.00 (0.996 to three significant figures) as shown in figure 4 does not mean that deviations from the regression line, or norm, are not significant. The separate regression equations in figure 9 for insectivores, prosimians, and anthropoids are significantly different from the group regression. Small deviations may signify nonsignificant deviations from a norm, but they may also mean that there are real differences. For these data, the differences reflect the fact that the forebrain is an approximately constant fraction of the whole brain in the three groups for which we have significant amounts of data: 53 percent in insectivores, 66 percent in prosimians, and 74 percent in anthropoid primates, and these are clearly not trivial differences.

I separated the elephant shrews from insectivores in this graph, but you can see that the insectivore regression would account for the elephant shrew data, at least that for the largest specimen. In the remainder of the analysis I treat elephant shrews as insectivores.

The analysis of the size of the cerebellum in these species is presented in figure 10. As in figures 4 and 9, the main message about the cerebellum is the orderliness of its size in this group of mammals, although the pattern of size relationships is reversed. Insectivores seem to be a bit more cerebellarized, as it were, than prosimians, and the anthropoids are the poor relations. The meaning of the relationship is not obvious; cerebellar functions are traditionally thought of as related to motor control, and one might expect the very agile anthropoids to have at least as much cerebellum per unit brain size as the other groups. As one learns more about cerebellar

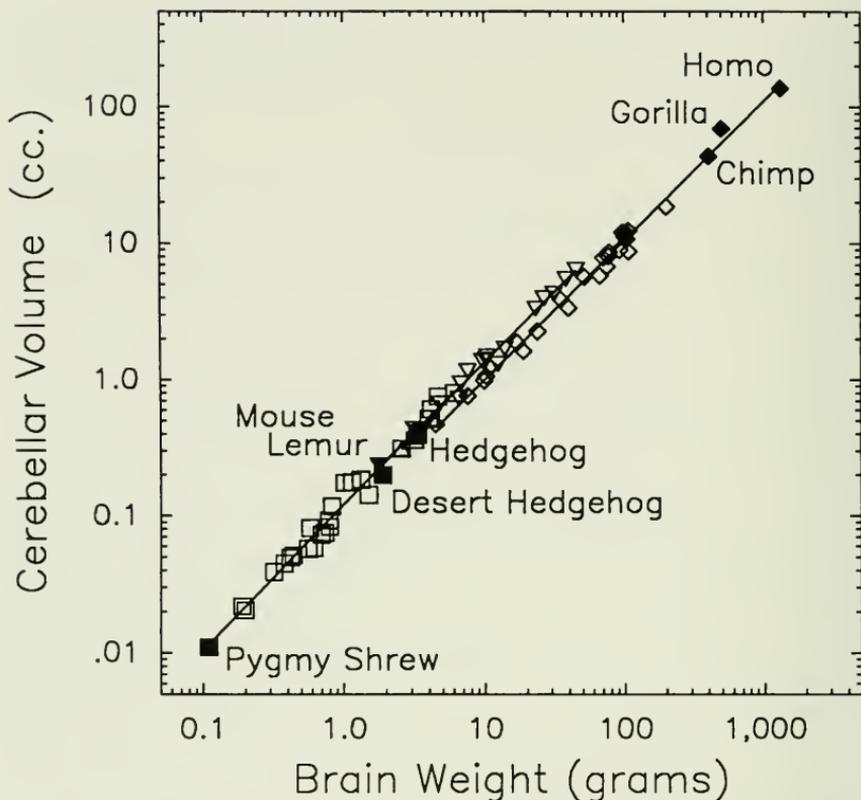


Fig. 10. Cerebellar volume as a function of brain size in 76 species of mammals. Symbols as in fig. 9, except that elephant shrews are treated as insectivores. Regression equations (assuming errors only in Y) and correlation coefficients: entire sample:  $Y = 0.12 X^{0.99}$ ,  $r = 0.997$ ; insectivores:  $Y = 0.12 X^{1.06}$ ,  $r = 0.991$ ; prosimians:  $Y = 0.12 X^{1.03}$ ,  $r = 0.995$ ; anthropoids:  $Y = 0.09 X^{1.02}$ ,  $r = 0.996$ . Data from Stephan et al. (1981).

functions that are involved in higher mental processes, this is doubly puzzling. But the facts are there in figure 10. We humans are not prize specimens, even among the higher primates, despite our handiness with tools. A little on the numbers: Stephan et al. report the human cerebellum as 137 cc in volume. In anthropoid primates the coefficients for the regression equation are 0.09521 and 1.0201, which would predict the human cerebellum to be 146 cc, so we are a bit less cerebellarized than expected for our group—not significantly low, but certainly not high.

There is a fairly simple explanation for the low “cerebellarization” of higher primates, which has to do more with brain specialization and total brain size than the contribution of the cerebellum to brain size. Anthropoids have unusually large brains for their body sizes—about twice as large as prosimians, for example, and five or six times as large as insectivores. This encephalization in anthropoids is probably related primarily to expanded visual functions and other brain functions in which the cerebellum is only marginally involved. Anthropoid primates are not undercerebellarized. Rather they are overvisualized, as it were, so their gross brain size is greater than one would expect, other things being equal. Using brain size as the independent variable to estimate the size of the cerebellum as a dependent variable is in this case misleading. A better independent variable would be a fraction of the total brain size that would exclude some of the encephalization component in gross brain size that is related to vision in anthropoids.

Although there exist, in principle, better estimators of the size of the cerebellum than total brain size, we should not lose sight of how good gross brain size is as an estimator. We need only keep in mind that the errors of estimation, though small, are not necessarily insignificant.

### *Uniformity and Diversity: Hippocampus and Olfactory Bulbs*

An analysis of the size of the hippocampus in different species is interesting in a different way from that of the more prominent structures. It is, first, a structure that will never be revealed in a fossil endocast, because it is entirely hidden under the mantle of other cortex, and it could be enlightening to determine the extent to which the size of hidden structures can be estimated from gross brain size. Second, the hippocampus may be an unusually important component of the brain in the control of “higher mental processes,” integrating information from other parts of the brain. As mentioned earlier, it is the brain structure most clearly implicated in memory, and yet it is “primitive” cortex rather than neocortex. Finally, the analysis is of a relatively small structure in the brain as estimated from the size of the whole brain, which stretches our notion of “first

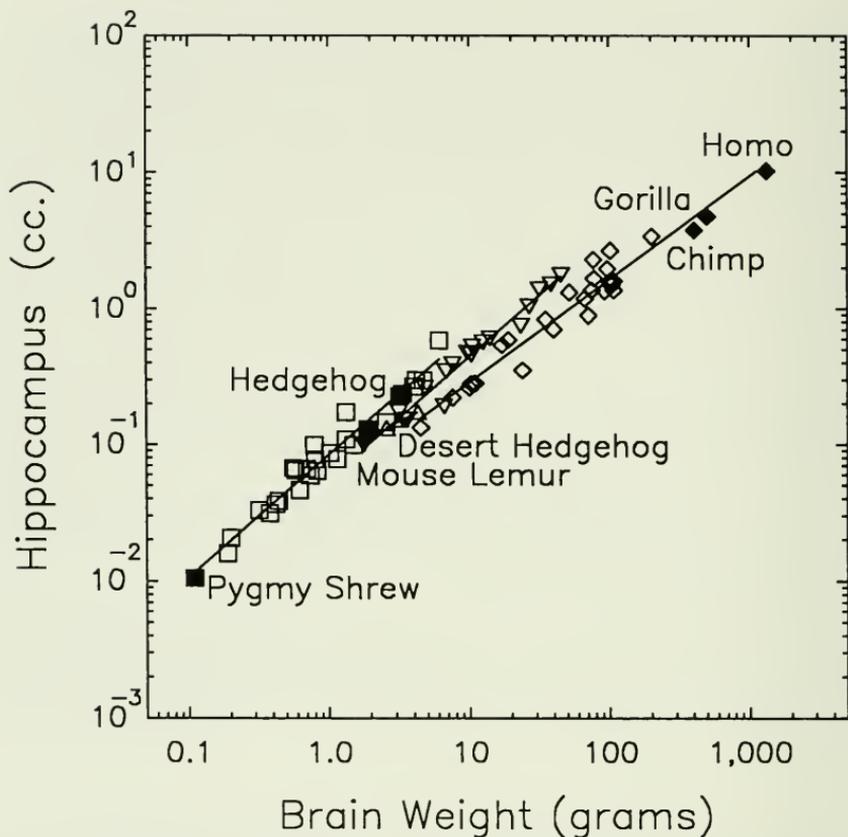


Fig. 11. Hippocampus volume as a function of brain size in 76 species of mammals. Symbols as in fig. 10. Regression equations (assuming errors only in Y) and correlation coefficients: entire sample:  $Y = 0.08 X^{0.69}$ ,  $r = 0.980$ ; insectivores:  $Y = 0.08 X^{0.90}$ ,  $r = 0.980$ ; prosimians:  $Y = 0.06 X^{0.90}$ ,  $r = 0.983$ ; anthropoids:  $Y = 0.05 X^{0.76}$ ,  $r = 0.974$ . Data from Stephan et al. (1981).

approximations.” The relationship of the size of the hippocampus to total brain size in our sample of 76 species of mammals is graphed in figure 11.

Although not quite as orderly as those seen earlier, the relationship is still an impressive demonstration of the uniformity of the structure of the brain in different species. It is clear that the hippocampus is not unusually large in humans, nor is it unusually small. Stephan et al. reported its volume as 10.3 cc, and the regression equation for anthropoids (coefficients: 0.05000, 0.75753) predicts a volume of

11.6 cc for a primate with a brain of human size. Most significantly, it is clear that the hippocampus is a fairly constant part of the brain in all of the species in our sample.

Other hidden brain structures, such as basal ganglia, provide more impressive evidence of the uniformities of brain structure across species. I chose to show hippocampus, because its place in the architecture of the brain is important for my analysis of the evolution of language. For that I will make old-fashioned statements about "olfactory brain," putting hippocampus in that category ("rhinencephalon") to help us think about olfaction in a particular evolutionary and behavioral context.

The second part of the morphometric analysis in this section is on the olfactory bulbs. I present it in connection with my view on language, and, incidentally, as an almost unique example of diversity of organization. Differences in the size of the olfactory bulbs are the best example that I can find of important differences in mammalian brain structures that are visible on endocasts, and you can think of the next graph as a relief from the dreary uniformity that we have encountered thus far. The results are pleasingly chaotic, but not too hard to analyze. The data are mainly from Stephan et al. (1981) as in the previous illustrations, but since I will also be concerned with olfaction in carnivores for my analysis of the origins of language, I have added a few points that I had determined on the endocasts of six carnivores (Jerison, 1973: table 11.3). The full data set is in figure 12.

The outstanding features of the graph are, first, the unusual decrease in relative size of the olfactory bulbs in anthropoids, and second, the appropriateness of the insectivore regression for characterizing carnivore data. Insectivores seem to represent a mammalian norm in olfactory capacities, and the primate condition should evidently be viewed as a specialized adaptation involving reduced olfactory representation and function. I have no explanation for this primate specialization, but the fossil record of the brain as revealed in endocasts is that olfaction was already reduced in Miocene anthropoids, more than 15 mya, but not in the one Oligocene anthropoid endocast that is known. Reduced olfactory bulbs appear to be a primitive shared trait for the living species of monkeys, apes, and

*Homo sapiens*. Living humans are unusually poorly endowed in this regard, even when compared with most other living anthropoids.

