Animal Intelligence as Encephalization [and Discussion]

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Animal intelligence as encephalization

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There is no consensus on the nature of animal intelligence despite a century of research, though recent work on cognitive capacities of dolphins and great apes seems to be on one right track. The most precise quantitative analyses have been of relative brain size, or structural encephalization, undertaken to find biological correlates of mind in animals. Encephalization and its evolution are remarkably orderly, and if the idea of intelligence were unknown it would have to be invented to explain encephalization. The scientific question is: what behaviour or dimensions of behaviour evolved when encephalization evolved? The answer: the relatively unusual behaviours that require increased neural information processing capacity, beyond that attributable to differences among species in body size. In this perspective, the different behaviours that depend on augmented processing capacity in different species are evidence of different intelligences (in the plural) that have evolved.

Structural encephalization is a morphological phenomenon, the enlargement of the brain beyond that expected from the enlargement of the body. Since brain size is proportional to neural information processing capacity (between species; see below), the evolution of encephalization was, essentially, the evolution of an increase in information processing capacity. This is obviously important for the evolution of animal intelligence, and it is one of the reasons for the interest in encephalization.

Among vertebrate species, brain size is determined mainly by body size. The relation is described as the brain–body allometric function, which has been estimated from the regression of log brain size against log body size in appropriate samples of species (Martin 1983). Encephalization is then the increase in brain size beyond that expected from the allometric brain–body relation. As a quantitative exercise, encephalization, or the increase in *relative* brain size, is often determined by calculating the residual for a species relative to the allometric regression; the residual is an 'encephalization quotient' (Jerison 1985).

The importance of relative brain size, or encephalization, has been recognized since classical times (see Jerison (1973, 1982) for historical reviews). In this essay I follow an outline implicit in a seminal statement by Karl Lashley, in his presidential address on the evolution of mind, presented before the American Society of Naturalists. He stated the issues as follows.

> The only neurological character for which a correlation with behavioral capacity is supported by significant evidence is the total mass of tissue, or rather, the index of cephalization...which seems to represent the amount of brain tissue in excess of that required for transmitting impulses to and from the integrative centres. (Lashley 1949, p. 33.)

I have a sentimental reason for organizing this essay according to Lashley's outline, because my first work in this area was inspired by these words. But I am also convinced that his approach leads to fundamental insights into the nature of intelligence as a biological phenomenon. 'Behavioural capacity' is clearly the same as 'animal intelligence', the central issue in this discussion. The index of cephalization is an encephalization quotient, which I will treat in a qualitative, pictorial way, rather than with numerical residuals. (To compute residuals we have to make assumptions that unnecessarily complicate the analysis and are not really needed here (see Jerison 1985).) The idea of 'excess brain tissue' takes us to the meaning of absolute brain size. This essay on intelligence, encephalization, and brain size may be thought of as a set of variations on Lashley's theme. I will change only the order of the topics, first discussing the evolution of encephalization and the meaning of brain size as background for the later discussion of animal intelligence.

Lashley began with the idea of behavioural capacity, or intelligence, as if there was consensus about its meaning. In the search for a neurological correlate for this 'well-understood' trait, he noted that at mid-century the only correlate that had been discovered was encephalization, but further research could presumably lead to the discovery of more and finer correlates. I propose that encephalization is, in fact, the fundamental trait and that it may be fruitless to seek finer correlates of intelligence. Finally, although there is no real consensus on intelligence, some unusual features of both human and animal intelligence about which we can agree may be better understood if we assume that the biological foundations of intelligence are in encephalization. I, therefore, begin with the neural correlate, and conclude by analysing animal intelligence in terms of encephalization.

