ON THEORY IN COMPARATIVE PSYCHOLOGY

The fundamental theory of comparative psychology is the Darwinian theory of evolution by natural selection. Shortly after Darwin published The Origin of Species in 1859 (see Darwin, 1985), his "bulldog," Thomas Huxley, anticipated this conclusion in a frequently reprinted "lecture to workingmen" delivered in 1860:

> I have endeavoured to show that no absolute structural line of demarcation, wider than that between the animals which immediately succeed us in the scale, can be drawn between the animal world and ourselves; and I may add the expression of my belief that the attempt to draw a psychical distinction is equally futile, and that even the highest faculties of feeling and intellect begin to germinate in lower forms of life (Huxley,1899, p. 152)

Huxley's belief about the evolution of feelings and mind has been vindicated by a century and a half of research in ethology and comparative psychology. In this essay I present my own understanding of the issues. I include data supporting my views, primarily by referring to two recent chapters published elsewhere (Jerison, in press a, b), to several older reviews (Jerison, 1982, 1991), and to my book of a quarter of a century ago (Jerison, 1973). I make no effort to offer comprehensive summaries or adequate critiques of the views of others who have analyzed the evolution of behavior or presented theories of comparative psychology, although I will of course cite the work that is most relevant for my perspective. My purpose is to relate my work on the evolution of brain size to our goal of understanding comparative psychology.

First, the evolutionary process. Three decades ago, in a review of theoretical issues, Hodos and Campbell (1969) alerted us to the danger of unsophisticated acceptance of an Aristotelian scale of nature as the model for what happened in evolution. The problem may be reflected in Huxley's phrase, "begin to germinate," which suggests a direction and inevitable advance in evolution from lower to higher forms. The phrase is unfortunate. The correct present view is that genetically determined traits that can be identified in living species all have evolutionary histories and were derived from related traits in earlier species. When one can identify an evolutionary phylogeny, it can be true that later species are at a higher "grade" with respect to some traits than earlier species, but it is a tricky question that requires much more discussion than is appropriate for this essay (Gould, 1976).

The "higher" faculties in the human species were surely derived from related, perhaps "lower" but at least different, traits in ancestor species. Evolutionary novelties are understood as relatively small genetic modifications of earlier traits, which are nevertheless manifested phenotypically as dramatically different traits. In Jerison (in press a) I present a hypothetical example of a small genetic modification of a trait and the way it would produce a dramatic phenotypic effect, an effect that could distinguish humans from apes.

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

As with almost all organismic traits, behavioral or morphological, phenotypes are produced by an interaction of the genotypes with the environments in which the genetic instructions are carried out. The genotypes are always definable in principle by the structure of certain molecules, chains of nucleotides, which are the classical genes. These form the genetic code. They are the blueprint, as it were, for generating the phenotypes: organs and organisms. The evolutionary rules governing genotypic variation and change within a species emphasize random mutations rather than natural selection. Their evolution can usually be ascribed to genetic drift. Selection operates on the phenotypes, however, and serves to change the frequencies of the corresponding genotypes across generations of a species to increase the likelihood of reproductive success. Natural selection is thus directional; its direction is determined by environmental effects, and it can be thought of as a mechanism that enables genetic systems to track a changing environment.

In a nutshell, that is how evolution works. There is nothing special about the traits that concern comparative psychologists, nothing to require special versions of evolutionary theory to understand the place of those traits in the history of life. Evolutionary theory remains the basic theory for comparative psychology, most easily appreciated for genetically determined traits. There is a matter of emphasis, however, in that the genotypes of few behavioral traits are well understood, and their phenotypic expression is determined to a significant extent by postnatal developmental factors. For many of the traits of special interest to comparative psychologists, it is probably usually the case that the genotypes are themselves complex and do not normally involve single genes.

The Special Problem of Comparative Psychology

From its beginnings as an experimentally oriented scientific discipline, comparative psychology has been devoted to the analysis of learning in different animal species (e.g., Lubbock, 1888, Thorndike, 1898). It emphasized traits that were obviously environmentally determined. How could such traits be studied as having evolved? The answer was to create a construct, "learning ability," which could presumably be genetically determined and which might have evolved in different ways and to different extents in different species. There could have been "higher" and "lower" grades of learning ability.

The first problem for theory in comparative psychology arises from the strange discoveries about learning ability. Much of Macphail's (1982) marvelous review of comparative vertebrate intelligence is concerned with the research literature on this topic. His conclusion, simply put, is that the fundamentals of learning are similar in all vertebrate species in which they have been studied. Researchers on the fundamentals of learning, whether or not they sympathize with Macphail's conclusions, appear to accept it pragmatically in their choice of species. The fundamentals of conditioning have been analyzed most intriguingly in sea slugs (Byrne, 1987) and fruit flies (Tully, Preat, Boynton, & Del Vecchio, 1994), extending Macphail's judgment to invertebrates. Because of this apparent uniformity across species, the neurochemical correlates of the operation of the fundamentals are being studied in these less "complex" animals. Their nervous systems are smaller and have fewer elements. And the fundamentals of learning appear to be the same in all metazoans.

If one is concerned with other dimensions of behavior, such as social behavior or animal communication, one reaches a similar conclusion. Most metazoan animals are social, and the fundamentals of simple sociality may be evident even in the analysis of microorganisms. We have known this for more than half a century (Allee, 1931). Almost all animals are known to communicate at least some information either to conspecifics or to other species in the form of sexual displays, warning calls, threat gestures, and so forth. One of the great discoveries about the ethology and comparative psychology of animal communication, the dance of the bees (von Frisch, 1950), was recognized by the award of a Nobel prize, and common principles derived from an evolutionary framework became the foundation of sociobiology (Wilson, 1975) and its offspring, modern "evolutionary psychology" (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998). One can catalog behavioral dimensions for sociality and for communication, but can one develop an evolutionary scheme in which a comparative analysis is helpful? It is hard to suggest a positive answer.

During the past decade a dominant effort among evolutionists has been to determine phylogenetic relationships, or cladistics (Patterson, 1987). This is performed by analyzing a traits-by-species data matrix: a listing of the presence or absence of traits in a variety of species, which may include quantitative values of traits where these are available. The relationships among the species with respect to the traits are then subjected to various computational schemes to determine a most likely phylogeny to relate the species. Any set of behavioral, morphological, and molecular traits can be used in the trait-matrix, as can any sample of species. Behavioral traits that have been used for such analysis usually involve relatively small differences among species with respect to fixed action patterns (Brooks & MacLennan, 1991). I am not aware of any behavioral traits involving higher mental processes as having been used in this way. Macphail's conclusion about the difficulty of differentiating species with respect to intelligence appears to be correct enough to make such traits difficult to use for cladistics.

Although it involves no fundamental challenge to evolutionary analysis, the common understanding of the importance of environmental factors for human behavior can lead to skepticism about invoking a theory so reliant on genetics for understanding the mind. We know intuitively, for example, that aspects of language must be genetically determined, because it is a universal human trait, and we recognize the validity of efforts to understand the evolution of the "language sense." On the other hand, our intuition is equally strong and obviously valid about the importance of the environment, since the actual language that one uses depends on where one was reared. Any theory of comparative psychology must be concerned with the multiple causal systems that control behavior in different species, and should address the problem of how systems involving both genetic and environmental controls evolve. The approach that I adopt, which treats facts about brains as elements of a theory of mind, does not avoid the problem. It meets the challenge, because both structure and function of a mature brain, at least in birds and mammals, is determined by an elaborate interaction between genetic systems and operations of the developing brain. The brain is a perfect organ to analyze as a structure shaped by the interaction between nature and nurture. An outstanding example is the way the visual system develops in mammals. The number of cortical neurons in this system are probably determined by genetic instructions, but their survival and the way they respond to stimulation are both determined to a major extent by the visual information that is received during critical periods of an animal's development (Hubel, 1988). The formal evolutionary issues relevant for comparative psychology are, to a significant extent, the same as these issues for comparative neurology, and the nature-nurture issue is not ignored if our models for psychology are neurological.