In our evolutionary history as anthropoids, although the olfactory bulbs became much reduced, the hippocampus evidently remained relatively normal in size. Having normal hippocampus but reduced olfactory bulbs implies a differentiation of "olfactory" functions, in which information from the external world, mediated by the olfactory bulbs, is attenuated, although further processing of *that kind of information* by the more central structure, that is, the hippocampus, remains normal. For my speculations on the origin of language, the central issue is on the kind of information that the earliest hominids needed for their way of life and the extent to which it was of the type that normally involved a significant olfactory dimension for information about the external world.

#### *Uniformity and Diversity in Brain Organization: Conclusions*

With the exception of the relative size of the olfactory bulbs, the brain's gross structural organization appears to be remarkably uniform across species of mammals. In analyzing organization, however, the problem is to avoid mistaking these uniformities for identities. It evidently requires relatively small changes in the quantitative measurements that I have reported to support major differences among species in neural control. This must be the case, because there are major differences in behavior patterns among all of the species that provided the data for this section. There must be correlated differences in their nervous systems, which are not detected in my analysis. Since this is the kind of analysis that can be applied to fossil data, it is clear that many behavioral differences will simply not be available for analysis from the data on fossil brains. But do not despair. In the next section I will describe a class of differences, measured as "encephalization," which are eminently analyzable.

The uniformities appear as first approximations in our analysis, and we should appreciate the differences among levels of approximation. For example, according to our data (fig. 9), the first approximation represented by fitting a single straight line to the data implies that the forebrain fraction of the brain increases as the brain

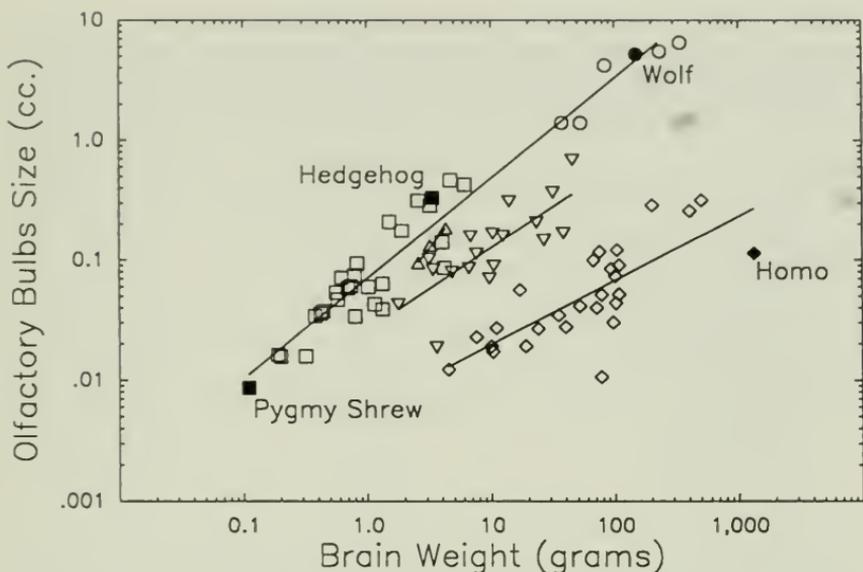


Fig. 12. Volume of the olfactory bulb as a function of brain size in 82 species of mammals. (O). Carnivores; other symbols as in fig. 10. Some statistics: insectivore regression:  $Y = 0.07 X^{0.91}$ ,  $r = 0.903$ ; combined insectivore + carnivore regression:  $Y = 0.07 X^{0.84}$ ,  $r = 0.971$ . Correlations, all data,  $r = 0.291$ ; prosimians  $r = 0.783$ ; anthropoids  $r = 0.768$ . Data from Jerison (1973) and Stephan et al. (1981).

becomes larger (the meaning of the exponent of  $1.07 > 1.00$ ). It is only with the help of a more detailed analysis, performed separately on different groups of species, that we recognize that the first approximation is probably misleading. The fundamental fact that underlies the approximation appears to be that within particular groups of species, the forebrain is a fixed fraction of the brain size, but the fraction happens to be largest in our larger-brained primate species (Anthropoidea), intermediate in our smaller brained primates (Prosimiae), and smallest in our very small brained insectivore species. Fitting a single line to our entire sample results in a steeper slope "between-groups" than is present within each of the subsamples.

To suggest a comprehensive view of these relationships, I present a multivariate analysis, a "principal components" factor analysis of 12 morphological variables (logarithmic data) listed in table 1. The data are on the same 76 species from Stephan et al. (1981). The factor analysis was performed with the factor program in SYSTAT (Wilkinson, 1989).

TABLE 1  
**Factor Loadings and Percent Variance Explained by Two Principal Components (Factors) in Brain and Body in 76 Species of Mammals**

	Factor 1	Factor 2
	(General brain size)	(Olfactory bulbs)
Neocortex	0.991	0.059
Total brain weight	0.989	0.137
Diencephalon	0.987	0.144
Basal ganglia	0.987	0.133
Cerebellum	0.983	0.168
Mesencephalon	0.972	0.196
Medulla	0.966	0.224
Hippocampus	0.962	0.239
Schizocortex	0.954	0.274
Body weight	0.939	0.285
Piriform lobe	0.899	0.399
Olfactory bulbs	0.157	0.985
Percent total variance	85.855	12.668

Note: Varimax rotation. Data from Stephan et al. (1981).

Although this is stretching the analysis a bit, I will discuss the factors in table 1 as if they were fundamental causal variables, which are represented to different extents in the brains of the different species. From this perspective, almost all of the variance (98.5 percent) in the data summarized in table 1 is "explained" by just two factors. The first of these, accounting for 85.8 percent of the variance, can be described as a general brain size factor. It is represented most strongly in the amount of neocortex, but almost as strongly in total brain weight. It is a "general" factor in the sense that it is strongly represented in all of the brain structures, with the exception of the olfactory bulbs, and also in body weight. This corresponds to the general impression from the analyses in the previous sections that the parts of the brain hang together rather well, and when one part is enlarged the rest of the brain tends to be enlarged as well.

The second factor, accounting for 12.7 percent of the variance, is an olfactory bulb factor. It is represented primarily by the olfactory bulbs, with a modest representation in the parts of the brain that are classic "rhinencephalon" (piriform lobes, schizocortex, and hippocampus) and in body weight.

We can think quantitatively about each of the structures by asking what fraction of their variance is accounted for by each factor. The fraction is the square of the factor loading. Thus factor 1 accounted for 98.2 percent of the variance ( $0.991^2$ ) in neocortex across the 76 species, and factor 2 accounted for essentially none (0.3 percent). The remaining 1.5 percent of neocortex variance is in residual factors, which we may think of as error factors. Factor 1 accounted for 79 percent or more of the variance in the other brain structures, with the exception of the olfactory bulbs (2.5 percent). Factor 2 accounted for 97 percent of the variance in olfactory bulbs, hence my naming it an olfactory bulb factor. This factor accounted for between 5.7 and 15.9 percent of the variance in the other rhinencephalic structures.

The general conclusion about the organization of the brain is that it is orderly enough to justify the use of gross brain size as a kind of statistic to estimate the sizes of other parts of the brain, excepting only the olfactory bulbs. We have seen from figure 4, and the discussion of uniformity in the corpus callosum and elsewhere, that brain size estimates the total information processing capacity of the brain in a species. Its efficiency as a statistic for estimating the size of the parts of the brain implies that the partitioning of processing capacity is relatively uniform in different species. Brain size, thus, estimates both processing capacity and the organization of processing capacity. Small (residual) departures from estimated capacity can be significant. Nevertheless, as a first approximation, it is clearly the case that if we know how large a mammalian brain is we know its processing capacity and can make reasonable guesses about its organization.

## ALLOMETRY AND ENCEPHALIZATION

The analysis that I just discussed tells us what to expect of a brain if we know its size. The analysis that I present now is of brain-body relations. It tells us in a very general way why brains are as large as they are. It also provides a statistical knife, as it were, for dissecting the brain. The "cut" is into two components, distinguished conceptually but not anatomically (Jerison, 1977, 1985a). One component

may be thought of as involved primarily in the control of general bodily functions (an allometric component from brain-body allometry). The second can be identified with higher mental processes, or mind—or at the very least with neural control not related to body size (an encephalization component). Such an analysis of brain-body relations provides a quantitative framework that can be applied to the fossil evidence on the evolution of the brain.

The main factor determining brain size in mammalian species is body size, and an allometric equation describes this basic relationship. Deviations from allometry represent degrees of encephalization. The usual modern approach to allometry is to fit a straight line to the logarithms of body and brain sizes in a sample of species. The equation of the line is the brain-body allometric equation. The most common measure of encephalization, the “encephalization quotient” EQ (Jerison, 1973), is the ratio of actual brain size to expected brain size when expected brain size is estimated by the allometric equation. In statistical language, the quotient is a “residual” computed from the regression of log brain size on log body size. In large samples of mammalian species, about 90 percent of the variance in brain size is “explained” by body size and about 10 percent by encephalization. The analysis is “between-species.” Encephalization is a character of a species; it is usually meaningless to discuss differences within a species in encephalization.

Allometry and encephalization do not have to be defined by regression equations or residuals, but most of the recent work on brain evolution involving brain-body allometry uses this approach, which might be called “parametric,” since it involves the estimation of the parameters of a normal probability distribution. Although I rely on a nonparametric analysis in much of my evolutionary analysis, I will begin with an analysis and critique of this parametric quantification (cf., Deacon, 1990; Harvey, 1988; Hofman, 1989; Martin, 1983; Pagel and Harvey, 1988, 1989), because it is the source of many insights, a few problems, and some interesting controversy. As in the last graphs, I begin with data from Stephan et al. (1981).

The work by Stephan’s group is especially relevant for evolutionary analysis because of the species they used. They worked with insectivores to represent a primitive grade of brain evolution and

to provide an evolutionary perspective on the human brain. We now recognize that the issues are more complex (Cracraft and Eldredge, 1979; Patterson, 1987), but insectivores appear to be a reasonable if not ideal model for the base group from which most placental species evolved (Johnson et al., 1982). They resemble the earliest mammals both skeletally (Savage and Long, 1986) and in their endocasts (Jerison, 1990; Kielan-Jaworowska, 1986). Although primates are presently a highly encephalized order of mammals, they are also a very ancient order, probably derived during the late Cretaceous period from a species comparable to living insectivores or tree shrews. Comparisons between insectivores and primates are, thus, very appropriate for our topic.

### *Allometry and Encephalization in Insectivores and Primates*

The quantification of encephalization in insectivores and primates is summarized in figure 13A–D. In contrast with the previous graphs, brain size is now treated as the dependent variable, and body size is the independent variable. The four graphs present the same data, fitted in different ways, to illustrate several parametric approaches. As in most of the previous graphs, the fits by regression analysis shown in figures 13A and 13B are remarkably good. The separate fits to insectivores and the two groups of primates and the fit to the entire sample of 76 species are equally good, all supported by correlations of at least 0.96. It is also clear by inspection that the three species of tree shrews are at a prosimian rather than insectivore grade of encephalization; elephant shrews are at an insectivore grade.