1. Structural encephalization

Brain and body masses are known for hundreds of species of vertebrates and provide the fundamental data on structural encephalization. Minimum convex polygons drawn to contain the log data of each class provide the simplest and clearest picture of how the allometric and encephalization factors determine brain size. Figure 1 summarizes such data in the major living

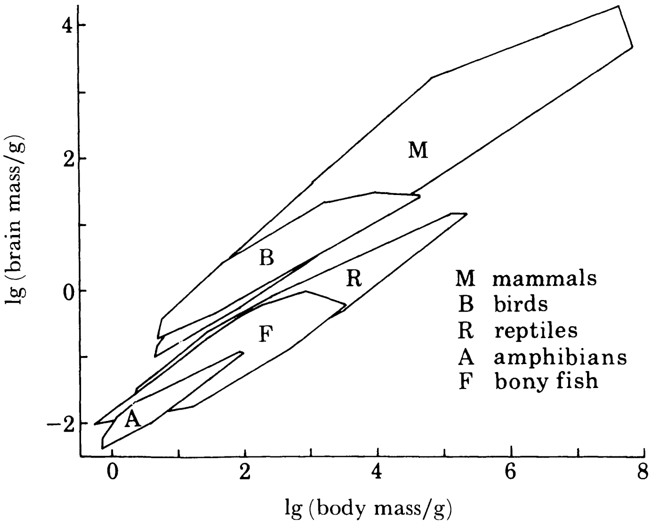

Figure 1. Brain–body relations in living species from five vertebrate classes. Mammals and birds from Martin (1981, 309 species of placental mammals and 180 species of birds); bony fish (Ridet 1973; 46 species), amphibians (Thireau 1975; 40 species), and reptiles (Platel 1979; 48 species). The polygons are minimum convex hulls drawn about the data of each class. See also Jerison (1973).

groups. This graph can be interpreted as a map of evolutionary opportunities in brain–body relations that have been realized in living species. It shows the regions in 'brain–body space' occupied by living species that are at various grades of encephalization and summarizes the present adaptive radiation of vertebrates. When supplemented by fossil data the graph suggests the constraints on the evolution of the brain–body system that limit the amount of brain that can evolve in a species.

The arrangement of the polygons justifies the division of the vertebrates into 'higher' and 'lower' groups with respect to encephalization. The angular orientation of the polygons, easily imagined as dispersions about regression lines, expresses the allometric factor, and the vertical displacement of the higher from the lower sets of polygons expresses the encephalization factor.

Were they added to figure 1, data on the classes Chondrichthyes and Agnatha, the cartilaginous fish and jawless fish (see, for example, Ebbesson & Northcutt 1976; Northcutt 1981), would complete this picture of the present adaptive radiation of vertebrates with respect to encephalization. The chondrichthian polygon lies between those for lower and higher vertebrates and overlaps both. Some sting rays are at a mammalian or avian grade, and that favourite 'primitive generalized vertebrate' of the comparative anatomy class, the dogfish (*Squalus*), is more encephalized than any of the 'lower vertebrates', lying near the lower bound of the higher vertebrate polygons. Sharks are, thus, intermediate rather than lower or higher. A chondrichthian polygon was omitted from the graph for didactic reasons, to maintain the clarity of the distinction of lower from higher vertebrates with respect to encephalization.

Data on living lampreys (*Petromyzon*) fall well below the 'lower' vertebrate polygon. Interpreted as an evolutionary record this could imply that the transition from an agnathan to gnathostome grade may have been the first advance in encephalization in vertebrates, since the earliest fossil vertebrates of about 450 million years ago were agnathans, and the jawed fish did not appear until about 50 million years later. Living agnathans, which are parasitic, are usually thought of as degenerate descendants of free-living species, however, and it may be that the ancestral agnathans were comparable to living fish in encephalization. The issue is of the kind that can sometimes be resolved by the fossil record.

Mappings such as those in figure 1 are the framework for interpreting an extensive fossil record on brain size, developed from the analysis of fossil endocranial casts (endocasts) for which the cranial cavity is the mould. From studies on living species we know that in birds and almost all mammals endocasts provide excellent pictures of the external surfaces of freshly dissected brains. These are less adequate in lower vertebrates, but are often good enough to enable one to estimate total brain size. Hundreds of fossil vertebrate endocasts are available for study, and together they provide a detailed record of the history and evolution of the brain (Blumenberg 1983; Edinger 1975; Hopson 1979; Jerison 1973; Radinsky 1979). Although there is occasionally some disagreement on method, it is relatively easy to estimate body size in fossil species in which enough skeletal material has been preserved. It is, therefore, possible to analyse the evolution of encephalization in fossil species by determining the extent to which their data fall into appropriate polygons of the type shown in figure 1.