Brain Evolution as an Approach to Behavioral Evolution

My work on brain evolution provides an alternative to a purely behavioral theoretical analysis of the evolution of mind. I undertook it without intending to develop a theory, but it works as theory by tying mind to a feature of the brain that is especially suitable for an evolutionary analysis. The connection is based on the idea that brain size can serve as a neural surrogate for behavioral variables, a kind of statistic for the analysis of mind as its "parameter." It is a bit of a stretch, but the basic ideas are a century old, modernized only by the development and application of better morphometrics, modern neuroscience, and more sophisticated mathematical and statistical analytic methods. It does not lead to a comprehensive theory in the grand tradition, but it makes many intuitions about comparative behavior understandable, and it leads to inferences that provide useful insights into what evolved when "mind" evolved.

I was led to the approach by Karl Lashley (1949), who discussed "persistent problems in the evolution of mind" in his presidential address to the American Society of Naturalists:

> The only neurological character for which a correlation with behavioral capacity in different animals is supported by significant evidence is the total mass of tissue, or rather, the index of cephalization, measured by the ratio of brain to [the 2/3-power of] body weight, which seems to represent the amount of brain tissue in excess of that required for transmitting impulses to and from the integrative centers.[Lashley, 1949, p.33]

I tried very hard to find out why this simple brain trait worked as Lashley described it, and it was in that connection that I recognized that brain size functioned as a kind of statistic for other brain traits as parameters. Its extension to "mind traits" is the hypothetical leap that makes it a theory of mind, and that its evolutionary history is easy to analyze makes it a useful approach to the evolution of mind. The success of this effort was due to a few simple facts about the brain and its work, which could have been demonstrated early in the history of the neurosciences, though their significance is still often unrecognized (cf., e.g. Gazzaniga, 1995, who represents a consensus about how complex brains are, a consensus that refuses to recognize that some important things about brains are surprisingly simple.)

Brain size is a natural statistic that estimates the total neural information-processing capacity of an animal as well as other important quantitative aspects of structure and function in living brains (Jerison, 1991). This conclusion is based on mammalian data, but it can be extended to all vertebrates, because all vertebrates are, in a way, bundles of cells. The way their bodies work is a kind of summation of the work of their cells. Most living cells are approximately the same size (within an order of magnitude), and they are packed efficiently in organs. The size of cells is limited by physical constraints on the membranes that bound them, and efficient packing density is a normal optimizing effect in living systems. As a result, when an organ is assembled, its size appears to be determined by the same controlling mechanism or genetic program that puts together other organs of the body, as well as the whole animal. There is more to this story, of course, and it is well told by a number of authors (e.g., Aiello & Wheeler, 1995; Schmidt-Nielsen, 1984).

To illustrate more specifically how brain size works as a natural statistic, consider Figure 1, which is a graph that combines data from Brodmann (1913), Elias & Schwartz (1971), Ridgway (1981), and Ridgway & Brownson (1984) on the relationship between total cortical surface and brain size. The 50 species are from the orders Artiodactyla, Carnivora, Cetacea, Edentata, Insectivora, Marsupialia, Monotremata, Perissodactyla, Primates, Proboscidea, and Rodentia. It is clear that if one knows the size of the brain in a mammal one can estimate the area of the brain's cortical surface, across species, with remarkable accuracy. That kind of estimation is what good statistics are supposed to provide.

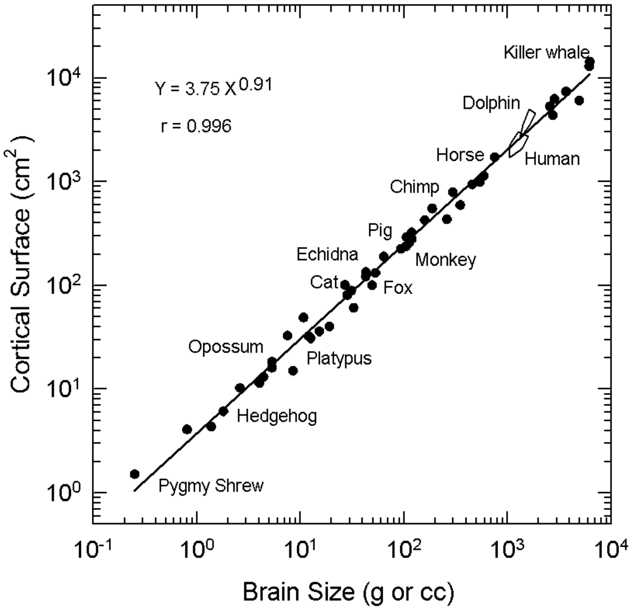

Figure 1. The relationship between cortical surface and gross brain size in 50 species of mammals. Each point represents a species. In addition, two labeled minimum convex polygons indicate within-species variability in humans (N = 23) and dolphins (Tursiops truncatus, N = 13). Several species are labeled by name to indicate the diversity of the sample. (From Jerison, in press a, by permission.)

The surface-volume relationship used to illustrate the efficiency of brain size as a statistic is worth a few more remarks. Its most important implication is for the relationship of brain size to neural information processing capacity. It also shows, perhaps surprisingly, that the human brain is less convoluted than expected for a mammal in our brain-size range.

The relationship to processing capacity follows from a kind of syllogism about how neural information is organized in the cerebral cortex. The unit of information may be defined at various levels, such as the synapse or the neuron. At another level, the cortical column is identified as a higher order unit. The number of cortical columns in a mammal's brain should be directly related to the information processing capacity of that brain, and since cortical columns are fairly uniform in diameter (Szentagothai, 1978), their number must be proportional to the cortical surface area. Figure 1 shows that total brain size estimates the surface area, and hence it estimates the neural information processing capacity of a brain. Other data sets are available that lead to the same conclusion if we consider the single neuron or the synapse as the unit of information (Jerison, 1991, in press a, b).

One is led to the conclusion on convolutedness by the position of the small human data polygon in Figure 1, which lies significantly below the regression line. That the slope of the regression line is 0.91 rather than 2/3 means that, between-species, mammalian brains differ in shape when they are different in size. (The log surface-volume "regression" slope for bodies of the same shape that differ in volume is always exactly 2/3.) The difference in shape, which takes the form of a change in surface area beyond that required for a change in volume, is obviously produced by the folding of the cortical surface into convolutions. The orderliness of the effect evidenced by the high correlation coefficient indicates that within the mammals essentially all (about 99 per cent) of the variance between-species in cortical surface area, i.e., convolutedness, is accounted for by brain size. A species exactly on the regression line has the expected amount of folding, but a species, such as the human species, that lies below the regression line has less than the expected amount of folding. It is less convoluted than expected. (See Jerison, 1991, for additional discussion).

Structure of the Theory

My brain-based analysis of the evolution of mind, which is a theory for comparative psychology, begins with the assumption that behavioral information and neural information are equivalent, that they are related to one another quantitatively and in a simple way. Behavioral information has been defined in the cognitive sciences by formal information theory (Shannon & Weaver, 1949). It is a function of the number of yes-no changes of state in a channel through which it is transmitted. The behavioral definition works for many cognitive phenomena, as documented in the annual publications of the Attention and Performance symposia beginning three decades ago (Sanders, 1967). Neural information is similarly defined as digital information, the all-or-none action potentials that can be recorded with suitable equipment from single nerve cells. Although there is also important neural analog information (changes in electrical potential at the membrane and neurotransmitter functions, for example), the idea of all-or-none units of information transmission in the nervous system has been a useful organizing principle in neurophysiology for all of the twentieth century.

The point is that as theory one can consider the neural and behavioral flow of information as parallel events, and whatever one can learn about one of these can be applied to one's understanding of the other. To use statements about neural events as equivalents for behavioral events is analogous to the classical scientific method of representing physical events by mathematical operations. Physical theories take advantage of the simplifications provided by the logical structure of the mathematical operations. The nervous system is not as elegant a logical analog as a mathematical system, but it is more easily understood than behavioral or mental systems that operate in parallel with it. A set of statements about the nervous system may then stand in for the comparable statements about behavior or the mind. Brain size, the gross weight or volume of a whole brain, has been my usual neural measure, and my analysis has exploited the simplicity of that measure.

In my analysis of the evolution of the brain I have used many facts about the relations among different animal species with respect to gross brain size, which I have treated as a statistic that estimates other facts about the brain (Jerison, 1973, 1991, 1997). The central assertion of the analysis is that brain size estimates total information processing capacity, following the argument presented in the previous section in which this assertion was explained for neural information. It can then be invoked as a theoretical statement for behavioral information. It implies a definition of intelligence as follows:

> Definition: Intelligence is the behavioral consequence of the total neural-information processing capacity in representative adults of a species, adjusted for the capacity to control routine bodily functions.