The fact of encephalization is evident in the vertical displacement of the lines that are fitted to the three groups (figure 13A), but we cannot compare the groups quantitatively, because both the slopes and intercepts are different, although, again by inspection, we can recognize the qualitative difference. Fitting a single line to all of the data (figure 13B) is faulty for the same reason as in figure 9; the slope of 0.91 is an obvious artifact of small body size in the sample of small-brained insectivores and larger body size in the sample of large-brained anthropoids.

For quantitative comparisons of the groups, we can force the lines

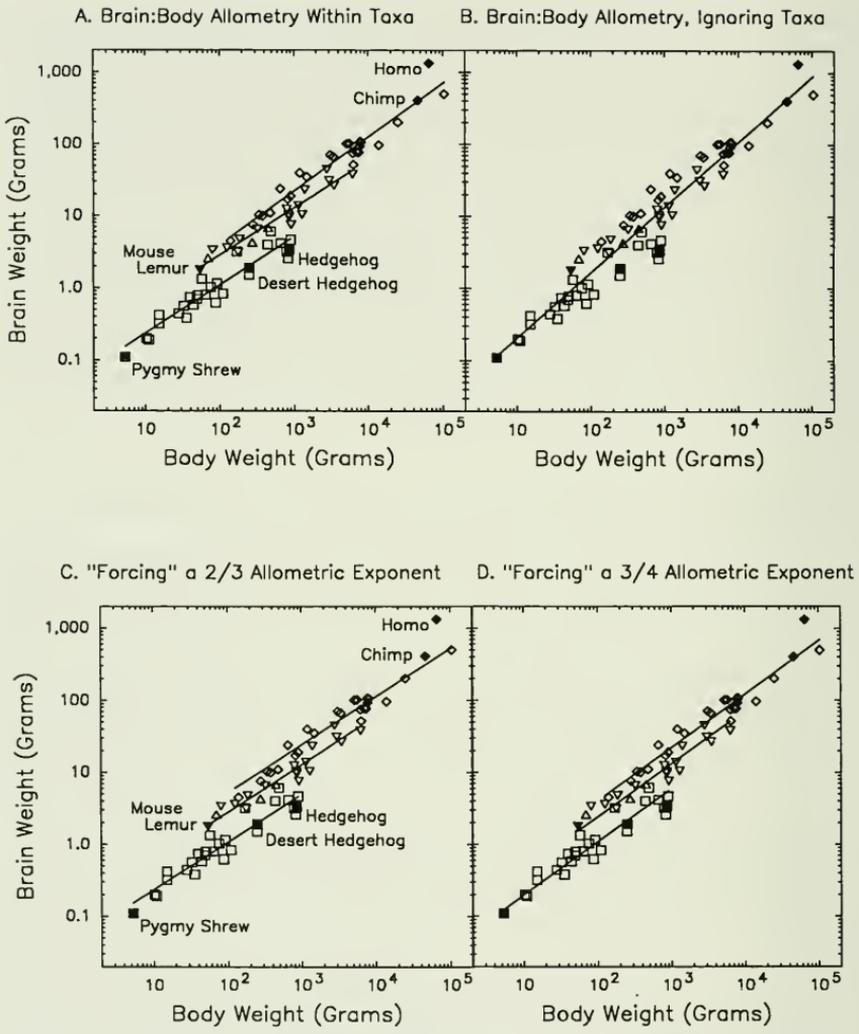


Fig. 13. Brain size as a function of body size in 76 species of mammals, symbols as in fig. 10. Data from Stephan et al. (1981). The graphs indicate several different ways of describing the data with regression equations. Fitted regression equations (assuming errors only in Y) and correlation coefficients for the separate taxa (fig. 13A): insectivores:  $Y = 0.05 X^{0.67}$ ,  $r = 0.946$ ; prosimians:  $Y = 0.14 X^{0.66}$ ,  $r = 0.960$ ; anthropoids:  $Y = 0.13 X^{0.75}$ ,  $r = 0.972$ . For the entire sample, lumping the taxa (fig. 13B):  $Y = 0.05 X^{0.91}$ ,  $r = 0.966$ . "Forced" regressions (figs. 13C and 13D) are drawn through the centroids of the taxa, with exponents (slopes) of 2/3 and 3/4. At 2/3, intercepts (proportional to EQ) are 0.05, 0.06, 0.12, 0.13, and 0.24 for insectivores, water shrews, tree shrews, prosimians, and anthropoids, respectively. At 3/4, intercepts are 0.03, 0.04, 0.077, 0.074, and 0.12. The effect on EQ estimates is trivial.

to have equal slopes (exponents), and I show this in figures 13C and 13D, in which parallel lines are drawn through the centroids (geometric means) of each group. The lines are at slopes of  $2/3$  and  $3/4$ , the slopes that have been discussed and analyzed during the past two decades.

Let me first contrast these results with those of figure 9, above, in which the same groups were compared with respect to the amount of forebrain per unit brain size. In that illustration we saw that the forebrain becomes a somewhat larger fraction of the brain in the insectivore-prosimian-anthropoid "progression," with an increase of about 10 percent per grade. In the graphs of figure 13, we can see an approximate doubling in relative brain size (encephalization) in the same series. Figure 13 shows that the available amount of information processing capacity per unit body size increased; figure 9 shows how that increase affected the way in which information processing capacity was organized. There was reorganization by changing the "investment" in capacity handled by forebrain as opposed to the rest of the brain. Investing in forebrain is not necessarily a more efficient way to handle information, although it implies an increased investment in "higher" functions that are typically forebrain functions.

The quantitative relations show that only a relatively small part of the additional capacity was invested in the forebrain and in the functions that it controls. (Doubling brain size corresponded to only a 10 percent rise in forebrain size.) At a given size, whether determined by allometry or encephalization, the brain tends to be organized in the same way. To illustrate, I will compare an insectivore and a prosimian that have brains similar in size. Our 250 g desert hedgehog (*Hemiechinus*) had a 1.9 g brain. If the 54 g mouse lemur (*Microcebus*) were an insectivore rather than a prosimian, we would expect its brain to weigh only 0.7 g, but, in fact its brain weighed 1.8 g. In this case our primate was a bit more than twice as encephalized as an insectivore of its body size. Is the fact that brain size in the desert hedgehog is explained by allometry and in the lemur by encephalization reflected in the organization of their brains with respect to the size of the forebrain? The actual volume of the desert hedgehog's forebrain was 1.22 cc; the mouse lemur's forebrain was

1.20 cc. This is an example of how little it can matter for a brain's organization whether its size was determined by the allometric correlation with body size or was a result of encephalization.

### *The Allometric Exponent*

We have seen in figure 13 that to compare species or groups of species with respect to encephalization we must specify a single exponent for the allometric equation. On log-log coordinates that exponent is a slope, and we must use the same slope for all the subsets to obtain a set of parallel lines that are separated by amounts of encephalization. There has been a good deal of discussion in recent years about the correct value for the exponent (e.g., Hofman, 1989; Martin, 1983), which rejects the  $2/3$  exponent used for many years (Snell, 1891; von Bonin, 1937; Jerison, 1973), and accepts instead a value of  $3/4$ , determined empirically by regression analysis on large samples of mammals (Eisenberg, 1981; Martin, 1981). In most instances the choice of  $2/3$  or  $3/4$  has very little effect on the analysis of encephalization, and this is illustrated in the relations between the "forced" intercepts in figure 13. The groups differ by about a factor of about 2 with either exponent.

The choice of exponent is important primarily for theoretical analysis. If the exponent is  $3/4$ , an implied surface-volume relationship that can be related to the brain's function in mapping may not be supported. Mapping involves converting information about volumes into information about surfaces, and the  $2/3$  exponent has a place in such conversions (Jerison, 1977). There is no theoretical explanation for a  $3/4$  exponent, but that is the empirical allometric exponent in the function that relates basal metabolic rate to body size (Kleiber, 1947). This suggests a metabolic determinant of brain size in mammals, although that is subject to other criticisms (McNab and Eisenberg, 1989).

There is a clue in the graphs in figures 9 and 13 on the meaning of a "true" exponent and on a correct way to use exponents for theoretical analyses. If "true" refers to an empirical result for the largest available sample, we would have concluded from figure 9 that the true exponent for forebrain-whole brain relations was 1.07.

The evidence from the subsamples, however, seems compelling that an exponent of almost exactly 1.0 represents the situation more correctly. The difference is that with an exponent of 1.07 we would conclude that it makes no difference if the brain is from an insectivore or primate, and that there is a general trend, independent of taxonomy, for larger brains to have somewhat more forebrain than do smaller brains. If we take 1.0 as the true exponent, it means that there is a pattern of brain organization within each taxon such that the forebrain is always a constant fraction of the whole brain. The groups would then be differentiated, and the basis would be (partly) the value of that fraction. We would conclude that insectivores have relatively less forebrain than prosimians and that prosimians have relatively less than anthropoids.

The two possible conclusions from the data of figure 9 can be thought of as hypotheses about factors determining the organization of the brain. There is nothing in figure 9 to suggest that one or the other hypothesis is better, although our insights as biologists may incline us to prefer the exponent of 1.0 because of its simple implications for how the size of the forebrain is determined. The line of reasoning is that a fixed-fraction adaptation is part of the mammalian bodyplan, and that natural selection conserves that body plan while modifying a growth factor in different groups to change the fate of the forebrain fraction. The modification would be involved in the transformation of an insectivore species into a prosimian and a prosimian species into an anthropoid. Such transformations are consistent with our knowledge of evolutionary history, about the ancestry and relations of these groups.

In the analysis of encephalization in figure 13, we would have to propose an allometric exponent of 0.91 (fig. 13B), were we to take sample size as the criterion for acceptability. As in figure 9, there would be no reason to support exponents of 0.65, 0.66, or 0.75 (the subgroup exponents) as more fundamental on statistical grounds, although they are closer to the consensus about a "true" exponent.

In my view a "true" exponent should be a theoretical value, based on a theory of brain size (see Jerison, 1977), and all empirical exponents should be related to the theoretical value. I continue to support the choice of a value of  $2/3$  as a didactic device to emphasize

TABLE 2  
**Factor Loadings and Percent Variance Explained for Brain and Body by Three Principal Components (Factors) in 76 Species of Mammals (in Order of Loading on Factor 3)**

	Factor 1	Factor 2	Factor 3
	(Allometric size)	(Olfactory bulbs)	(Encephalization)
EQ (re 2/3 exponent)	0.540	-0.084	0.837
Total brain weight	0.919	0.129	0.369
Neocortex	0.922	0.051	0.366
Basal ganglia	0.924	0.124	0.349
Cerebellum	0.922	0.157	0.346
Piriform lobe	0.836	0.394	0.343
Diencephalon	0.931	0.132	0.330
Mesencephalon	0.918	0.185	0.326
Hippocampus	0.920	0.224	0.294
Schizocortex	0.912	0.259	0.294
Medulla	0.932	0.206	0.276
Total body weight	0.925	0.261	0.217
Olfactory bulbs	0.196	0.978	-0.042
Percent total variance	73.391	11.207	14.173

Note: Varimax rotation. Data from Stephan et al. (1981).

mapping. It can be shown that if 2/3 is fundamental, empirical values such as 3/4 should be found in empirical analyses of large samples of mammals (Jerison, 1985b), but this is not necessarily the best value to use for the analysis of encephalization. The issue is related to the evolution of mind only because the quantitative estimation of encephalization is as a residual relative to an allometric estimation of expected brain size, and for that estimation the only real requirement is that a single exponent be used, because otherwise a residual would be meaningless.