In general, the differentiation between lower and higher living vertebrates as shown in figure 1 occurs in the same way in fossil species as in living species from the same groups. The most important additional information from the fossils is that early species of birds and mammals were at, or perhaps even slightly below the lower margins of the polygons for the living populations, indicating that encephalization occurred but not to the same extent as in 'average' living species. One fossil shark studied by R. Zangerl (personal communication), which lived about 250 million years ago, was probably as encephalized as living dogfish, suggesting that the sharks were the first vertebrate species to 'experiment' with encephalization as an adaptation. Other 'experiments' with enlarged brains occurred in certain dinosaurs (Ornithomimidae; see Russell 1972), and some of the mammal-like reptiles (Therapsida) may also have been encephalized beyond the present reptilian grade (Hopson 1979; Kemp 1979; cf. Quiroga 1980). The orientation of the polygons for lower and higher vertebrates when fossil data are added is the same as in living species, and the vertical displacement is similar (Hopson 1977, 1979; Jerison 1973). Such analyses lead to some straightforward conclusions, which can destroy old myths. For example, dinosaurs as a group were normal reptiles in relative brain size, and a few were even as large-brained as some living birds. The dinosaurs did not become extinct because of their small brains.

The question of the differentiation between an agnathan and gnathostome grade raised earlier is, unfortunately, not resolvable by the fossil record. I reviewed that fossil evidence some years ago (Jerison 1973) and concluded that agnathan endocasts, though impressed as beautiful patterns on the armoured fossil skulls (Stensiö 1963), were inadequate for judgements about brain size.

The orderliness of the evolution of encephalization as indicated by the analysis of fossil endocasts is impressive. I have discussed the issue in several reviews as well as in my monograph of a decade ago (Jerison 1973, 1982, 1985). With some exceptions, most other reviewers (see Armstrong & Falk 1982; Blumenberg 1983; Hopson 1977, 1979; Passingham 1982; Radinsky 1979; Tobias 1971) have also been impressed with this orderliness. The major conclusions are the following.

(i) A basal lower vertebrate grade of encephalization evolved in the earliest bony fish, amphibians and reptiles and has continued to the present as a steady-state or equilibrium maintained for a least 350 million years. Since about two-thirds of living vertebrate species are members of these three classes of vertebrates, this basal grade is the norm for vertebrates.

(ii) There are variations in encephalization within the lower vertebrate groups, the most interesting being between herbivorous and carnivorous dinosaurs. The carnivores were apparently significantly more encephalized.

(iii) The earliest fossil birds and mammals with known endocasts had evolved to a higher grade, representing at least three or four times as much brain as in lower vertebrate species of comparable body size. This progressive or 'anagenetic' evolution occurred at least 150 million years ago, and in the case of the mammals may have begun with their reptilian ancestors at least 50 million years earlier.

(iv) Within the mammals there is a good fossil record of the brain, which is consistent with a picture of steady-states punctuated by rapid evolution to higher grades. However, many grades of encephalization are represented in living mammalian species, with some (opossum, hedgehog) at the same grade as the earliest of the mammals.

(v) Two unusual conclusions are evident in the history of encephalization in primates. First, primates have always been a brainy order, perhaps doing with their brains what many other species did by morphological specializations. Second, the evolution of encephalization in the primates followed rather than preceded or even accompanied other adaptations by primates to their niches. Washburn (1978) has pointed this out as a feature of hominid evolution, but it appears to have been true for prosimians and simians as well (Jerison 1979).

(vi) The highest grade of encephalization is shared by humans and bottlenosed dolphins (*Tursiops truncatus*). The sapient grade was attained about 200000 years ago, but cetaceans may have reached their highest grade 18 million years ago.

(vii) Encephalization in the hominids is a phenomenon of the past three to five million years, and its rapidity appears to have been unique in vertebrate evolution.

(viii) These results suggest two complementary conclusions. First, the long steady-states that occurred in most groups indicate that, on the whole, encephalization was not a major element in vertebrate evolution. A particular grade of encephalization tended to be maintained once it was achieved. On the other hand, its appearance in many different and distantly related groups is evidence of some Darwinian 'fitness' for encephalization.