With relatively few assumptions, which are easy to justify, the definition leads to an operational definition of intelligence as a measurable trait that evolved in animals. It is, first of all, a species trait, measured as an average value for adult animals. The data of Figure 1 enable us to measure total processing capacity by gross brain size. The adjustment for routine bodily functions required by the definition is determined from the regression of log brain size on log body size, and is called a brain-body allometric function. Intelligence in a species is then the residual from the regression. Because the data are logarithmic, the residual is the quotient of measured brain weight divided by the expected brain weight as determined by the regression. That residual is called encephalization, and since it is a quotient it is an encephalization quotient, or EQ. There are, as you can imagine, many refined statements about how to do the regression analysis, which species must be sampled, and criticisms of the use of so simple a method, but the basic definition remains intact, given agreements about the refinements. The most valid criticism, with which I strongly agree, is of the oversimplifications, which ignore important details about the organization of brains. For more on the statistical and mathematical methods, see Harvey & Pagel (1991), and for more on the application to brain evolution see Jerison (1991) and Martin (1990).

The oversimplification is, of course, in the suggestion of the discredited "mass action" as a model for brain function. We have learned too well the lessons of the intricate organization of localized system within the brain to accept mass action as a correct model. However, that it works as I will show as a model for the brain's evolution and the evolution of mind implies a certain fundamental truth about mass action, which is worth examining. It can be justified partly as a way to acknowledge that the major neural control systems involved in "higher mental processes" are spread through many parts of the brain (Goldman-Rakic, 1988). But mass action as related to encephalization has a more interesting implication for comparative psychology. At a gross level, we know that brains reach their adult size in different species for different reasons. A given level of encephalization is an outcome of convergent evolution, reached by different evolutionary paths. Bats and mice have brains of similar size, yet the bat's neocortex is largely specialized for audition (Grinnell, 1995), whereas a mouse's is a "normal" mammalian brain with all of the sensory and motor areas represented approximately correctly (Braitenberg & Schüz, 1998). Procyonids provide another example of comparable encephalization that reflects different specializations. The coati mundi's sensorimotor cortex has an expanded snout region reflecting the role of its rhinarium in exploring its environment, whereas the raccoon's has comparably expanded representation of its forepaws, as a handler of fish and other objects in a primate-like way (Johnson, 1990; Welker, 1990).

I have called such specialized expansion the principle of "proper mass," that the amount of neural tissue encumbered by a process is related to the importance of the process in the life of an animal. But since encephalization is a kind of summing across such specializations, if we consider encephalization as a measure of animal intelligence, we accept the important idea that this intelligence is a plural phenomenon, that there are different kinds of intelligences that have evolved in different species. The definition, therefore, requires that we accept a limitation on the possibility of developing a unitary comparative psychology. I believe that the limitation is unavoidable as a fact of evolution, and I believe it correct to acknowledge it in a theory of comparative psychology.

If we accept the definition, its most powerful applications may be to inferences from fossil data as direct evidence on the evolution of mind. One can measure brain size in fossil birds and mammals, and estimate body size in the same species. This has been done in many vertebrate species (Edinger, 1975, Hopson 1979, Jerison, 1973, Radinsky, 1978). It has been an especially notable approach to analyzing the fossil evidence in the human lineage (Falk, 1992; Conroy, Weber, Seidler, Tobias, Kane, & Brunsben, 1998).

A "fossil brain" in a mammal or bird is actually a cast molded by the cranial cavity, and in most species these are shaped like freshly dissected brains with dura intact, and their size is about the same as that of a brain. Body size is estimated from skeletal remains and is probably no less adequate than measurements on a living animal. In any case, one can include data on fossils in the analysis of encephalization, which is important for one's ability to develop evolutionary scenarios to explain the changes that can be identified.

Inference about the Evolution of Mind

I summarize all presently available vertebrate brain-body data in Figure 2. The data are from over 2,000 species. In many graphs, such as that of Figure 4, below, the picture appears simpler because one graphs only groups relevant to one's theme, and these groups may be nonoverlapping. In viewing the comprehensive graph of Figure 2, one should keep in mind that the total number of known vertebrate species is close to 50,000. There are perhaps 25,000 bony fish (Osteichthyes) species, more than 9,000 birds (Aves), nearly 5,000 mammals (Mammalia)., more than 6,000 reptiles (Reptilia), more than 4,000 amphibians (Amphibia), about 700 species of cartilaginous fish (Chondrichthyes), comprising the sharks, rays, and skates, and about 70 species of jawless fish (Agnatha), the lampreys and hagfish. The sample in Figure 2 is fairly representative except that there are, perhaps understandably since this is an essay by a mammal for other mammals, mammalocentric -- too many mammal species compared to the others. I have also added electric fish, separately from other bony fish, as an additional complication, although its simplicities should be evident.

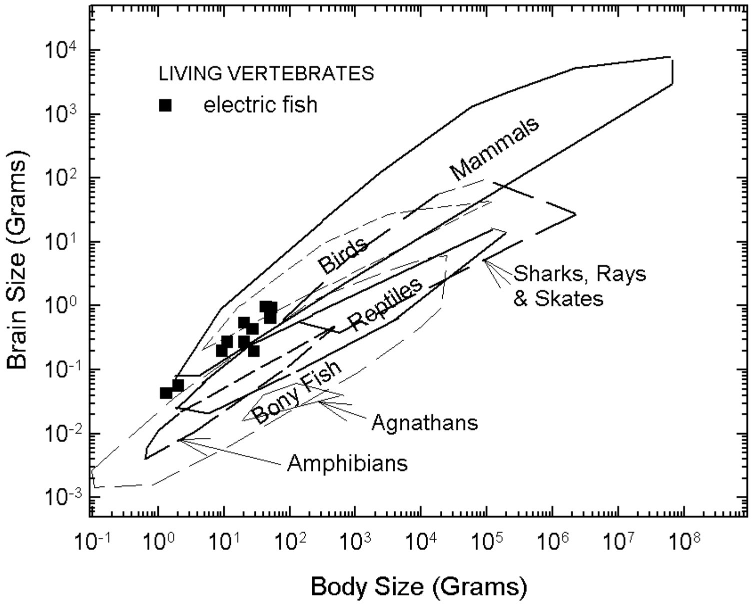

Figure 2. Brain-body relations in 2,018 living vertebrate species enclosed in minimum convex polygons. The samples are 647 mammals, 180 birds, 1,027 bony fish, 41 amphibians, 59 reptiles, 59 cartilaginous fish (sharks, rays, and skates), and 5 agnathans, or jawless fish. Electric fish are Mormyriformes,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

There are many unusual inferences about animal mind and its evolution that can be developed from this simple approach. One unusual inference is on present relationships among living vertebrates. A first general inference: Mammals and birds are similar in "intelligence" as defined here; the relatively small number of species of sharks and their relatives also include many species in the mammalian range of encephalization, and comparative psychologists might well consider that a challenge for their perspective. From the fossil record, the first evolutionary "experiment" with intelligence was in a shark species that lived over 250 million years ago. (This fossil shark is not identified as a point in Figure 2.) We are no longer surprised by the overlapping distributions of mammals and birds, in view of the performance of Pepperberg's (1994) gray parrot and the way pigeons, rats, and people function in Skinner boxes (Skinner, 1957).

The graph of the present situation in living vertebrates in Figure 2 is based on all presently available data. The data of each group are represented by convex polygons drawn to contain all of the individual data. This procedure is illustrated in Figure 4, below, for the living reptile polygon. To the extent that the polygons are distinct one distinguishes the groups from one another, and from Figure 2 we can see the extent to which one is justified in discussing "lower" versus "higher" vertebrates. The sharks and electric fish confound the picture, but the distinction is generally easy to maintain.

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

Of the other living species, the electric fish (Mormyriformes) are also unusual in relative brain size. There is a good clue to the source of their encephalization from comparative neuroanatomy. The electric organs, used by different species of these fish in sensing a variety of things, such as conspecifics, the flow of water, and so forth, project to an enlarged cerebellum, which could be mistaken for cerebrum (Butler & Hodos, 1996). It is a challenge to ethologists and comparative psychologists to measure and analyze the utility of the neural extra processing performed by that system. The analogy might be to the enlarged inferior colliculi in bats specialized for echolocation, since these structures are especially implicated in auditory analysis. We could, in principle, relate their size to the amount of information they handle. The forebrain in these bats is not unusually enlarged, but it is specialized for auditory analysis with enlarged auditory projection areas compared to other sensory areas (Grinnell (1995).