### *Encephalization Quotients*

To present the relationship between encephalization and the component structures of the brain I performed a multivariate analysis of the same kind as in table 1, but added an encephalization quotient to the variates in the analysis. Encephalization in a species was measured as its typical brain size divided by the term,  $0.12 P^{2/3}$ ,

where  $P$  is body size in grams. The results, using an exponent of  $2/3$  for computing all EQs, are summarized in table 2. (Essentially the same results are obtained with a  $3/4$  exponent and a multiplier of 0.055.)

We must keep in mind that EQ is a residual, and the correlation coefficient,  $r = 0.966$ , between log brain and log body size in our sample of 76 species (fig. 13) indicates that EQ would account for less than 8 percent of the variance in brain size if it were taken with respect to the "best-fitting" slope of 0.91. It accounts for a bit more when the residuals are with respect to the slope of  $2/3$ , but most of the variance would still be attributed to the allometric effect, that is, the correlation with body size. From table 1 we might, therefore, have guessed that about 10 percent of the general brain size variance and 10 percent of the olfactory bulb variance would be partitioned out when we removed the "residual" variance of encephalization. Table 2 shows that the encephalization variance was created only from the general brain size component of table 1. The 86 percent of variance analyzed in table 1 as related to brain size is reduced to 73 percent in table 2, with 14 percent of the variance associated with encephalization. It is appropriate, therefore, to call the first factor an allometric size factor, which would represent the allometric component of brain size. Note that the loadings for brain size and body size are almost identical, as one would expect for such a factor.

The fraction of variance identified with the olfactory bulbs remained about the same at a bit over 10 percent, and was independent of encephalization and of allometry. We could have anticipated this from the appearance of figure 12; it should be interpreted primarily as reflecting our unusual sample of species, in which the size of the olfactory bulbs was determined more by taxonomic status than anything else, because of the heavy sampling of anthropoids. Had we used more "normal" orders of mammals (e.g., carnivores and ungulates), it is likely that the olfactory bulbs would have had a significant loading on the allometric size factor. But in no case would we expect the size of the olfactory bulbs to be related to encephalization (Jerison, 1990).

Uniformity of organization is evident in table 2 in the similar pattern of loadings for the brain structures (not EQ) on both factors

1 and 3. The effect of encephalization was similar for all of the parts of the brain with the exception of the olfactory bulbs. It is represented most strongly in the measure of neocortex (as expected), but it is represented in every other part of the brain proper. The result also indicates that bivariate graphs involving either brain or body on the abscissa and a part of the brain other than the olfactory bulbs on the ordinate will resemble figure 9. More can be said about multivariate analysis, but that can be left for another occasion.

## EVOLUTION OF ENCEPHALIZATION

When species differ in brain size and are similar in body size, we define the difference as encephalization. Since encephalization is a fraction of gross brain size, it represents the fraction of processing capacity that is not determined by body size. Although I have not developed the theory here (see Jerison, 1977; 1985b), most differences in encephalization should be attributed to differences in the extent of mapping in the brain.

We can recognize encephalization in graphs of brain and body data that present clouds of points of brain and body sizes in different species (see fig. 14). We do not really need the regression lines in figure 13 to recognize anthropoids as more encephalized than prosimians and both primate suborders as more encephalized than insectivores. The analysis of encephalization can be pictorial and not numerical.

My remaining analysis does not depend on computed regression coefficients or encephalization quotients. I rely on graphic rather than numerical methods to summarize the data. It is possible to compute the numbers, but I prefer not to, because an array of numbers implies precise knowledge that is not really available for these data. I will graph the patterns of encephalization in living vertebrates, and the graphs will be the background against which to view the fossil evidence on the evolution of the brain.

With the exception of human data, each of the 200 or so points in figure 14 represents a single living species; the data are from Quiring (1950) and the graph is from my book (Jerison, 1973). The human data are on 42 men and the entire range is framed by the

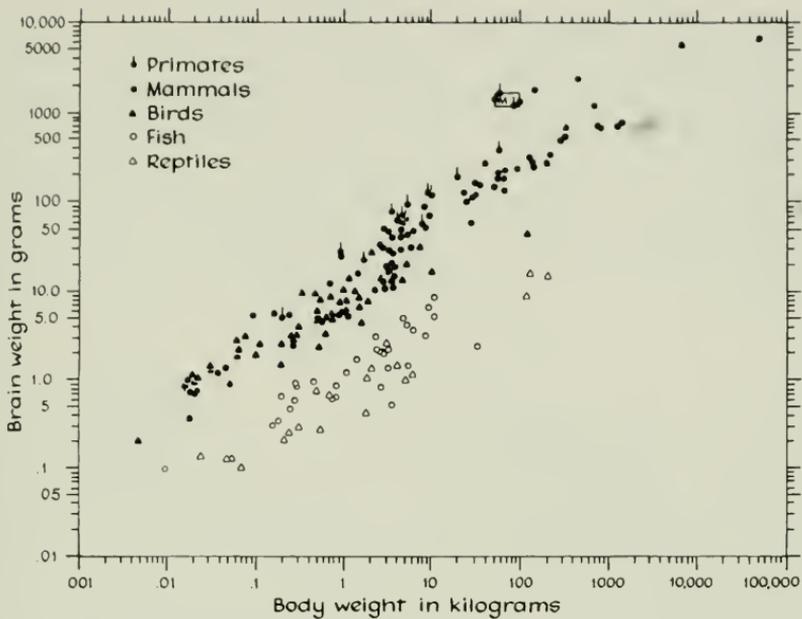


Fig. 14. Brain weights and body weights in 198 species of vertebrates, graphed on logarithmic coordinates. (Data from Quiring, 1950, graph from Jerison, 1973, reprinted by permission)

rectangle marked M. As you can see, the variability within our species, notorious as it is reputed to be, is small and unimpressive when seen against the background of the other data. The size of the data points in other species can represent within-species variability.

There are two outstanding regularities in the graph. The first is the angular orientation of the clouds of points for the classes of vertebrates, which is the graphic representation of brain-body allometry. The second effect is the separation of the clouds of points of birds and mammals on the one hand and of reptiles and bony fish on the other. That vertical separation represents encephalization. Allometry and encephalization are thus represented graphically, without further “parametric” or numerical analysis.

The size of brain and body of each species graphed in figure 14 can be thought of as a response by natural selection to the diversity of the environmental niches to which species became adapted. A graphed point would be a qualitative measure of the response, and

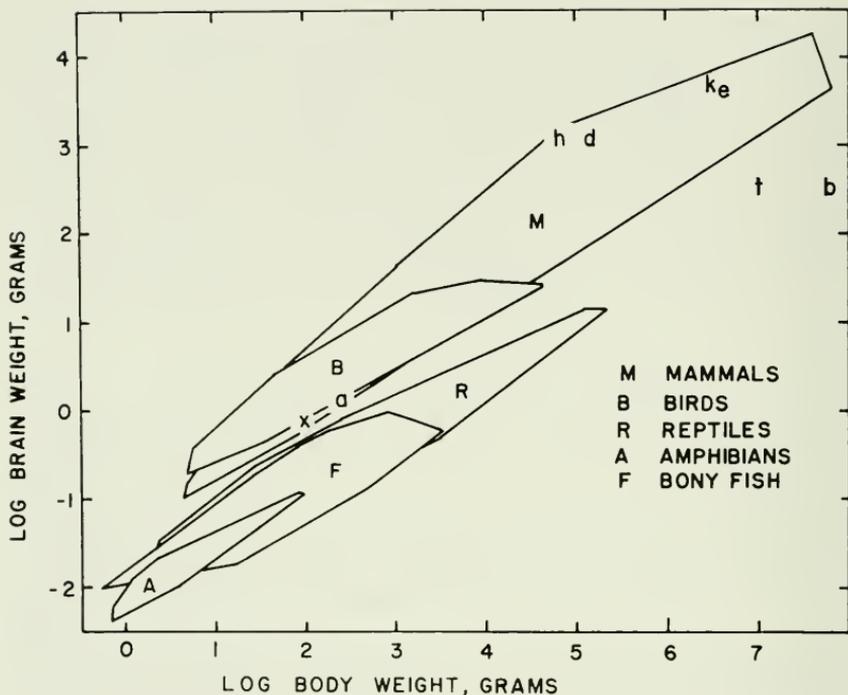


Fig. 15. Brain-body relations in 623 living vertebrate species enclosed in minimum convex polygons. The samples are 309 mammals, 180 birds, 46 bony fish, 40 amphibians, and 48 reptiles. Additional data are: *d*, *Tursiops truncatus* (bottle nose dolphin); *e*, elephant; *h*, humans; *k*, *Orcinus orca* (killer whale), two dinosaurs (*t*, *Tyrannosaurus*, *b*, *Brachiosaurus*); *x*, the 150-million year old mammal, *Triconodon*, and *a*, the early bird, *Archaeopteryx*. (From Jerison, 1987, reprinted by permission)

the regions in this adaptive "brain-body space" occupied by each class of vertebrates represents the range of responses to evolutionary opportunities that have taken place in that group. We may visualize these effects most clearly, without curve-fitting, by drawing convex polygons about appropriate sets of points. I present such polygons in figure 15 from a larger data set (Jerison, 1987).

The polygons in figure 15 are regions in brain-body "space," and they describe regions of realized evolutionary opportunities at the present time. All living mammals are within the mammalian polygon, birds within the bird polygon, and so on. To anticipate the addition of a time dimension to this evolutionary view, I have added points representing fossil species: two dinosaurs, *Tyrannosaurus* and

*Brachiosaurus*, the earliest bird, *Archaeopteryx*, and the earliest mammal on which we have evidence of the brain, the upper Jurassic *Triconodon*. I have also indicated some well-known living mammalian points: humans, dolphins, killer whales, and elephants. As you may guess, the largest and smallest birds in the sample are an ostrich and a hummingbird. The largest mammal is a blue whale, and the smallest is the pygmy shrew. I will now consider some of the fossil evidence on the evolution of the brain in the context of these polygons.

### *Dinosaur Brains*

To illustrate the data and the very simple method, I begin with the always fascinating dinosaurs, and I analyze their evolution as a problem in brain evolution. The essence of the analysis was in figure 15, in the minimum convex polygon that enclosed the available data on living reptiles and the two points added for *Tyrannosaurus* and *Brachiosaurus*. The scientific issue is: Did dinosaurs become extinct because of their small (“walnut-sized”) brains? This old saw of popular science can be analyzed by first answering a related question: Did dinosaurs have small brains? I had asked a similar question at the beginning of this lecture, about the 35 million year old fossil mammal, *Bathogenys reevesi*, and answered by comparing the brain of *Bathogenys* with that of living domestic cats, which were probably about the same body size. The answer for *Bathogenys* was “Yes, it was small-brained, at least when compared with cats.” The problem with dinosaurs is that there are no living reptiles in the size range of those graphed in figure 15, and we have to control for body size by performing an allometric analysis. But we do not need a regression analysis. It will be enough to use the allometry evident in the orientation of the convex polygons.