2. THE MEANING OF BRAIN SIZE

As a first approximation, gross brain size is a kind of statistical estimator of total neural information processing capacity. The evidence is from the mammalian brain, in which the necessary quantitative analyses have been performed, but elementary ideas on how nerve cells must be packed into brains suggest that the perspective is appropriate for all vertebrates.

Brain size estimates the processing capacity of a brain because of the statistical orderliness of the brain's structure. Several aspects of that orderliness in the mammalian brain are especially relevant for information-processing. There is, first, a 'basic uniformity in the structure of the neocortex' described by Rockel *et al.* (1980), who showed that the various regions of the cortex in various mammals follow a common structural plan, with regional variations. Secondly, the neocortex is organized into columnar modules, which extend through the full depth of the cortex and are about 250 μm in diameter. Modules seem to be units of information processing (Eccles 1979; Mountcastle 1978; Szentagothai 1978), analogous to chips in computers. The number of modules is proportional to the cortical surface area, and processing-capacity should, therefore, be proportional to the total cortical surface area. For this reason a third feature of the brain's orderly structure is especially important, namely that at the between-species level the cortical surface area is determined almost entirely by brain size. The correlation (log data) is $r = 0.995$ (Jerison 1983). The syllogism is now complete: information processing capacity is determined by cortical surface area (in mammals), and cortical surface area is determined by brain size. Brain size, therefore, determines processing capacity. Since the analysis is statistical, it is more appropriate to conclude that brain size 'estimates' rather than 'determines' processing capacity.

Derived from evidence on mammals, these ideas may be extended to other vertebrates by considering the packing of neurons and glial cells into brains. Despite the obvious oversimplification, it is appropriate to assume a general statistical similarity among brain cells, at least to the extent of defining an average cell. With respect to packing, a large population of neurons and glial cells may be treated as approximately the same as an equal number of average cells. For the analysis of packing one can work with information on the total volume of an average neuron–glial unit and represent it by its equivalent sphere. The packing of such spherical model cells into a brain would then be analogous to the packing of spheres in any container. (Such a model is oddly appropriate. The mathematical solution of this packing problem is that up to about three-quarters of the space in a container can be taken up by the spheres (Sloan 1984). Evidence from the analysis of the volume of the extracellular space in the brain (Nicholson

1979) is consistent with that percentage.) Within the mammals, neuron density and the ratio of neurons to glia are both related in an orderly way to brain size, as would be expected from this geometrical model (Jerison 1985). There is no reason to assume major differences for those relations in other vertebrate classes, and the analysis is, essentially, one of parsimony. How are cells packed into their available spaces? Lacking contrary evidence, we should assume the packing is efficient, and geometrically similar for all cells in all brains, at least to the extent to permit the assumption that the number of units of information-processing in different brains is always related to the size of the brain. We may, therefore, treat the results on mammals as appropriate models for other vertebrate brains.

In the analysis of encephalization the total size of the brain is divided, statistically, into two fractions, one related to body size and the remainder (residual) to 'encephalization'. The correlation of brain size with processing capacity refers to the entire brain, however, and not solely to a component related to encephalization. The allometric and encephalization components are statistical estimators of how, not where, processing capacity is divided. It would be impossible to state, on the basis of the analysis presented thus far, whether any particular bit of brain tissue belongs to the allometric component or the encephalization component. It would be inappropriate, certainly, to think of the allometric component as sensorimotor and the encephalization component as referring to association systems if these are considered as localized grossly in different parts of the brain. In accordance with recent analyses (Diamond 1979), it is more appropriate to think of various blocks or columns of tissue as contributing to both projection and association functions, and the biometric division into allometric and encephalization factors might correspond, approximately, to a partitioning of the work of a columnar modular unit into sensorimotor and association activities.

To explain encephalization it is sometimes assumed that it is the result of reorganization of the mammalian brain that followed the evolution and subsequent enlargement of the uniquely mammalian cerebral cortex of the forebrain. This is at best an oversimplification. Many brain structures, including the forebrain, became larger in mammalian encephalization. The enlargements are correlated, and an outstanding example is the cerebellum in mammals, the size of which is closely related to the size of the forebrain. The evidence is in figure 2.