A second and unusual inference from such data can be made by adding evidence from fossils, as shown in Figure 4, below: Dinosaurs did not become extinct because of their stupidity. Their "intelligence" defined by their encephalization was appropriate for reptiles of their body size, and there were some species of dinosaurs that were relatively large brained, perhaps in the size range of living birds (Jerison, in press, a, b, Hopson, 1977). This inference is also interesting in the light of recent conclusions about the relationship of dinosaurs to reptiles and birds.

Most paleontologists have become convinced from their study of the fossil record that birds should be treated as a surviving group of dinosaurs, specialized by feathers and flight and relatively small body size for unusual niches, but this is not well-supported by the evidence of encephalization. Most dinosaur species, as I just mentioned, were in the reptilian range, and the few that were in the avian range (ornithomimids, or "ostrich-dinosaurs") are known from less than 100 million years ago, much later in history than the earliest birds. I illustrate fossil data on encephalization in Figure 4, below, which is also relevant to mammalian encephalization, but do not indicate information on fossil birds. Only a few are known and all specimens lie within the polygon of living birds in Figure 2. They lie near the lower edge of the polygon, but are above the reptile polygon. We know nothing about encephalization in the small dinosaurs most closely related to birds, such as Compsognathus (Ostrom, 1976), a fossil that was a possible contemporary of the earliest bird, and we need the information to clarify the relationships with respect to brain evolution. These were events of more than 150 million years ago, the age of the earliest bird, Archaeopteryx, which was as encephalized as the smallest-brained of living birds, pigeons and gallinaceous birds.

There had to be a transition between a reptilian and avian grade of encephalization, and one needs a fossil record of that period between 150 and 200 million years ago when the transition probably occurred. Within the birds, the enlargement of forebrain characterizing all living birds, the Wulst which is probably homologous to mammalian primary visual cortex, was not present in Archaeopteryx, although it appears in birds known from the late Cretaceous, about 75 million years ago. Brain enlargement that evolved when Wulst evolved presumably had behavioral significance, related to this increase in information processing capacity, but we have no idea what advantages accrued. We may have a sense of their effect by examining the reptile-mammal transition about which there is somewhat more information.

The transition periods are especially interesting for suggesting the specialized neurobehavioral adaptations that might have been met by the evolution of new forms. I have tried to analyze the available information about the beginnings of encephalization in mammals compared to their immediate ancestors among reptiles, the mammallike reptiles (Therapsida). It was possible to develop a scenario that can explain the origins of major mammalian neural, and perhaps behavioral, adaptations, and I will review that scenario in a later section. From an evolutionist's perspective the scenario has features that can be identified in a comparable scenario explaining the evolution of language in the earliest human ancestors, which I will also present. But first, a few more inferences, and a general conclusion about the evolution of behavior and mind as it can be inferred from the analysis of encephalization.

A third inference from the analysis of gross data, evident in Figure 3, below, and based on comparative neuroanatomy, is genuinely surprising. Contrary to recently published claims (Deacon, 1997), the human species does not have unusually enlarged prefrontal neocortex. Although it is large, human prefrontal neocortex is exactly as large as expected in a brain as enlarged (encephalized) as the human brain. Since behavioral functions of prefrontal neocortex are now well understood (Krasnegor, Lyon, & Goldman-Rakic, 1997), the behavioral implications of this result are especially interesting. Despite the small size of the sample, the graph in Figure 3, redrawn from Uylings and Van Eden (1990), is impressive, because the relationship reflected in the almost perfect correlation is so strong. The interpretation is straightforward. If a mammalian brain evolves to human size, it must have prefrontal neocortex that is the size of human prefrontal neocortex because of the way prefrontal cortex is

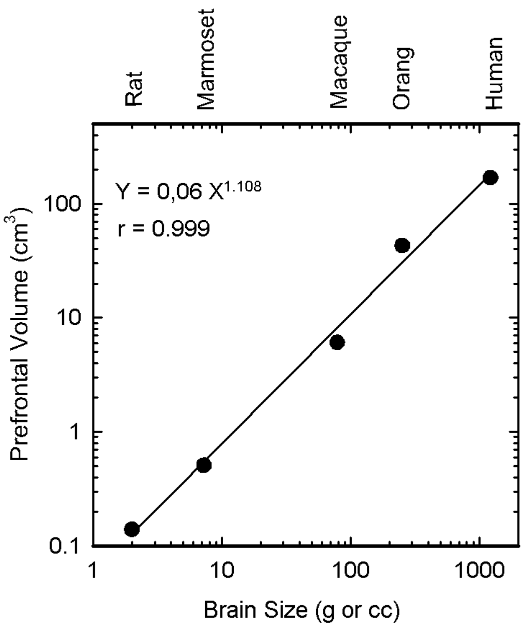

Figure 3. Volume of prefrontal neocortex as a function of brain size. Redrawn from Uylings & Van Eden (1990).

connected to the rest of the brain. There is a kind of symmetry, like the fact that the walls of one side of a rectangular building have to be as tall as the walls of the other side.

The size of prefrontal neocortex reflects the way the brain works in the control of information. If the information is distributed through many regions (Goldman-Rakic, 1988), the size of each region must be determined by how extensively it is connected with other regions. Prefrontal neocortex is often described as an executive organ for brain functions: it controls what many other parts of the brain do. The size of this controller system has to be related the size of the systems that it controls. Because of its extensive network of controls to other parts of the brain, enlargement almost anywhere in the brain for any reason would be reflected in an appropriate corresponding enlargement of prefrontal cortex. The human brain is, in fact, a normal primate brain in all respects except gross size. Given its gross size, however, the sizes of its parts must be appropriately enlarged and this includes the human prefrontal neocortex. The brain "hangs together" and works as a unified system in which the sizes of the parts are appropriate to one another and to the size of the whole brain (Jerison, 1997).

From the quantitative analysis of fossil evidence there are other important inferences, some of which have been common "knowledge" for many years but unsupported by actual evidence. For example, it has usually been assumed that neocortex expanded during mammalian evolution, but only when I analyzed the data quantitatively was I able to support that assumption. I was able to show that the conventional wisdom was correct by analyzing fossil endocranial casts. In mammalian endocasts, neocortex can be identified as cortex dorsal to the rhinal fissure, and this fissure is often recognizable in an endocast. Until I performed the quantitative analysis the situation was in doubt, and very experienced and competent students of this kind of fossil evidence had rejected the idea that such changes had been demonstrated (Radinsky, 1978). The measurements that I could make were primitive, based on two-dimensional lateral views of a large sample of endocasts, but their adequacy for the problem was supported by the fact that in this same sample of species the olfactory bulbs did not change in relative size (Jerison, 1990). The relative size of the neocortical area in two-dimensional projection clearly was greater in later progressive species than in earlier more primitive species during the 60 million years of mammalian evolution that I was able to examine. I have exploited this particular result when I developed a scenario for the evolution of human language, which I present later in this chapter.

Evolutionary Events

The geological and fossil records are now quite well known, and one can present reasonably definite accounts of significant times of change in vertebrate evolution during the past 500 million years. The eras are the Paleozoic (550 to 250 million years ago), the Mesozoic (250 to 65 million years ago, and the Cenozoic (the past from 65 million years ago to the present). These are subdivided into periods (e.g., Jurassic, Tertiary, etc.) and epochs (e.g., Eocene, Pliocene, etc.), which I will date if I mention specific events. If the words are unfamiliar one can always go to a dictionary.

The earliest vertebrates were jawless fish of about 450 million years ago, and the first land vertebrates were amphibians, which appeared between 350 to 400 million years ago. Reptiles appeared about 50 million years later. Because fossil endocasts are available for analysis, and because brains evolved as appropriately engineered organs for their work of controlling the body, one can correlate the evolution of the brain with other events in the history of life. Although there were important changes in the organization of the brain during the Paleozoic era, there is no evidence of measurable encephalization, except in the ~~Permian~~ Carboniferous shark (about ~~250~~ 300 million years old) mentioned earlier. Most species were ~~"lower vertebrates"~~ comparable to their relatives that are alive today. Intelligence as I have defined it did not change significantly during the entire evolutionary history of the “lower” vertebrates (Jerison, 1973). But the variety of behaviors in living species of “lower” vertebrates, which are also at this grade of encephalization illustrates the behavioral diversity that can be supported by an unexpanded nervous system.