We answer by examining the appearance of reptile polygons with and without dinosaurs. Hopson (1977) published the polygons of figure 16. He showed the effect of adding dinosaur data to the polygon for living reptiles; we can ignore the “regression line” at slope 2/3 through that polygon. As you can see, adding dinosaurs extended the living reptile polygon to include larger body sizes but did not

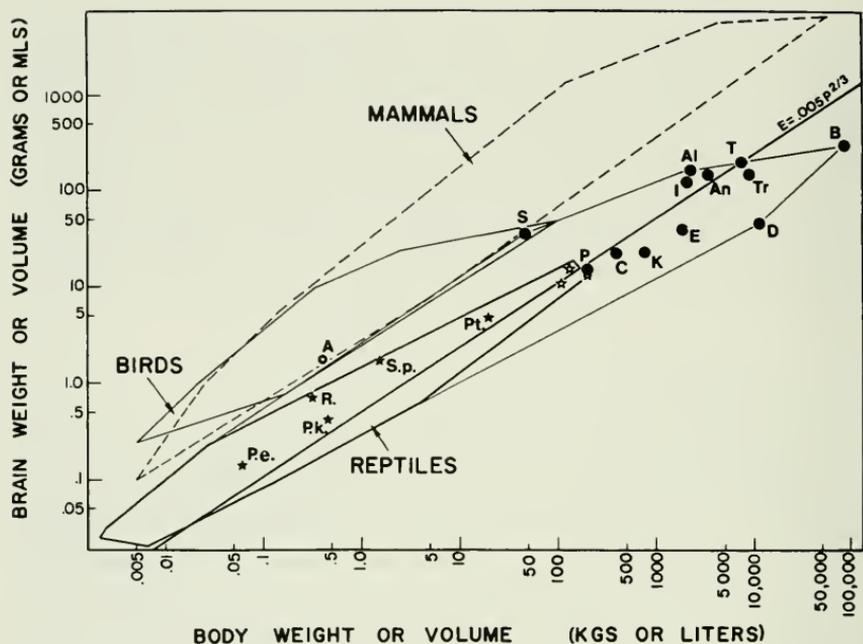


Fig. 16. Fossil reptile data added to mammalian, avian, and reptilian brain-body polygons. (A., *Archaeopteryx*, the earliest bird.)

Pterosaurs (★): P.e., *Pterodactylus elegans*; P.k., *Pterodactylus kochi*; Pt., *Pteranodon* sp.; R., *Rhamphorynchus*; S.p., *Scaphognathus purdoni*.

Dinosaurs (●): Carnosaurs: Al, *Allosaurus*; T, *Tyrannosaurus*. Coelosaur: S, *Stenonychosaurus*. Sauropods: B, *Brachiosaurus*; D, *Diplodocus*. Ornithopods: An, *Anatosaurus*, C, *Camptosaurus*, I, *Iguanodon*. Ankylosaur: E, *Euplocephalus*. Stegosaur: K, *Kentrosaurus*. Ceratopsians: P, *Protoceratops*; T, *Triceratops*. (From Hopson, 1977, reprinted by permission)

affect its orientation, and it altered its shape only slightly. The lower brain-size margin of the reptilian polygon remained the same, but its upper limits became somewhat higher, reaching the lower avian and mammalian limits. This is attributable to the recently reported datum on the ostrich-like dinosaur *Stenonychosaurus* (Russell, 1972), which appears to have been comparable in brain and body size to living ostriches.

With this simple procedure we have our answers: Dinosaurs were at least normal reptiles with respect to brain size. If they were distinguished in this respect, it was that some species had evolved unusually *large* brains, and these species were at a low avian, almost

mammalian, grade of encephalization. Since much less encephalized reptiles survive, we answer our main question: We cannot attribute the dinosaurs' extinctions to their "walnut-sized" brains. We have not asked, but we can nevertheless add: since dinosaurs were reptiles, from a mammal's perspective dinosaur brains were small, but the brains of the great thunder lizards were not walnut-sized. The *Tyrannosaurus* brain probably weighed a pound and a half—comparable to a walnut's weight only if walnuts were made of uranium. A grapefruit would be a better model for its size.

### *Early Encephalization: Sharks, and Mesozoic Birds and Mammals*

Most fish are known only as flattened fossils in which the endocasts cannot be properly analyzed for size. The only good fossil endocasts from bony fish are from very small unflattened specimens, and these are strikingly similar to those of living species in both size and shape and lie within the same convex polygon (fig. 15) as living fish. Perhaps surprisingly, the earliest "experiment" with enlarged brains seems to have occurred in supposedly primitive cartilaginous fish, according to evidence on Paleozoic (about 300 mya) sharks. The species *Cobelodus aculeatus* is a relatively uncrushed fossil, and Zangerl and Case (1976) compared its endocast with that of the living horned shark (*Heterodontus*). Although the fossil's endocast has not been measured (its body was about 80 cm long), both its brain and body appear to have been similar in size to those of the horned shark, which would put them above the highest grade of encephalization of living bony fish (Ebbesson and Northcutt, 1976) and above that of any other fossil vertebrate of their time.

It was not clear to me from examining Zangerl and Case's illustrations that the *Cobelodus* brain was organized in ways radically different from that of the horned shark, but Zangerl and Case believe that the fossil's brain was more enlarged in the cerebellar area and less in the forebrain area. Brain organization at this gross level is significantly more variable in fish than in birds or mammals, and it is impossible to suggest a proper interpretation of such a difference, even if it is present. Processing capacity by the entire brain of *Cob-*

*elodus* was almost certainly high compared to living bony fish. *Cob-elodus* probably represented an advance in encephalization. In a cladistic analysis of the relationships among living sharks, Northcutt (1989) indicated that the earliest sharks were likely to have been smaller-brained and comparable to bony fish. The evidence of *Cob-elodus* indicates that at least one group of early sharks may have become more encephalized.

The evidence on encephalization in birds is clearer. There is no question that they were more encephalized than their reptilian ancestors. Two endocasts are known for the earliest bird, *Archaeopteryx*, which lived about 150 mya. The better known one is at the British Museum (Natural History). From my reconstruction (Jerison, 1973; cf. Whetstone, 1983) I estimated its endocast volume as 0.9 cc and body weight as between 250 and 500 g, with the latter as a maximum. Hopson estimated the endocast as twice as large, and body size toward the lower end (about 300 g). The *Archaeopteryx* point in figure 15 is my estimate and slightly below the lower avian boundary but above the upper edge of living reptiles. Hopson estimated it (fig. 16) as clearly within the range of living birds. His estimate incorporates suggestions from the newer data on the second *Archaeopteryx* with known endocast, the Eichstätt specimen (Wellnhofer, 1974). Although I am not yet satisfied about whether my older estimate or Hopson's newer one is correct, both estimates agree in placing *Archaeopteryx* above the grade of encephalization achieved by any reptiles in that body size range. The much larger ostrichlike dinosaurs, mentioned earlier, may also have been in the avian range of encephalization.

The earliest evidence on the mammalian brain, on the upper Jurassic *Triconodon mordax*, indicates that this mammal species was about four times as encephalized as a reptile of its body size and that it was in the range of encephalization of living opossums and hedgehogs (Jerison, 1973; cf. Crompton et al., 1978). Later Mesozoic mammalian endocasts (Kielan-Jaworowska, 1986) are at that grade or higher, and it seems to be true that the lowest grade of encephalization in living mammals has always been a minimum for the mammalian bodyplan. Although no Mesozoic mammals seemed to depart very much from that minimum, all Mesozoic

mammals, like all later mammals, were more encephalized than any reptile.

Although the fossil evidence of the mammalian brain is of the same vintage as that of birds, mammals probably preceded birds in the history of life by about 50 million years. (Endocasts are less common than jaws and teeth in the fossil record, and the evidence on mammalian origins is mainly mandibular and dental.) When I first reviewed the evidence (Jerison, 1973), the immediate ancestors of the mammals among the mammallike reptiles seemed to me at a reptilian grade of encephalization. There is new information on mammallike reptile endocasts (Kemp, 1979, 1982; Quiroga, 1980; cf., Jerison, 1985, 1990), which suggests that a mammalian grade was reached by at least some mammallike reptiles. The advance must have occurred at some time during the transition from reptiles to mammals, of course, and it may have occurred in more than one mammallike reptile lineage. We are certain only that it occurred in the lineage of the true mammals, and we know that it had already appeared 150 mya.

I am concerned primarily with mammalian encephalization, and the evidence on Mesozoic mammals is impressive on two major points. From at least 150 mya to the end of the Mesozoic, about 65 mya, there was no obvious or important mammalian encephalization beyond the advance from a reptilian to a minimal mammalian grade. Despite their adaptive radiation into many niches, Mesozoic mammals were similar to one another in relative brain size. I should add that they were all small-bodied compared to living mammals, never larger than domestic cats and much smaller than almost all of their contemporaries among the ruling reptiles of the Mesozoic. Their body sizes are important for our understanding of the selection pressures on mammalian evolution during the Mesozoic and for the origin of "mind" in mammals.

The second major point is that there are many living mammals that are no more encephalized than the earliest on which we have evidence, and some are spectacularly successful in their niches. The Virginia opossum and the European hedgehog are outstanding examples, familiar from the remains of their encounters with automobiles on American and European highways, which provide grue-

some evidence of their evolutionary fitness. Their fecundity must be impressive for them to contribute so significantly to the population of road kills.

Mammalian adaptations can be successful without expansion of the brain beyond the grade established 150 (or 200) mya. After the initial advance from a reptilian grade, there was a remarkable stasis in the evolution of encephalization in mammals in all species until the end of the Mesozoic, which has continued in some species to our own time.

### *Encephalization in Tertiary Mammals*

With the extinction of almost all large land vertebrates at the end of the Mesozoic, about 65 mya, there followed an exuberant adaptive radiation of mammals. Within the first few million years of the Tertiary many large-bodied species appeared, and by the middle Paleocene, species of archaic ungulates as large as living rhinos (the pantodont *Titanoides*) had appeared. (Species are "archaic" if they are members of orders that are entirely extinct. The designation is objective and not evaluative.)

With the exception of the earliest primates that had appeared, brain size in the early Tertiary was determined entirely by allometric factors, and encephalization did not increase. For example, one of the largest of the archaic ungulates, the late Eocene uintathere *Tetheopsis ingens* weighed about 2000 kg, and its endocast was approximate 350 cc in volume. If one imagines an average insectivore evolving to such large size, the equations of figure 13 would lead us to expect it to have a much larger brain—over 800 cc. Bauchot (1978) has pointed out that very large species tend to have smaller brains than expected according to the usual allometric analyses, although in this instance the "error" seems unusually large. The least encephalized of living species is probably the Virginia opossum, with a 6 g brain and 4 kg body. Taking it as the model for *Tetheopsis* would lead one to expect the uintathere to have a 380 g brain. The point is that there had been no important encephalization until relatively late in mammalian history. We can imagine the mammalian radiations of the early Tertiary period as having resulted in archaic

species in which the size of the brain was determined entirely by allometric effects—enlarged hedgehogs or opossums, as it were, with respect to encephalization.