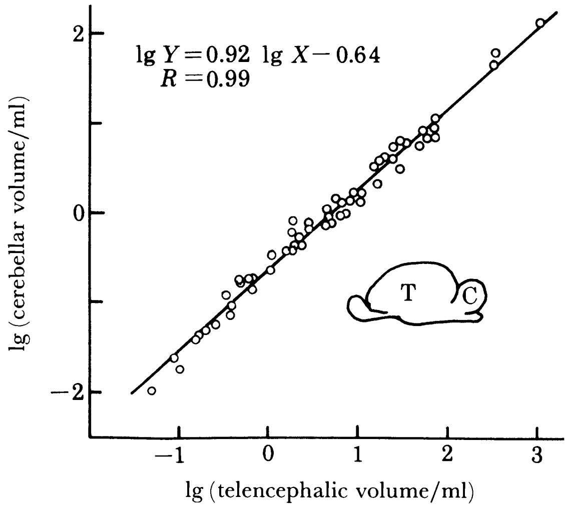

Figure 2. Cerebellar volume as a function of telencephalic volume in 63 species of mammals (24 insectivores and 59 primates). Data from Stephan *et al.* (1970). Telencephalic volume is exclusive of the olfactory bulbs. Inset sketch of mammalian brain indicates telencephalon (T) and cerebellum (C).

Figure 2 may be an example of what Mountcastle (1978) has described as the 'distributed' network in brain function, that many widely separated units contribute to the normal functions of the brain. The cerebellum is involved in conditioning and learning (McCormick & Thompson 1984), for example, indicating that it may have important functions in 'higher mental processes' beyond its traditional role as a motor control system. In any case, the enlargement of the cerebellum contributed significantly to structural encephalization in mammals. I summarized the results of multivariate analyses of structures contributing to brain function and of the correlated evolution of these structures in encephalization (Jerison 1973, pp. 63–81), and later reviews are included in Armstrong & Falk (1982).

Up to this point the brain has been treated as if it were similar in all species, and as if size alone was important in its function. This is, of course, another simplification, introduced partly because the concern here is mainly with effects of size and also because the importance of the size of biological systems, including the brain, is often under-emphasized. Brains of different species are organized differently, just as the behaviours of different species are different; the structural reorganization of the brain is consistent with the reorganization of behaviour. For example, the superior colliculi of the visual systems of reptiles and birds and some fish are so enlarged relative to the rest of the brain that they are called optic *lobes*, comparable in size to lobes of the forebrain, and sometimes larger than the entire forebrain in some species of fish and reptiles. It is more or less true that the mass of neural systems related to specialized behaviours is proportional to the importance of the behaviour for a species (cf. the 'principle of proper mass', in Jerison 1973).

Thinking statistically, we recognize gross brain size as a natural biological statistic, which estimates many significant parameters. One of these is the surface area of the neocortex in mammals, and another, at a different level of analysis, is total information processing capacity of a brain. As might be expected, brain size is a good estimator of the sizes of most of the parts of the brain, including cerebellum. Furthermore, differences in organization that occur often average out, in a sense, so that different species may be equally encephalized but for different reasons. Relatively enlarged visual system in a 'visual' species may be comparable in volume to relatively enlarged auditory system in another, 'auditory', species, and the two species could be equally encephalized despite their different specializations.

Reorganization in the brain is the basic correlate of most of the interesting variations among species in their behavioural adaptations, and the brain tissue related to these specializations could contribute to both the allometric and encephalization factors. When the specialization requires very large amounts of neural tissue it may be reflected directly in the encephalization factor. It is likely that encephalization in monkeys and apes, for example, which is about twice as great as in 'average' living mammals, results mainly from the enormous expansion of the visual system of the brain in higher primates. Equal amounts of encephalization could and normally do result from very different patterns of specialization. The extra processing capacity involved in encephalization may be allocated to very different behavioural adaptations.

We should consider now a more general question: why did encephalization evolve? It is, after all, an expensive adaptation for the economy of an organism, requiring metabolically demanding neural tissue rather than energetically 'cheaper' bone, muscle or other tissues that are required for many behavioural adaptations. The answer must be in the requirement for specialized neural control systems, and the question becomes: what kinds of neural control systems require very large amounts of tissue?