The earliest birds appeared in the late Jurassic period, about 150 million years ago evolving from dinosaurian roots, and the earliest mammals in the late Triassic period, about 225 million years ago evolving from the rather different therapsid ("mammallike") reptiles. Birds and mammals were encephalized relative to their closest relatives among the reptiles, with brains two to four times the size of reptiles of comparable body size.

There were major environmental changes at transition times during this history. The most extensive occurred at the end of the Paleozoic era, at the transition from the Permian to the Triassic period, about 250 million years ago. The most popularly recognized extinction, which may have resulted in the final extinction of dinosaurs, occurred about 65 million years ago and was probably caused by a comet or asteroid striking a region near the Yucatan peninsula of Mexico. The latter is called the K-T event (from the German: Kreidezeit-Tertiärzeit) that ended the Cretaceous period of the Mesozoic era and initiated the Tertiary period of the Cenozoic era. Less dramatic extinctions occurred at other transition times. An important one is known have occurred about 35 million years ago, at the transition from the Eocene to Oligocene epochs of the Cenozoic era, during the adaptive radiation of "progressive" mammal species, which I will discuss shortly.

Vertebrate tetrapod encephalization began in the earliest mammalian species which are known from about 225 million year ago. Endocasts have not yet been prepared from those fossils, but from the appearance of the skull one recognizes expansion of the cranial cavity appropriate to the grade of encephalization of the least encephalized of living mammals. The oldest known mammalian endocast is about 150,000,000 years old, from the species Triconodon mordax, a member of a group unrelated to any living mammal, but it is as encephalized as living hedgehogs and opossums. The earliest placental mammals probably appeared about 100 million years ago, and their endocasts are known from at least 75 million years ago (Kielan-Jaworowska, 1986; Jerison, 1990, in press a). All Mesozoic mammals were small, generally the size of mice or rats, and the largest was the size of a house cat. They were all encephalized to about the same extent, two to four times that of reptiles. This level of encephalization was stable for all of the Mesozoic and for the first 10 million years of the Cenozoic, an interval of about 170 million years, illustrating the conservatism of brain evolution.

For completeness I outline now the evidence on major mammalian encephalization during the Tertiary period of the Cenozoic era. There is insufficient space to discuss this record in detail or to suggest scenarios to explain it. That was a major goal of my book on the subject, which I published a quarter of a century ago (Jerison, 1973). Mesozoic and early Cenozoic mammals were at a kind of steady-state of the evolution of encephalization with brains averaging about 1/3 the size of average living species. The grade persists today among all insectivores and many marsupials, and is best represented by the Virginia opossum (Didelphis marsupialis).

I have graphed most of the available data on that grade of evolution in Figure 4. I also show some data on dinosaurs and illustrate with the data on living reptiles the way such data are analyzed non-parametrically with convex polygons. The long period of stability in encephalization suggests that the mammals had discovered rather stable niches, and that after the end of the Mesozoic, following the great extinction of larger land animals such as dinosaurs, they radiated into new niches with relatively little requirement for enhanced capacities at processing information.

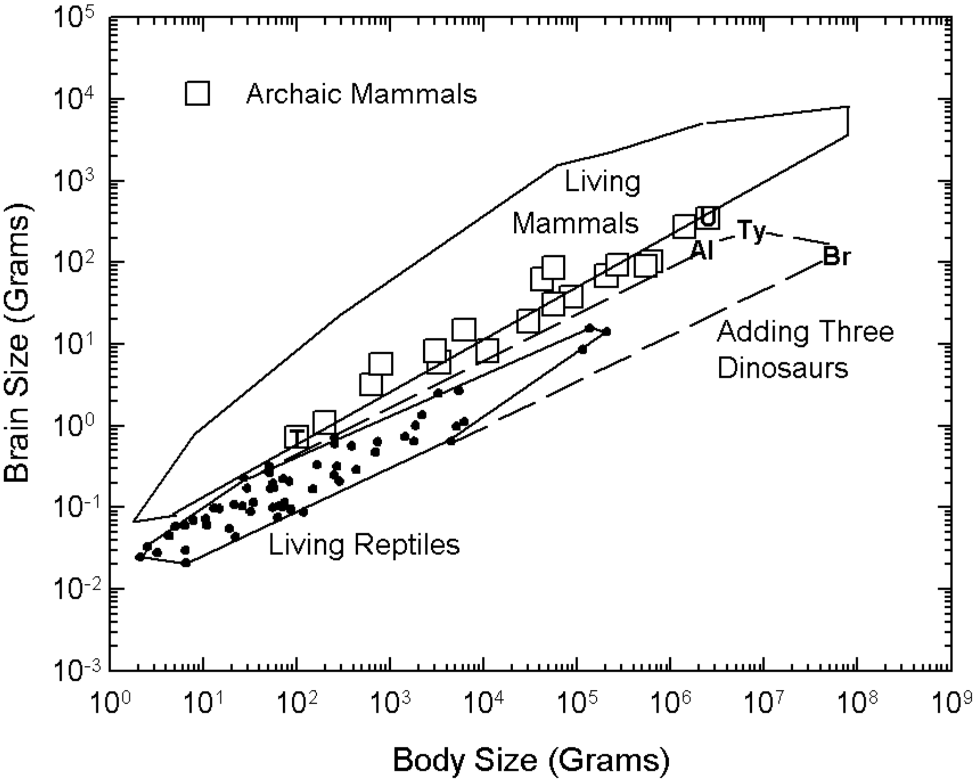

Figure 4. Brain-body relations in mammals and reptiles, each class enclosed in a minimum convex polygon. Labeled archaic mammals are the Mesozoic Triconodon mordax (T) and the early Cenozoic Uintatherium anceps (U). Labeled dinosaurs are Allosaurus (Al), Tyrannosaurus (Ty), and Brachiosaurus (Br). Data points on living reptiles illustrate the construction of a minimum convex polygon of minimum area to contain all the points within a polygon with no interior angles greater than 180 degrees. Adding the dinosaurs merely extended the reptilian polygon to be more like that of mammals, when the body size range was extended.

Primates are among the most ancient of living orders of mammals, with suggestions that they may have appeared during the Cretaceous period at the end of the Mesozoic, as long as 70 million years ago. They are relatively common fossils of the Eocene epoch (extending between 55 to 35 million years ago). Primates appear always to have been more encephalized than their contemporaries, and this was true of the many lemur-like species that had appeared during the Eocene. Their contemporaries averaged EQ of about 0.3 or 0.4, whereas the Eocene primates ranged between 0.5 and 0.8 on this measure of encephalization. Primate brains of the time also had distinctly modern shapes, surprisingly similar to those of living lemurs. However, all of the living orders of mammals had appeared by that time, at least 35 million years ago, and some advance in encephalization can be recognized in these species. During the late Eocene there is evidence of the earliest of the anthropoid primates, but encephalization in these animals was still in the range of their lemuroid contemporaries, about EQ = 0.5.

There was increasing diversification in mammalian adaptation during the Eocene epoch, and although they had not reached a primate grade, other progressive orders of mammals had appeared and their species were somewhat more encephalized than the archaic orders, which is evident even on casual inspection of their endocasts (Radinsky, 1978; Jerison, 1990). (The descriptions "archaic" and "progressive" refer merely to whether an order has become extinct.) The brain evolved conservatively, and the pattern of change is best described as punctuated equilibria for most vertebrate lineages, with long periods of stasis in relative brain size. The rapid recent evolution of encephalization in the human lineage, beginning in the Pliocene epoch about 4 million years ago, was unusual.