Encephalization in most other mammalian orders began somewhat later, during the Eocene and Oligocene, beginning about 50 mya. The pattern is clearest in carnivores and ungulates. For example, in the horse lineage, the earliest known species, the “eohippus” (*Hyracotherium* or *Protorohippus*) of the lower Eocene had a brain that was intermediate in size between one’s expectation from hedgehogs and from average living mammals. By the middle Oligocene, about 30 mya, *Mesohippus* was at the same grade of encephalization as average living mammals. The later horse species have all been average mammals in the same sense, showing no further encephalization. The pattern was similar in the even-toed ungulates, the order Artiodactyla.

Carnivore encephalization is also easily traced. The earliest true carnivores and the archaic carnivore order Creodonta were intermediate in encephalization, but by the end of the Oligocene the true carnivores were at the grade of average living mammals and have remained at that grade. Creodonts were smaller brained on the average, although some creodont species were at an average grade (Jerison, 1973, 1990; cf., Radinsky, 1977a).

The evolution of encephalization in various vertebrate groups is summarized in figure 17: long periods of equilibrium, and where encephalization is evident its probably rapid course in a group. We can note the long stasis in Mesozoic mammals and the persistence of their grade of encephalization in some living species. Advances in grade in the mammals in the Cenozoic, between 65 mya and the present, occurred separately in several groups. The graph is somewhat misleading on this point, because it was constructed by determining mean grades of encephalization for the indicated groups during major intervals, such as the entire Eocene or Oligocene, and it does not represent changes within those intervals or the diversity of encephalization within groups. However, it can be thought of as indicating the amount of selection for brain enlargement taking place during a period, with the representation reflected in the presence of species at a particular grade. For example, we might read the graph

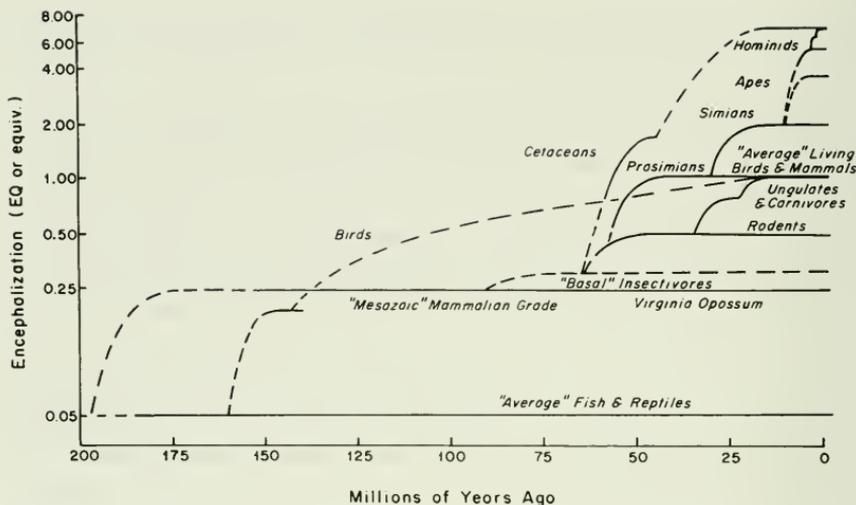


Fig. 17. The time course of encephalization in vertebrates. Encephalization quotients are approximate relative to average living mammals, in which the quotient is defined as 1.0.

on ungulates and carnivores as indicating that during the Oligocene, a successful species had to be approximately 75 percent as encephalized as living ungulates and carnivores. Successful rodents or insectivores were less encephalized then, just as they are now.

### *Cetaceans and Primates*

The highest grades of encephalization among vertebrates have been achieved in cetaceans and primates: in dolphins and hominids, respectively. The history of dolphin encephalization is not known, but from evidence in other cetaceans it seems likely that very impressive encephalization, close to the present highest levels, occurred during the major cetacean adaptive radiations of the Miocene, between 15 and 20 million years ago (Jerison, 1973, 1983).

Although there is some controversy on the primate record (Radinsky, 1977b, 1979; Jerison, 1979; cf., Pickford, 1988), there is little question that early in the Eocene there were significantly encephalized prosimians. The tarsierlike *Tetonius* of the lower Eocene was as encephalized as some living prosimians, although the adapids of the later Eocene were less encephalized: intermediate between an

insectivore and prosimian grade and relatively small brained for primates. Earlier, in the Paleocene, plesiadapids, which are usually considered to be primates, had appeared, and although their endocasts are still unknown, the external configuration of the cranium was rounder; the species appears to have been more encephalized than any of its contemporaries. By the end of the Oligocene, fossil prosimians at about the same grade of encephalization as living lemuroid species had evolved.

The earliest anthropoid primates are known from the late Eocene, and their brains from the middle Oligocene with the appearance of *Aegyptopithecus* (Radinsky, 1979). This early anthropoid was at a prosimian rather than anthropoid grade of encephalization. Encephalization evidently lagged behind skeletal features at that period of primate evolution. The pattern was to be repeated in the hominid lineage (Pickford, 1988).

Hominid encephalization was a much later phenomenon. There is evidence of slight encephalization beyond a great-ape grade in the earliest known hominids, which lived about 3.5 million years ago (Falk, 1987; Tobias, 1981). These were australopithecines and are "hominid" rather than "pongid" for dental and skeletal reasons, not because of enlarged brains. As in the earliest anthropoids, brain evolution appears to have lagged behind other skeletal features.

The major expansion of the hominid brain seems to have begun about 2 mya, with the appearance of *Homo habilis*. Brain size within the range of living humans was achieved within the next million years by the pithecanthropines, *H. erectus*, and it is possible that some increases occurred during its "life" as a species (Falk, 1987). There are technical questions here on the meaning of "species" (Campbell, 1972), but later fossil pithecanthropines may have been bigger brained than earlier ones, suggesting selection for brain size in the "anagenetic" evolution of the species. The general conclusion about the increase in brain size in primates, however, is that encephalization probably lagged behind other events in speciation, which would mean that some primate niches were not initially characterized by selection for brain size, but that encephalization was associated with improved adaptation to those niches.

The fossil record on the hominid brain ends with fossil *Homo*

*sapiens*. The record here is quite good, and it appears to be true that the neandertals were larger brained than living humans (Kennedy, in press). The earliest *Homo sapiens*, represented by the Swanscombe skull, lived about 250,000 years ago. Differences in brain size among earlier and later populations within the species, however, are not large enough to be interpreted in relation to brain function (Falk, 1987; Holloway, 1981; Kochetkova, 1978). Our best judgment about human brain size is that it reached its present grade with the first appearance of *Homo sapiens*, including the subspecies *H. s. neanderthalensis*.

Hominid species are all in the same body size range, with the exception of the earliest australopithecines, which were somewhat smaller, weighing as little as 20 or 25 kg. Because of the uniformity in body size, differences in brain size represent encephalization. In living humans, within each sex there appears to be no allometric effect at all. There is a sex difference in human brain size (about one standard deviation; male brains average about 125 g heavier than female brains) that is not really understood, but it may be related to body size differences. There are smaller but significant race differences which are also not understood.

The quantitative increases in brain size in hominids (fig. 18) were from somewhat less than 500 cc for the early australopithecines of 2 to 3 mya, rising to a bit over 500 cc (reflecting allometry rather than encephalization) in robust australopithecines of 1.5 to 2 mya. Brain size also rose at that time in *H. habilis*, about 2 mya, to about 750 cc, and then to the range of 800 to 1100 cc in the pithecanthropines, between 1.6 and 0.5 mya. Living and fossil *H. sapiens* (including the neandertals) had endocranial volumes ranging between about 1100 and 1800 cc.

Larger human brains (and cranial cavities) are known, but they and the upper extreme of the living human range—brains weighing more than about 1600 g—may be caused by pathology or postmortem edema (Whitaker, personal commun.). In any case, at the present time there is very little evidence that relates brain size to the quality of mind within the human species, except in cases of microcephaly, hydrocephaly, and senility. Although it is difficult to demonstrate, because of the difficulties of between-species scaling on a dimension

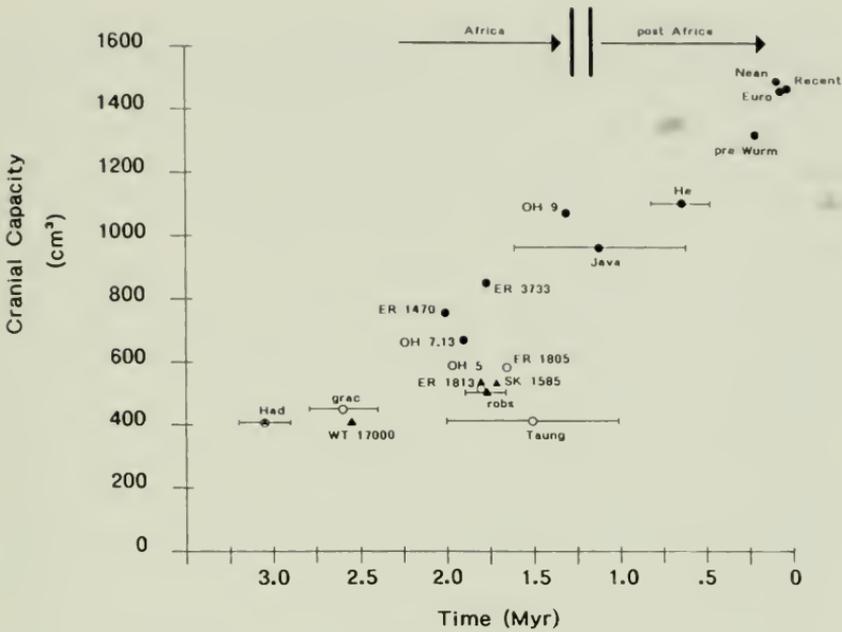


Fig. 18. Mean cranial capacity as a function of time for hominids. (▲), robust australopithecines; (○), gracile australopithecines; (●), genus *Homo*. **Had**, Hadar specimens; **grac**, gracile australopithecines; **robs**, robust australopithecines; for other abbreviations, see Falk, 1987. Horizontal bars indicate time ranges. (From Falk, 1987, reprinted by permission)

of mind (Macphail, 1982), one must interpret between-species differences in encephalization as indicating differences among species in mind or intelligence, whereas normal within-species differences do not have clearly significant behavioral correlates (but see Hahn et al., 1979). This is the case for all vertebrate species including the several hominid species (Jerison, 1985a).

### ENCEPHALIZATION AND THE EVOLUTION OF MIND

The graph of the evolution of vertebrate encephalization (fig. 17) points to several critical periods when there were important advances in grade. I will discuss two of these: encephalization at the reptile-mammal boundary, which probably occurred about 200 mya, and hominid encephalization at the transition from a pongid to an australopithecine grade, or from the latter to a *Homo* grade, 2–4 mya.