The evidence on mammalian brains is that their enormous masses are involved mainly in the works of the projection systems (Diamond 1979; Merzenich & Kaas 1980). The information that they process would be characterized as sensory and motor. This suggests that the work of the brain involves perceptual systems, which operate on sensory and motor information that is transmitted in the nervous system. The amount of information is enormous, involving thousands of millions of changes of state every second, which must somehow be related to the changing information received through sensory and motor surfaces about the external environment, often by a moving animal. In reviewing the problem (Jerison 1973) I thought that Craik's (1943) discussion was helpful, that one could think of the work of the brain as constructing a model of a possible world in which the changing pattern of the detailed neural information that is being processed finds its place in an understandable way. In modern terms this would be described as a hierarchically organized system, in which events such as the activity of single neurons, or even modular columns of neurons, are organized at lower levels of the hierarchy, and the 'possible world' is represented at higher levels as part of a more complex model. The complex model, in fact, is a real world of ordinary experience containing, for example, 'objects' in 'space' and 'time'. Objects, space and time are chunks of information, as it were, more useful than the elementary data (Simon 1974).

Gross brain size may, thus, be thought of as having two kinds of meaning. First, it is the morphological measure of neural information processing capacity, reflecting the orderly packing of processing units within brains. Second, it is a quantity which, upon reaching some particular size and handling some specifiable amount of information, handles that information by creating a representation of a possible world, within which the patterns of neural activity make sense. This second meaning is, in fact, nothing less than the creation of a reality, of a real world within which the events of a lifetime take place. Familiar computer analogies would have 'pattern recognition' as part of that work, although it would be more accurate to call it 'pattern construction'. The patterns created by a brain would be much more interesting, with many more dimensions than the visual and auditory patterns created by computers. The brain's patterns have emotional and motivational dimensions, anticipatory dimensions, and even dreams and hallucinations. For our purpose, however, the point to emphasize is that it is functions such as these that require the enormous amounts of tissue that are in the brain.

3. INTELLIGENCE

Encephalization was discovered in the search for neurological correlates of intelligence, and it is easier to analyse encephalization. It has an identifiable evolutionary history and unusual but interesting features as a 'character' under natural selection. Animal intelligence and the problems in its analysis may be much better understood if we reverse the implicit causal arrow and think of it as the behavioural correlate of encephalization. The evidence of encephalization is so clear that were we ignorant of behaviours that might be correlated with it, or were we lacking in intuitions about the behaviours, we would find it necessary to invent a category of behaviour related to encephalization.

Evolutionary traits are often analysed for their phyletic histories to determine 'cladistics' and lineages. Although this can be done for encephalization in the hominid lineage, it is not an easy exercise for other animal groups (cf. Radinsky 1979). There is no feature in its definition that would require a taxonomic label to help describe a grade of encephalization that is identified in a species. Deer and wolves are equally encephalized, for example; they are average mammals joined by lemurs among the primates and even by crows. Encephalization is a measure of capacity, independent of the way the capacity is used, and it may be treated as a trait for 'anagenetic' rather than 'cladistic' analysis (Gould 1976). Deer and wolves and lemurs and crows are more or less equal on this quantitative trait.

This provides the first insight about animal intelligence. When distantly related animal species are comparable in excess neural information processing capacity, that is, in encephalization, we should identify the species as comparable in intelligence. Yet the near equality in encephalization may be based on radically different adaptations. Some species of deer and wolves (to retain that example, useful in many contexts in this discussion) live in ecological balance, as prey and predator species (Mech 1970), and the fact of the balance, which depends on appropriate behavioural adaptations, suggests that they should be equated behaviourally despite the different repertoires of the species. In that sense their approximate equality in encephalization reflects their behavioural grades and is useful as part of the characterization of each species.

The insight is that comparable *amounts* of intelligence in different species may not (and normally would not) reflect comparable *kinds* of intelligence. Many and various intelligences (in the plural) must have evolved in conjunction with evolving environments and with brains and behaviours adapted to those environments.