The transition from the Eocene to the Oligocene epoch 35 million years ago, signaled a significant effect on the appearance of the mammalian brain as well as on its relative size. Geologically the time is known as the Grand Coupure, a period of significant mountain building and related activity. Perhaps this explains the enlarged and more modern-looking brains represented as fossil endocasts in many species. But the convolutions are identifiably arranged as in modern species, and the degree of encephalization appeared to reach the level of the living descendant species. The record is quite good for the orders Carnivora, Artiodactyla, and Perissodactyla, the living carnivores and ungulates. Major gyri and sulci are clearly identifiable, and labeling systems used for living brains are easy to apply to the fossils. Encephalization had approached or reached the level of average living mammals, defined as EQ = 1.0. There is only one well-studied primate species of that age, the 30 million year old Rooneyia, a tarsier-like form that had lived in Texas. Its skull and brain are both larger than but remarkably like that of living species, and its encephalization has been determined as at least EQ=1.5. By the transition from the Oligocene to the Miocene epoch (about 20 million years ago), the level of encephalization in mammals was comparable to that of their living descendants, excepting only the major developments in the human lineage, which can be traced to the beginning of the Pliocene, with evidence on the brain available beginning almost 4 million years ago. I review that record briefly, later, as part of a speculation on the evolution of language.

Selection for Encephalization: Reptiles into Mammals

Brain tissue is metabolically among the most expensive of bodily tissues (Aiello & Wheeler, 1995). Evolution is often thought of as an optimizing process in which costs are balanced by benefits, and the question is: "What benefits were associated with the enlargement of the brain in these mammals to make its energetic cost worthwhile? The answer has to be speculative, of course, since we were not on the scene when the critical events occurred. The issue is to present a reasonable scenario. With a few calculations on living brains, I develop such a scenario on the basis of how reptiles and mammals presently use information about the environment to guide their movements. I follow the uniformitarian hypothesis, a version of parsimony that states that the laws of nature in the past were the same as in the present (Simpson, 1970).

During much of the Paleozoic era the synapsids and therapsids, the "mammallike reptiles," were the dominant land vertebrates. Archosaurians, or "ruling reptiles" including dinosaurs, first appeared at the end of that era. The mammallike reptiles became extinct at about the middle of the Mesozoic era, and the archosaurians had become extremely diversified by that time and throughout that era. The behavioral scenario to describe the changing environments tracked by natural selection begins by recognizing that most Paleozoic reptiles were diurnal and relied primarily on visual information to guide their movements. I suggest that the therapsids became extinct when the ruling reptiles displaced them in diurnal niches, and that aberrant nocturnal "therapsids" that we know retrospectively as mammals survived. The earliest mammals had evolved adaptations for nocturnal niches in which they did not face competition or predation from archosaurians.

Life in nocturnal niches depends on sensory modalities other than vision. I am concerned here only with sensory-perceptual adaptations, although other adaptations such as endothermy and the evolution of small body size are also obviously important. For my scenario I calculate the amount of neural machinery required for nonvisual senses to be computationally equivalent to the visual system. For convenience, I work with auditory information, as if the earliest mammals were batlike in relying on echolocation. We know that living bats construct a three-dimensional world from such auditory information, and that their world is comparable to our visual world (Grinnell, 1995). Visual and auditory senses for distance information might both be spatial senses, but the neural machinery for vision and audition is packaged in different ways.

The neural control of visual information in amphibians and reptiles involves significant amounts of information processing that occurs in the neural retina of the eye (Lettvin, Maturana, McCulloch, & Pitts, 1959). Additional processing is performed at subcortical neural centers such as the superior colliculi, and although some analysis may take place in their forebrains, these species have no cerebral cortex. Processing at the level of the colliculi appears understandable in the framework of signal detection theory as distinguishing neural signals from neural noise (Ewert, 1974; Roth, 1987).

From data on living species, one can estimate that there were several hundred thousand retinal ganglion cells in each eye of the reptilian forbears of the mammals. There may have been several million nerve cells in other layers of the neural retina (cf. Polyak, 1957; Roth, 1987) and comparably large numbers of photoreceptors. The computational problem is to determine the effect on the organization of the brain if one were to replace the reptilian diurnal neural retinal system with other neural sensory systems. This had to be accomplished by early mammals if their movements after dark were to be coordinated with information about the environment.

If in the earliest mammals the auditory system were to evolve as a primary system for distance information, the sensory information and the location of the neural control networks would be quite different from that in the visual system. In living reptiles there are only between 50 and 1,000 sense cells (hair cells) in each cochlea, indicating that hearing has a relatively minor role in their lives (Wever, 1978). However, even in mammals such as bats, where we know that the auditory system is critically important, there are only about 35,000 sense cells (hair cells) in each cochlea. This number, so much smaller than the number of photoreceptors, is typical for all living mammals.

The neural analysis by any sensory system converts sensory data into information about the external environment, and the initial information received by the sense cells has to be analyzed by neural networks elsewhere in the system. This analysis itself could be similar in auditory and visual systems. We know how that analysis can take place in the neural control in Ewert's toads, a signal detection analysis of neural data in the colliculi, which enables them to "know" how to catch a fly. The amount of analysis might be similar for an equivalent analysis with the auditory system, for example, in the way echolocating bats catch moths (Grinnell, 1995). This is more detail than we need to know about how the system might function, however. Our problems are only how large the system must be and where it would be packed.

These are packaging problems. It may take as many as 5,000,000 neurons in each retina of a reptile, or 10,000,000 neurons in all, to process information about the environment useful for the control of movement. We can assume (as a first approximation, of course) that this is the number of neurons that would be required to do the same job with auditory and other nonvisual modalities. In no nonvisual system is there a peripheral structure comparable to the neural retina as a place to pack the neurons of the network. For example, in the peripheral auditory apparatus there is space beneath the basilar membrane of the cochlea for the auditory bipolar cells, but no more than the same number of bipolars as hair cells can be stored there.

The argument also follows, with somewhat more detail, from the hierarchical structure of the networks. Retinal photoreceptors in reptiles communicate directly with as many as 1,000,000 first order retinal bipolar neurons, which then communicate with even more "association neurons" in the retina, and it is these that communicate with the ganglion cells, which are the cell bodies of the optic nerve. The retinal neurons for processing visual information are, thus, second, third, or fourth order neurons in a synaptic chain. The comparable hierarchy in the auditory system in all living vertebrates has a maximum of 70,000 first order bipolar neurons peripheral to the brain in the spiral ganglion. The second, third, and fourth order auditory neurons are all in the brain, proper. They are in the medulla, midbrain and thalamus in lower vertebrates, and in mammals there is an additional level of neural processing in the neocortex. If the early mammals were to do with hearing (and other modalities) what their reptilian ancestors did with vision they had to evolve networks to do the equivalent processing, presumably with a similar hierarchical structure. As we have seen, something of the order of 10,000,000 neurons are in the retinal neural networks, and for the other modalities to do the job, this is the number that would have to be packed in the brain.

This is the same as the total number of cortical neurons in the half-gram mouse brain (Braitenberg & Schüz, 1998). If we were to provide neural machinery for the information-processing performed in the neural retina of a reptile to processing done by nonvisual neural machinery in the brain proper, we would have to add the equivalent of a mouse brain to the pre-mammalian reptile brain. We have to add about 0.5 g of brain.

With these numbers we can turn to quantitative data on fossils (Jerison, 1973). To model the reptilian ancestors of mammals I take the unusually small (for early reptiles) lower Triassic (about 250 million years ago) therapsid, Thrinaxodon, which weighed about 500 g and had an 0.4 g brain. As the early mammal, I take the upper Jurassic (about 150 million years ago) Triconodon, which may have been a bit large for a mammal of the time. It weighed about 100 g and had an 0.7 g brain. Evolving from a Thrinaxodon-sized therapsid to a Triconodon-sized mammal required a half order of magnitude reduction in body size and an appropriately adjusted brain size. From a regression analysis of the data of Figure 4, I can estimate the expected brain size in a 100 g reptile as 0.15 g. To transform the therapsid into Triconodon we would add the difference between 0.7 g and 0.15 g, or 0.55 grams of brain, a four or five-fold increase in brain size. The transformation added a mouse-sized brain, as it were, the right amount according to our calculations.

Mammalian Intelligence

We now have a complete answer. The amount of encephalization that occurred when the earliest mammals evolved can be explained as a solution of a packaging problem of where to put the extra processing machinery for the sensory systems (10,000,000 neurons) that had to replace or supplement vision. From comparative neuroanatomy we infer that the extra machinery was packed into a new neural forebrain structure that evolved in mammals, the cerebral cortex. However, sometimes even a simple solution has complications, and one effect of this kind of packaging may be the major clue to the relationship of encephalization to intelligence.