Since I have published my views on these issues before (Jerison, 1973, 1982a, 1985a,b), I will only outline my analysis of why things went the way they did. But I want to emphasize that in each case there is a real problem in explaining the enormous increases in processing capacity. Remember the data on the mouse. Just half a gram of brain represented 40 million neurons. That is about the amount that would have to be added to the brain of a 100 g reptile to convert it into the brain of a 100 g mammal. The change in the brain would be from about 0.15 g to 0.75 g, both tiny brains, but differing by a factor of five. What could possibly have happened to justify such expansion?

If evolution is parsimonious there must be a justification. We assume that organisms evolve to function efficiently and that they minimize the energy required for their adaptations. As a control system, the brain is profligate in its use of energy. The human brain, which is about 2 percent of the body's mass, is estimated to account for about 20 percent of the body's metabolism. If a job could be done with a minimal amount of neural control, parsimonious evolution would have moved toward such a method rather than toward encephalization, which increases neural control.

The issue is illustrated by vertebrate and invertebrate adaptations for flight. Vertebrate adaptations for flight involve very fine control of muscle systems that are continuously adjusted by the neural machinery. In insects, some of the wing movement is automatically determined by the placement of the wing linkages to the body proper, and aerodynamically appropriate movements are effected by dentlike movements that snap the wing into appropriate successive positions with less elaborate neural control (Wendler, 1983). The insect's system is biologically more efficient than that of vertebrates in the sense that it requires less investment in energetically expensive neural control devices. Encephalization would be expected to occur only if no cheaper way were available to solve an adaptational problem.

### *Reptiles into Mammals*

The explanation for the enlargement of the brain in mammals compared to their ancestors among the reptiles must involve the

perceptual-cognitive domain of information-processing as I discussed this earlier. It is only for such processing that really massive amounts of neural tissue must be available. We, therefore, seek a scenario in which the transition between mammallike reptiles and early mammals involved a species under natural selection for significantly more perceptual-cognitive processing than in normal reptiles.

A reasonably simple and straightforward suggestion is that the selection occurred in species that successfully invaded an adaptive zone of fossorial, crepuscular, and nocturnal niches. We must keep in mind that “normal” reptilian adaptations of Triassic species almost certainly involved primarily visual information about the external world and that a highly efficient eye-brain system had evolved in all reptiles to support such adaptations. These are the systems that still characterize most living reptiles—retinal daylight vision effected and supported by a well integrated retino-tectal and fore-brain system that is efficiently responsive to visual signals. A “reptile” evolving for comparably efficient activity with reduced or absent visual information would require other sources of data about events at a distance.

The special quantitative feature in this problem is that visual processing is done not only in the brain but in the retina of the eye, which is brain tissue that migrated out into the eyeball. The retinal “brain” is very large, and may have millions of neurons. If normal visual processing involves these several million retinal neurons, the same kind of processing with other sense modalities might require that many neurons too. But other systems do not have peripheral brains as part of their structure, so the extra neurons would have to be put inside the head. I have argued that this had to happen, and that the explanation for the first brain enlargement in mammals was as a solution of a packaging problem: where to put the neural machinery that would enable other sensory systems to do the job that is normally accomplished by diurnal vision. The extra half gram of brain may have been just what was needed to do that job.

I have taken the auditory system as my model for replacing the visual system and note that “peripheral” processing in the inner ear region is accomplished by just a few thousand nerve cells in asso-

ciation with the sensory hair cells of the inner ear. Further auditory information processing is accomplished in the brain proper at a bulbar, tectal, and where there is cortex as in mammals, at a cortical level. I have considered the auditory system as having become expanded in early mammals relative to their reptilian ancestors to handle the added information load through the evolution of expanded tectal and novel cortical auditory projections. A comparable argument for the olfactory system would involve, primarily, the expansion of the olfactory bulbs (cf. fig. 12) but also the remainder of the brain's olfactory system. The visual system could also become specialized for nocturnal life, by becoming sensitive to very low levels of illumination, and we can recognize this specialization in mammals in the evolution of the rod system of the retina.

We have to imagine a change from reptile to mammals that was minimal with respect to the requirements for neural control. We should imagine the early mammals as being slightly modified "reptiles" that used unusual sensory systems to navigate their environments the way normal reptiles managed with their visual systems. Their expanded brains were packed with neural machinery that did for other senses what the retino-tectal and associated forebrain system did for the visual information used by diurnal reptiles. Information from these other senses would then be integrated with otherwise reptilian behavior systems for coping with and navigating through their environments, and the information from the novel senses would be used in ways comparable to the ways that the visual system is used by reptiles: providing information about objects and events at a distance.

Most species of mammallike reptiles were evidently replaced in diurnal niches by species of ruling reptiles by the middle of the Mesozoic. Although they were a dominant group at the end of the Paleozoic era, the mammallike reptiles became extinct sometime during the Jurassic period of the Mesozoic era, except for those that, transformed into true mammals, survived and flourished as species of tiny animals (much smaller than any of the reptiles) through the remainder of the Mesozoic. These survivors, numerous and diversified but always small, were the raw material for the exuberant mammalian radiations of the Cenozoic era.

## *Mind in the Early Mammals?*

Consider now the implications of a mammalian adaptation for integrating information received through multiple neurosensory channels about events at a distance. Were the information gathered through a single channel, such as the visual system in reptiles, it might be possible to imagine a tightly coupled arrangement in which visual inputs are associated with motor output to support reflex responses to the changing environment. If the mammalian adaptation is for several sensory modalities to combine to provide the information, different kinds of information would reach different parts of the brain and would have to be assembled and coordinated with the additional message that they provide information about the same features of the external world. How should the sources of information be identified? It would obviously be helpful to label them, regardless of the modality in which they are received and the parts of the brain in which they appear, with labels that identify all of the stimulation with the same environmental source.

The labels would be created by the brain, and they would have to designate “objects” of an external world. There would have to be additional labels for a coordinate system of the external world in which objects would be placed; these would label “space” and “time,” also constructions of the brain. (That the labels would refer to real space and real time in the external world is secondary. The point is that known space and time, as well as *known* objects, must be constructions of the brain.) There would have to be additional properties for the labels, or constructions. They would have to be able to persist over time, and it would have to be possible to store them and retrieve them—to remember them—when needed. The overall activity of labeling amounts to the construction of a real world containing real objects, which is exactly the function of mind as I have discussed it with you.

That the *knowledge* of reality is constructed from sense data seems almost self-evident when information about the external world is coordinated from the combined data of several sense modalities. But this may also be true even when the information appears to be limited to a single modality. We know enough about the complexity

of the visual system, for example, to appreciate that even if information about the external world is exclusively visual the experienced world may be constructed in the same sense as it is by combining the data from other systems. There are many dimensions within vision, dimensions of shape, color, and location and movement in three dimensions, and information about these dimensions may be distributed through much of the brain. In fact, one characteristic of the brain's normal work is the extent to which different regions participate in particular jobs.

The question we ask about the origin of mind is: When in the evolution of the brain did it become necessary to construct a representation of reality rather than work directly, in reflex fashion, with "raw" neural information? While most vertebrates almost certainly are adapted to use a representational method of handling information, with encephalization to an avian or mammalian grade, creating a model of reality would have become essential for coordinating information from the external world in an effective way. Although we need not imagine the origin of mind as exclusively a result of encephalization, it is appropriate to imagine mind as having become a much more complex construction in the mammals. Because of the extraordinarily great amount of neural information that has to be handled, we have to imagine that the processing is hierarchical and that the actual construction of a model of a real world is a function of some level or levels in the hierarchy.

Mind refers to knowledge of reality. I emphasize that this knowledge must be achieved by constructing a model of the real world and that the knowing is of the model rather than direct knowledge of the external world. The real external world is transformed into a model that can be experienced, and knowledge and action are referred to that model. We know that the model can sometimes be false or misleading, as in some illusions and in some familiar perceptual demonstrations. But most of the time the model works well as a framework for behavior. We don't normally know when it fails, because we don't normally know the external world independently of this construction by the brain. When we have independent knowledge, i.e., from the readings of physical instruments or from arranging patterns of stimulation for others to experience (i.e., per-

forming experiments on perception), we can recognize the constructed and sometimes fallible nature of our normal experience. I am arguing that the construction of such a mind was a necessary consequence of the adaptive demands faced by the earliest mammals. The adaptations for integrating information from several sense modalities about the same events at a distance were, in effect, the creation of mind as a knower of reality.

### *A Hominid Scenario: The Evolution of Language*

The evolution of a prehomimid anthropoid into a hominid species occurred perhaps 4 or 5 million years ago, and present evidence is that we humans share our prehomimid ancestor with living chimpanzees. This provides some clues about our mental origins, since we know a fair amount about the mental capacities of chimpanzees (Kummer and Goodall, 1985; Passingham, 1982; Premack and Woodruff, 1982). We know, for example, that we share with chimpanzees the conservation of mass as discussed by Piaget (Premack and Kennell, 1978); the ability to make, use, and train others to use primitive tools (Boesch and Boesch, 1983); and educability in the use of languagelike symbols (Savage-Rumbaugh et al., 1985). We also share the ability to learn to distinguish ourselves from others on the basis of fairly abstract information, such as that provided by a reflection in a mirror (Gallup, 1979), which indicates that the knowledge of the self as an object is rather well developed.

These shared behavioral traits were presumably in the repertoire of our common ancestor, which means that we evolved from a species that had the mental capacities required by those traits. Some, but not all, of these capacities are shared with the other two great ape genera, the orangs and gorillas, as well as with chimpanzees, but no one has yet demonstrated that other anthropoid primates, that is, monkeys and gibbons, possess them. The evidence is not all in on just how much is shared, nor does everyone agree on how to interpret the behavioral data as evidence of cognitive capacities, but we and the great apes appear to be closer relatives with respect to those capacities than either of us are to other anthropoids.

Among the more spectacular recent discoveries on our shared

capacities has been the educability of chimpanzees and other great apes in the use of "language" initiated under human tutelage as discussed by the Gardners and others (Gardner and Gardner, 1985). I am as impressed as everyone else by the remarkable performance, but I believe that the extraordinary performance of chimpanzees in languagelike activities involves other (impressive) cognitive capacities. My reactionary view (contradicting that of my friends in the ape-language field) is that our use of language is uniquely human, and I hold it on the basis of the logic of an evolutionary analysis and scenario.

My scenario follows the same general form as my analysis of the beginnings of mammalian encephalization. It begins with the neurological status of language, namely that it is controlled by an enormous *neocortical* system. As I emphasized earlier, I interpret neocortical control as implying that at the most fundamental level, the system that is being controlled is perceptual and cognitive. Human language is, therefore, to be considered a priori a perceptual-cognitive adaptation.

In seeking to identify selection pressures that were effective during the prehominid-hominid transition and were met by a languagelike adaptation, I sought to identify problems of adaptation that required unusual perceptual-cognitive capacities. I recognized, of course, that those capacities would not necessarily have resembled language as we know it although they had to evolve into such a language capacity. The role of language in human communication had to be secondary both in time and in importance according to this evolutionary analysis, since pressures for improved communication would have led to a different kind of initial adaptation, which would not have required much expansion of the brain for its control. But even in its beginnings, language may have been preadaptive for present human language and its place in communication, and it was according to my scenario.