That intelligences would be of various kinds is almost an axiom of evolutionary analysis, since adaptations evolve in the contexts of the environments in which they are effective, and species never occupy identical niches. The evolution of neural and sensorimotor adaptations provides many fine examples of uniqueness of species. The visual systems of deer and wolf, for example, may be similar in many ways, for example, in the structure of the sensory cells, neural networks of the retina, and the central nervous pathways and centres (cf. Merzenich & Kaas 1980). Yet these systems are significantly different: the deer, like most ungulate 'prey' species, probably has panoramic vision whereas the wolf's visual field is more nearly like the primate's proscenium stage (cf. Marler & Hamilton 1966). The visual system encumbers significant amounts of nervous tissues and, thus, contributes to brain size and measured encephalization. Neural machinery associated with the sensory systems and motor control systems as a group determines a large fraction of the mass of the whole brain. Equality of encephalization of deer and wolf, thus, implies that the neural control systems for the specialized adaptations, though different in the two species, sum to approximately equal amounts relative to body size.

Laboratory scientists should anticipate difficulties when attempting to compare species in intelligence, because it may be impossible, even in principle, to equate the environments used in testing different species. Behaviours and their control systems evolved in specific environmental contexts, as adaptations to specialized environments . The difference between 'intelligent' and 'unintelligent' behavioural adaptations is in the amount of neural tissue that they encumber, according to the present perspective, which may be uncorrelated with measurable differences in overt behaviour. Intelligence as a correlate of encephalization would be manifested in experience, rather than behaviour, in the realities created in the brain of a species, and although this view has its charms it obviously adds significantly to the difficulties of a scientific analysis requiring objective tests.

The first inference was, thus, that a variety of intelligences may be represented at a single grade of encephalization. A second inference from treating intelligence as the behavioural counterpart of encephalization is about the class of behaviours that is likely to be involved in the evolution of intelligence. Ever since Darwin and Romanes it has been normal to assume that 'brainy' behaviours involve the ability to profit from experience, the ability to learn. An enormous literature now indicates that animals of many different species can usually learn a particular task, and apparent differences among species in learning ability are determined as much by the skill of the animal trainer as by anything else. Operant conditioning procedures have been remarkably successful in training animals to act as if their performance was based on 'higher mental processes', even when it was demonstrably based on associative learning. The evidence is on the learning abilities of pigeons and other unencephalized species. Macphail (1982), Warren (1977) and many others have reviewed the sorry record of research correlating learning ability with 'phylogenetic level of advancement'. There is at best equivocal evidence of an orderly progression in the capacities of different species for conditioning and associative learning that corresponds with their degrees of encephalization (Bitterman 1975; Riddell 1979). More significantly, it is not clear that any of the simpler categories of learning are dependent on large amounts of nervous system, and the evolution of learning ability is not implicit in the evolution of encephalization.

There is empirical evidence for a relation between the grade of encephalization and what an animal appears to know when it copes with a task. This at least seems to be the case for learning sets performance in primates (Passingham 1982) and for Piagetian 'conservation of mass' as demonstrated in a chimpanzee (Premack & Woodruff 1978). Such results are entirely consistent with the view presented earlier about the kinds of brain functions that require very large amounts of brain tissue for their control. As pointed out in the previous section, the enlargement of vertebrate brains, especially the very great enlargement of the mammalian brain, can be related to the evolution of extensive sensorimotor 'projection' systems for all of the sensory modalities and for motor feedback. And the enlargement is involved not merely in the use of sensorimotor information but in the construction of representations of reality from neural data. The 'intelligence' that corresponds to higher grades of encephalization is one involving a knowledge of reality, or, in terms of the earlier discussion, the quality of the reality created by the brain to account for the information that is received.

I should, perhaps, make the point that the view of a brain as creating reality is not solipsistic. It does not deny an external reality. The fact of an external reality explains the uniformities in social behaviour and shared experiences. There are fundamental similarities among the operations of different nervous systems, and there are constancies in the environments to which nervous systems are exposed. The realities created by brains reflect these constraints. They are not chaotic but must be similar for different species and very similar for individuals of the same species. Your reality and mine are similar enough to leave little doubt that we share a view of a real external world that remains constant as we live our lives. Our perceptions and experiences are referred to that reality, and it is only in our more metaphysical moments that we question it.