Several different nonvisual systems would have contributed information for this scenario, in particular the auditory, olfactory, and tactile systems. In addition, the visual system could continue to provide information about the external environment for a nocturnal species, provided that it evolved to be sensitive to weak visual stimuli that are available in the evening or at night. The rod system of the retina, basically a mammalian specialization, is appropriate for these responses. There are, thus, four different neural systems to provide information about the external environment, and in living mammals they are packed into different regions in the cortex.

The complication for the operation of these systems occurs because the information from the different component systems would refer to a common set of events in the external environment. The neural response to the information from each modality would presumably be similar to that recorded from the superior colliculi of Ewert's (1974) toads. These consist of bursts of firing of nerve cells in a network, and there would be no way to identify the bursts as having originated in a common environmental event. The analysis of the information from several sensory systems would have to be integrated in some way, and more neural machinery would be required to effect the integration.

The integration presumably took the form of identifying common features in the information from each modality, such as a description of the source as an object in an external world. There would also have to be codes with regard to where the object was and when the object was sensed. In short, the integration would be by translating the neural patterns into a common code to represent events in the external world as objects placed in space and time. From a computational perspective, the brain's problem is a pattern recognition problem rather than a simple signal detection problem. In more classical terms, one might consider the problem as the creation of perceptual worlds or Umwelten (von Uexküll, 1934/57), and this seems to me a good characterization of the work of a mammalian brain, in particular of the cerebral cortex. In effect the brain's work is to create a real world, or in less dramatic terms, to provide knowledge about the real world. This is very different from a brain as a reflex machine implied by Ewert's toads.

If I were to go beyond my definition presented earlier in this chapter, it would be to restrict "intelligent" processing to pattern recognition. I would attempt to distinguish this kind of integrative activity from the brain's work as a reflex machine, although one assumes that both integrative and reflex activities occur in all mammalian brains. The critical added processing is the creation of a real world by the brain, as it were, or in less dramatic terms: the processing supports the integrative activity that enables an animal to know the real world. This seems to me a fundamental feature of intelligence in any animal. One reason to resist going beyond the working definition, however, is the difficulty one would face in attempting an operational "bottom up" approach within such a definition. At a fundamental level, one would have to specify purely neural distinctions between pattern recognition and signal detection. In direct analysis of neural activity it is impossible to make such a distinction. The computer analogy is to attempt to distinguish, in a blind test, between small samples of machine code for a pattern recognition program from samples of code during a signal detection program and to identify the programs. It is presumably possible, but it would be a formidable problem in cryptanalysis.

Brain and Perception

Since I have tied the evolution of intelligence to the evolution of encephalization, and since I analyze the major advance in encephalization that occurred when the mammals evolved as having involved a shift in perceptual modalities, I must comment on the brain's role in perception. It is conventional in neuropsychology to draw maps of the brain indicating localized sensory and motor areas, and in older maps one drew "silent areas" representing association cortex. That view has been recognized for several decades as unsustainable (Diamond, 1977). Association functions that relate the activities of sensory and motor systems to one another are intercalated among the sensory and motor areas, and those areas extend over almost the entire neocortex (Jones & Powell, 1970). There are no silent areas. Furthermore, we recognize that sensory analysis at the level of the neocortex usually involves multiple projections of superficially similar information. There are many duplicate maps of the body on the brain, including at least a dozen separate projections in the primate brain from different parts of the visual field (Zeki, 1993). If one had to describe neocortical functions in very few words it would be that they control perceptual and voluntary motor performance, and neocortex evolved in response to requirements to enhance such performance. The enhancement added the cognitive dimension.

"Images of mind" (Posner, 1994), determined by metabolic activity in the brain and recorded as PET and functional MRI scans of the living brain, show that foci of activity correlated with behavior and experience are spread through many parts of the brain. Although such images demonstrate localized activation by specialized human mental activities, the "local" regions are very extensive. There are about 15,000,000 neurons under a square centimeter of cortex (Rockel, Hiorns, & Powell, 1980), and a typical human brain scan localizes activity in at least several square centimeters of cortex. A "localization" thus involves a very wide area and very large amounts of processing capacity. One should note, too, the extent to which there are multiple activation patterns, which suggest interaction among parts of the brain. There are usually several regions of maximum activity rather than a single focal region responsive to a mental activity. The extent to which functions are localized is partly a function of the way the measurements are performed. Localized functions are measurable as activity in single nerve cells, but these cells are presumably parts of extensive networks of neurons. All or almost all of these networks process information from the external environment. Most significantly, these networks, which can be characterized as supporting perceptual and cognitive processing, can account for essentially all of the cortical surface.

In the quantitative example of mammalian encephalization as the solution to a packaging problem I "explained" the increase in brain size as related entirely to perceptual and cognitive processing. The additional tissue was assumed to be doing sensory analysis of the kind done in the neural retina of frogs (Lettvin et al., 1959) and that it was also integrating that analysis as knowledge of a real world. It is interesting that when one analyzes the work of the brain in living monkeys and humans, one also correlates neural activation with handling information from the external world. We describe the behavioral aspects of the work as attending and responding to images, sounds, words, and ideas (Posner, 1994). Returning to the computer analogy, the point can be made that good pattern recognition is the most demanding work that computers can do and requires the most processing capacity. One can reach a similar conclusion about brains. To generate knowledge of the external world, to perceive that world and understand its structure and function, is the brain's most demanding work and is the basic reason for the brain's enlargement. I have tried to show how this was true early in mammalian evolution, and I believe that it remains true in living mammals, including humans.

Hominid Encephalization 1. The Beginnings of Language

The evolution of a prehominid anthropoid into a hominid species occurred early in the Pliocene epoch, perhaps 4 or 5 million years ago. Present evidence is that we humans share our prehominid 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, 1978). 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., 1993). 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, like us, chimpanzees have a knowledge of self.

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 any 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." I am as impressed as everyone else by the remarkable performance, but I believe that the extraordinary performance of chimpanzees in languagelike activities involves different cognitive capacities than the ones we humans developed. 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. It is a theme that has its roots in the kind of analysis presented earlier of the origin of mammalian encephalization.

Hominid Encephalization 2. Size of the Neurolinguistic System

My analysis begins with the neurological status of language, namely, that it is controlled by an enormous neocortical system. As I argued earlier, very large neocortical systems evolved in mammals to control activity that should be described as perceptual and cognitive. I distinguish these from three other major psychological categories, namely <u>learning</u>, <u>social behavior</u>, and <u>communication</u>, which occur in all vertebrates and can be controlled by very small nervous systems. When their neural control is large, I think of perceptual-cognitive dimensions as having been added to, say, social behavior, or communication. From my perspective, human language is, therefore, a priori a perceptual-cognitive adaptation.

To identify selection pressures that were effective during the prehominid-hominid transition and that 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, because 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 pre-hominid or early hominid primate. 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.

Hominid Encephalization 3. Social Predation

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. Meeting those requirements would strain the neural processing capacity of an anthropoid primate species, however, despite its being more than twice as encephalized as wolves, because anthropoid primates had 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^2. 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 but the expected size suggested by data on other land mammals (Jerison, 1991). Wolves are, therefore, properly recognized for their excellent olfactory sensation and perception. The brain systems receiving the olfactory information include the piriform lobes and schizocortex, and eventually hippocampus. We know very little about how olfactory information is used in cognition, partly, of course, because we humans are peculiarly deficient in that sense modality. Our intuitions about how olfaction would work 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 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. The system would have access to all of the mapping and memory functions in which hippocampal control occurs. We should imagine the perceptual world constructed by a wolf from olfactory information as based on input from olfactory bulbs coupled with appropriate analysis by hippocampus, paleocortical, and neocortical structures. The wolf's "model of reality" would be an experienced real world that corresponds more to the one we humans build from visual information than to the one we build (or fail to build) from odors.