The first step in this evolutionary narrative is to suggest for the ancestral species an environmental niche characterized by adaptive requirements that would put unusual demands on the already large perceptual-cognitive brain system of a prehominid or early hominid. The environmental requirements, I propose, were in the climatic

change in the Mediterranean basin, which reduced the size of the normal forest habitat for a chimpanzee-like primate species—the prehominid of my scenario. As I imagine them, some individuals of the prehominid populations were adapted to live in the desertlike or savanna region at the forest's edge and were able to shift to a more carnivorous diet than that typical for primate species (cf., Pilbeam, 1984). It was in the neurogenetics of those individuals that I would identify the precursors of language.

The niche that was available was for a carnivorous predator, but the animals that invaded it successfully were social vocal primates similar to living chimpanzees, and not members of the order Carnivora. The model of a species adapted for such a niche is the well-studied timber wolf (Peters and Mech, 1975), a proper social carnivore, with a proper profile of morphological, neural, and behavioral adaptations for life in this niche. There are information-processing requirements for the adaptations that are fulfilled easily by wolves, which are average mammals in encephalization. But meeting those requirements would strain the neural processing capacity of an anthropoid primate species, despite its being more than twice as encephalized as wolves, because anthropoid primates lost the capacity to use certain critical information during the course of their evolution. My view is that the specialized information processing requirements were met in our hominid ancestors by a new adaptation that eventually evolved into human language.

The special demand of this niche is that it involves the navigation of a very large territory and range by a socially integrated group of predators to harvest prey in sufficient numbers to support the predators. In living wolves a typical territory is of the order of several hundred km<sup>2</sup>. In contrast, a typical daily range of living gorillas and chimpanzees for normal foraging may be only a few hundred square meters (Pickford, 1988). A successful predator must *know* its territory, and this means that it must have a good cognitive map of it and remember the map's history and status. The sensory and neural equipment of wolves, in contrast to that of apes, provides the clue for the new anthropoid adaptation that was required and which appeared in our hominid ancestors.

For their adaptations as social predators, wolves have an elaborate

scent-marking system coupled with “normal” olfactory bulbs (more than 50 times the size of the almost vestigial human olfactory bulbs) and presumably excellent olfactory sensation and perception. The brain systems receiving the olfactory information include the piriform lobes and schizocortex, and certainly hippocampus. We know very little about how olfactory information is used in cognition, since we humans are peculiarly deficient in that sense modality (see fig. 12), and our intuitions about it in “normal” mammals are bound to be inadequate. Olfactory information in living carnivores is known to be sufficient to enable individuals to identify other animals individually (Brown and Macdonald, 1985; Rasa, 1973; Roeder, 1983), and we probably should think of it as having a role comparable to that of vision in our lives. This means that it could be used to create maps formed with edges and borders and so forth, and populated by animals and other objects—at least we should imagine this as something that can be constructed from olfactory data.

The fate of these maps in controlling action would be comparable to that of a well-remembered map in our own lives. Mapping and memory about maps are among the functions that appear to involve important hippocampal control (Horn, 1985; Squire, 1987), and the system for wolves presumably involves significant sensory analysis of scent marks, coupled with the establishment of appropriate cognitive maps, with access to all of the mapping and memory functions in which hippocampal control occurs. We should imagine the real world constructed by a wolf from olfactory information to involve input from olfactory bulbs coupled with appropriate analysis by hippocampus, paleocortical, and neocortical structures to produce a “model of reality” that corresponds more to the one we can build from visual information than to the one we build (or fail to build) from odors.

The neurobiological problem of an anthropoid species adapting to a social predator’s niche is somewhat analogous to that of a visual “reptile” species adapting to a nocturnal (mammalian) niche. An anthropoid primate has the right central neural machinery for the adaptation—appropriately large hippocampus and related structures. But in figure 12 you see the evidence that the system as a whole, which is coupled peripherally to the olfactory bulbs, would

be unlikely to work well with the almost vestigial olfactory bulbs of anthropoids. (The adaptational problem is like that of a species with vestigial eyes and retina, evolving under selection pressures to have access to the central visual system.) A solution to the adaptational problem could take advantage of the fact that the hippocampus, which may be thought of as the neural central processing unit in the brain's control of the required cognitive adaptation, is a polysensory structure that can be accessed by other senses. My idea is that the transition to the hominid grade was correlated with the evolution of other peripheral access to the cognitive system that controls a predator's mapping of its range, and primarily by the use of the auditory-vocal channel, which is highly developed in primates.

It is an odd picture, but I think it works. Instead of urinating and sniffing (the scent-marking and sensing that wolves do), we can imagine our ancestor as marking with sounds and sensing the sounds—talking to itself, as it were, but in primitive tongues. The picture is odd, but no odder than another use of an auditory-vocal channel that evolved in some cetaceans and in insect-eating bats, in which echoes from vocalizations are used in the elaborate sonar system that evolved in these species, and from which they construct and know the external world. The picture for our ancestors would be adequate for access to the cognitive systems for mapping and remembering important features of the external world, that is, for knowing that world. The vocalizations would constitute a very small vocabulary but a vocabulary. A model for that might be the three “word” vocabulary of vervets to signal the presence of eagles, or leopards, or snakes. The hominid vocabulary would have to be larger to encode relevant environmental features, and less frenetic, not a danger signal that commanded escape but a knowledge signal that helped construct a map of the world.

The suggestion is, in summary, that an auditory-vocal system was established for marking and knowing a territory or range, that this system sent information to appropriate old-brain and neocortical systems, and that the information was integrated with other knowledge of the external world. (An important peculiarity of the system, only interjected here but worth much more discussion, would be that even at its “sense-data” stage, this system would be neocorti-

calized, because it would appear in a species in which the sensing and marking “vocabulary” was already neocorticalized.) It was a new perceptual-cognitive system and could interact with the very elaborate older system based on vision and touch and other senses, which was already in place. The latter system is the one that enables living chimpanzees to be so much like humans in so many ways, but it is a system that we probably know in a distorted way. Our own knowledge of the external world is much more elaborate—built not only from that sensory mapping that we probably share with other anthropoids and sometimes philosophize about, but by important inputs to the mapping that comes from our language “sense” as it has evolved in *Homo sapiens*.

This scenario offers a solution to an adaptational problem: how an anthropoid can succeed as a social predatory mammalian species without normal olfactory bulbs. It also has implications for other aspects of hominid evolution, because it describes a new cognitive system that is obviously usable for communication with conspecifics. Communication with the auditory-vocal channel is common in primates, as warning calls and other social messages that elicit a variety of behaviors. The communication by hominids using their range-marking system would be of a new kind, however, because the information transmitted by the auditory-vocal channel would be incorporated directly into the listener’s knowledge of the external world rather than act as a releaser or elicitor of specialized behavior. Let me elaborate on this odd notion.

As I have pointed out before, animal communication is normally a system of commands to other animals that can be thought of as having coevolved with the system of responses to those commands. The vervet calls are good examples of what I mean. We can think of the calls as danger signals that elicit appropriate escape action as the normal response. The cognitive dimension of this interaction could be completely absent; it probably is absent in most danger signals in most species, although for other reasons we can assume that it is present in vervets. In any case, normal animal communication need have no cognitive dimension.

The feature of human language that my scenario would emphasize is that it began as a cognitive rather than communicational adap-

tation. That it evolved into the characteristic communication system of our species implies that our communication is not like that of other mammals. Once the adaptation of using auditory and vocal signs to label the geographic environment had appeared, its utility for communication compared to normal communication with sign stimuli that release “instinctive” behaviors in other members of the species is fairly obvious. This cognitive system for knowing an extended range, when used to communicate with another animal, could communicate the knowledge of the range, or other knowledge. What individual A knew could become part of what individual B knew if B merely listened while A vocalized. The only other species in which something close to this is believed to occur are echo-locating bats, which can intercept one another’s calls and their echoes, and, in that sense, experience one another’s worlds. I have speculated that this sort of thing could have developed in dolphins as well, and that the additional neural machinery in the dolphin’s brain might process such information into something more nearly like human language (Jerison, 1986).

I should state this conclusion about language more dramatically. Since language contributes to our knowledge of reality in the same general way as information received by the conventional senses, such as the eye and ear, when we communicate with language we communicate information that contributes to our reality. The listener or reader receiving the message incorporates it into his or her reality and then *knows* the same world that we know as we communicate. Communication with language is, thus, a sharing of awareness or consciousness. We literally read minds when we read a realistic text and enter the minds of the characters as if we were living their fictional lives. This very common experience is really very odd, and it is one of the stranger features of the human mind.

### *Consciousness*

This view of language leads to an unusual view of the nature of human consciousness in an evolutionary framework. As I mentioned before, there are two aspects of consciousness. The first, and biologically most important, is in connection with one’s knowledge of

the external world and should be thought of as the problem of awareness, or representation, or imagery. Why do we know a pictorial world with solid objects and so on? I say that this is the more important biologically, because I believe that the evidence is overwhelming that all birds and mammals are conscious in this sense, and this may also be true for other vertebrates. I mentioned Herrnstein's work with pigeons, which can identify faces that people miss. Griffin (1976) has argued for a universality for this kind of consciousness, or awareness, in an appropriately persuasive way. From my perspective, this means that in most vertebrates, certainly in birds and mammals, the work of the brain includes the construction of a possible real world from sense data, and that "possible world" is the reality that the animal knows. The function of this construction is to make sense of an otherwise overwhelming mass of neural data that refers to the external world.

The other kind of consciousness involves an awareness of self that is unusual. It is not only the self as an object, which is really the same as any other object of which one may be aware or conscious in the first sense. It is the knowledge that the self is different from other objects in that it generates knowledge and knows that it knows. Why would this kind of self be created by a brain? A functional explanation is that this kind of self is necessary if one is to have human language as a dual adaptation for both perceptual/cognitive uses and for communication. Our knowledge of the external world is too important to be compromised by confusion about where it came from. If we can know another's external world simply by hearing (or reading) some statements, it is important that we be able to distinguish this known world from the reality that we know when our information comes through the usual sensory channels, e.g., when we see and hear and touch the external world. We can also know an external world by remembering it, and if our memories are verbalized that information, too, can enter into our awareness of the moment as information about the external world. The point is that language is so potent a medium for knowledge that it may be essential that knowledge carried by that medium be distinguished from other knowledge. By being self-conscious, we can distinguish images generated by the spoken or written word from images gen-

erated at the sensory and motor surfaces of the body in interaction with nonverbal external information. We can distinguish image from reality. It is another oddity about the mind that we don't always succeed in making the distinction, as any schizophrenic and many mystics and dreamers can tell us.

## CONCLUSION

Mind is a construction of the brain, and it evolved as the brain became enlarged during the course of evolution. Mind is a necessary brain adaptation that organizes otherwise unmanageable amounts of neural information into a representation of the external world. Many unusual specialized adaptations have appeared in the course of evolution in connection with the evolution of information processing with respect to the external world, and in mammals most of these almost certainly involved aspects of mind, such as awareness of reality. Human language is one such specialized adaptation, and according to my analysis it is the explanation for the unusual human experience of self-consciousness, that is, of the awareness that we are aware and that we are knowers—that we have minds.

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