There is a neurobiological problem for an anthropoid species adapting to a social predator's niche. An anthropoid primate has the right central neural machinery for the adaptation -- appropriately large hippocampus and related structures. But because the system as a whole in all mammals is normally coupled peripherally to the olfactory bulbs, it would be unlikely to work as well when coupled 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 a 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. The other access, I propose, was primarily by the use of the auditory-vocal channel, which is highly developed in anthropoid 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 could be with a very small vocabulary. A model for that might be the three "word" vocabulary of vervets to signal the presence of eagles, or leopards, or snakes (Cheney & Seyfarth, 1990). The hominid vocabulary would have to be larger to encode relevant environmental features, less rigid to be reponsive to more diverse 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. It would be a new perceptual-cognitive system. This new "language-sense" would interact with the very elaborate older mammalian perceptual-cognitive systems that are based on vision, touch, and other senses. The older systems enable chimpanzees to be so much like humans in so many ways, but we humans probably know them only in a distorted way. Our own knowledge of the external world is elaborated by the language dimension -- built not only from sensory mappings that we share with other anthropoids as well as most mammals, 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.

Hominid Encephalization 4. Language, Cognition, Communication, and Consciousness

As I have pointed out before, animal communication is normally a system of commands to other animals that can be thought of as having co-evolved 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 (Cheney & Seyfarth, 1990). In any case, normal animal communication could be a purely reflex system without a cognitive dimension.

The feature of human language that my scenario would emphasize is that it began as a cognitive rather than communicational adaptation. 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 is fairly obvious. 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.

This view of language leads to an unusual view of the nature of human consciousness in an evolutionary framework. 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? This is the more important biologically, because the evidence is overwhelming that all birds and mammals are conscious in this sense, and this may also be true for other vertebrates. Herrnstein (1985) has shown that pigeons can identify faces that people miss, presumably from pictorial cues. Griffin (1976) has argued persuasively for a universality for this kind of consciousness, or awareness. 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 such a 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, that is, when we see and hear and touch things. 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 generated 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.

Final Remarks

In view of my emphasis on the importance of encephalization for understanding the phenomena studied by comparative psychologists and as a foundation for theory, let me conclude, first, with some words of caution from the honeybee's world. In insects the analogues to the vertebrate brain appear to be head ganglia called mushroom bodies. These "brains" are largest in roaches, bees and wasps but contain no more than about 400,000 neurons (Erber, Homberg, & Gronenberg, 1987). Mice, which are among the smallest of vertebrates, have half-gram brains (about one-fiftieth of an ounce) with about 10,000,000 neocortical nerve cells, and 30,000,000 additional brain cells, mainly in the cerebellum. The data on the mouse are from Braitenberg & Schüz (1998), who also note that there are about 80,000,000,000 synapses in the mouse neocortex. The vertebrate numbers are very large. Those of insects are small. Yet behaviorally, in the analysis of learned behavior, honeybees cannot be distinguished from mice, rats, or other vertebrates on the tasks Macphail (1982) reviewed. Although he is not especially sympathetic toward Macphail's conclusions, Bitterman (1988) performed the required experimental analysis of the behavior of honeybees. Animals evidently do not live by brains alone, even for their "higher mental processes." The result is perplexing, and exposes an obvious gap in our understanding of intelligence. But in this essay on comparative psychology I have defined intelligence in terms of encephalization, which is measurable only in vertebrates, and I hope I am forgiven for simply excluding the clearly different set of adaptations and control that evolved in insects from this analysis. There is no fossil evidence at all on the evolution of "brain" size in insects. I agree with Bitterman's judgment that the result is due to convergent evolution, and would assume, further, that the neural mechanisms underlying the behavior are likely to be quite different in invertebrates and vertebrates.

The narratives to illustrate the value of my approach are conventional evolutionary scenarios, which seek features in the ecological niche "invaded" by an evolving species that make a particular adaptation more successful than the related adaptation of the ancestor species. In the most general terms, having a brain is an adaptation for controlling a body, for moving about in the world (if the animal is motile, as are most living vertebrates), and for exercising other forms of control. How does a larger brain improve an animal's chances to survive and reproduce? Human intuition usually attributes the improvement to the ability to think deeper and better thoughts, but that really makes no sense in the larger scheme of things. The improvement has to be related to better control of action and reaction tied to some environmental change that made the previously evolved method of neural control less effective than it was in the previous "normal" environment. It can never be anticipatory of greater opportunities but must be a response to a present challenge. If it appears to be anticipatory it must be understood as preadaptive, an evolutionary accident that made a valid and useful adaptation applicable to a different environmental challenge that had not affected its initial viability. My scenario on language emphasizes this view, since I reject the possibility of the origin of language in a requirement for communication. Such a requirement would have led to very different adaptations, with less uncertainty about the meaning of the message and a smaller investment in neural machinery.

In every instance, encephalization is a solution involving packing more material into the control system, and there has to be a reason for putting more in. My two narratives had different reasons because different environmental changes were being coped with. For the earliest mammals it was not so much a changed environment as the availability of an unexploited nocturnal environment. In my tale of human origins, including the place of language, I assumed a chimpanzee or gorilla-like life that was challenged by an environmental change that reduced the available habitat. Although some predation is a normal part of anthropoid life in the living chimpanzee, it is not the major requirement that I described in my scenario. I should note here that predation may not have been essential. A scavenger's life involving an extensive range would have essentially the same challenges for a chimpanzee-like primate.

My analysis also emphasizes that information-processing capacity is what is gained when there is encephalization. It emphasizes cognition rather than purely motor skills such as throwing (cf., Calvin, 1983; Wilkins & Wakefield, 1995), or scenarios about the nutritional systems that enable encephalization by improved nutritional capacities (Falk, 1992; Martin, 1990). I do not reject approaches emphasizing such dimensions, but I believe that the driving environmental forces that actually supported encephalization as an adaptation were those that could be met only by additions to the total information-processing capacity of the brain.

I have just noted the great difficulties that would be faced if one attempted to extend the analysis to insects, but there is no difficulty in the case of birds. There is a fair consensus now that the bird's forebrain is homologous to that of mammals, although the structure homologous to mammalian cortex is not layered and has the superficial appearance of enlarged basal ganglia (Karten, 1991). That structure, nevertheless, could support the control of avian behavior, which, like that of mammals, could only be effected by enlarging the control system. The details will, of course, be different in birds and in mammals, just as they are different among species of mammals, but the strategy of the analysis is the same.

To conclude, let me restate an important limitation of my approach that I think limits any theory of comparative psychology. Tying mind and its evolution to the evolution of encephalization rather than to that of small systems in the brain implies a particular, and I believe correct, view of what evolved when higher mental capacities evolved. Were we to focus on regional specializations in the brain, even on very large regions such as the prefrontal neocortex, we might consider a notion of modular control in which the subsystems that can be identified could have evolved independently of one another. The evidence of the brain and of the way it "hangs together" suggests that independent evolution of either behavioral or morphological modules did not occur. There could always be dominant modalities that might have driven the process, but the evolution of a modality had to be accompanied by the evolution of the systems connected to its operation.

The evolution of such a system involves a genetic code, and we have no sense of how a genetic code might specify the control complex mental performance. Codes can specify only simple things, such as the structure of molecules. I suggested the level of complexity that can be encoded in my example at the beginning of this chapter of how to generate the correct number of neocortical neurons in a hominoid. I have no idea how code could be written at a molecular level to specify localized functions of sensory-perceptual systems. Grand theories of comparative psychology should be evolutionary theories in which such codes are among the elements. My elements remain information-processing units, and my theorizing has been on how and why their number changed in vertebrates under natural selection.

Finally, an odd feature of the genetic code as it must be written to account for nature-nurture interactions is that it must, in some sense, include a representation of the environment. A code for neural growth might have the form: "grow branches in all directions but let only those branches survive that run into a particular biochemical environment. Another code might be written to lay down appropriate environments within which growth could occur. By mapping the layouts of the environment the details of growth could be regulated without having to have the full map encoded in the genetic material. The extent to which a mature nervous system is described by the genetic material is nevertheless remarkable, as indicated by the general uniformities of structure and function. All humans have language, presumably because of code in our genetic material. All mammals have identifiable and comparable maps in their brains that label information as visual, auditory, and so forth. All vertebrates have brains divided into at least forebrain, midbrain, and hindbrain. These must be uniformities imposed by the genetic code in each group, and variations in the codes are what evolved. All primates have visual cortex, but if they are deprived of visual experience it develops incorrectly, so the code to direct embryonic neurites growing in an embryonic brain to become elements of the visual cortex also depends upon (or assumes) the experience in some way. We have no idea how this is done. That is the problem of encoding the environment to be tracked by natural selection, and this confession of ignorance may be a good note on which to end.

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