Grades of encephalization presumably correspond to grades of complexity of information processing. These, in turn, correspond in some way to the complexity of the reality created by the brain, which may be another way to describe intelligence. There are problems here in taking evidence of the presence of unusual kinds of information processing as implying that the processing is difficult and can only be accomplished with very large amounts of brain tissue and the conclusion that this must be an example of complex processing. The issue arises in analysing exotic adaptations, of which echo-location is a good example.

Echo-location and sound-ranging in insect-eating bats and in toothed whales are adaptations for handling spatial information, which depend on the activity of an auditory–vocal system. The adaptation clearly requires a fair investment of neural machinery. Although much of the bat's brain is devoted to this class of information, the whale's investment must exceed the bat's by an enormous amount. It is sometimes suggested that the size of the brain in large whales, which is several times the size of the human brain, is a result of the processing capacity required for this exotic adaptation for handling information. But if it were merely a problem of handling information, whales could do the job with a much smaller investment in nervous tissue; they would need no more than the amount of tissue in a bat's brain. There must be more than echo-location that explains encephalization in whales, in which dolphins and killer whales are at approximately the human grade. We must infer that the reality created from this information in the whale is more elaborate, more complex, and at least very different from that produced by the bat's brain, that the realities of these species differ radically.

To extend the analogies we can compare human language as a sensory–vocal adaptation with sensory–vocal adaptations in other primates, indeed in other mammals. Specialized processing of auditory information and of vocalization is reasonably similar in different species, including the human species. The important difference is obviously in the way the information contributes to the realities that we construct. Our linguistic world is a unique reality-creating world, which is dramatically demonstrated by the facts of literacy: reading can enable one to enter a fictional world and live in it. We create worlds with language. The acoustic story of language is limited and is not much different from the acoustic story of vocalization and hearing in other species, but the cognitive story is another matter.

This leads to a final inference from encephalization as defining animal intelligence, an extension of the proposition that enlarged brains are enlarged because of their activity in the sensory–motor and perceptual domains of analysis. The inference might be stated more clearly by calling this domain by a better name, the cognitive domain. The idea is inherent in the hierarchical organization of large information handling systems, including large brains. In this view, following Craik's (1943) perspective as well as Simon's (1974), there is a major problem of organizing the information. The solution is by chunking, nesting subroutines within larger subroutines. The place of representation of the external world, the creation of a reality, in this scheme is as a method to make sense of an otherwise impossible amount of information. In ordinary experience some of this creation is consciousness or awareness of the external world, which we recognize as a simplification when we examine any part of that world carefully. There is always more detail revealed in careful examination and our knowledge expands as the examination continues. The elements of the world are the 'chunks' and they may have the form of objects, or of dimensions, or of any category within which experience is organized. The model of reality is made simple or elaborate, depending on the observer's requirements and those imposed by the information that is being handled.

This leads to the expectation that very encephalized animals may be something like us in having unusual adaptations for handling or constructing realities. Perhaps language is the most complex of human adaptations, and some of the unusual features of language as a medium of communication are clearly related to its role in the creation of a reality. In the following discussion let us keep in mind that the idea of creating reality is a dramatic way of describing the 'knowing' of reality, or cognition, and that this is a statement about neural activity at a high level of hierarchical organization. Although theoretical, based on word games, this is a *biological* rather than philosophical, psychological, or linguistic approach to language. Let us also note that the analysis of brain size indicates that it is only systems that ultimately contribute to cognitive functions, the knowing of reality, that account for very large amounts of nervous system, and that the very extensive representation of language in the brain argues for its role as a cognitive system.

The understanding of language in this biological perspective may be different from the usual understanding. Language is usually equated with communication, and discussions of animal communication and animal language are treated as equivalent. This may be a serious mistake that can lead to great confusion in the understanding of both language and communication. Here is my analysis.

Human language as a cognitive adaptation contributes to the reality constructed by each individual. In this respect it is like vision or olfaction or other senses. But language is also a major adaptation for communication. The implication is that we communicate by sharing parts of our real worlds, sharing consciousness with one another, because we share part of the information that we use in constructing our realities. We can verify this by the often repeated 'experiment' in which we have all participated and which I described earlier. When we read and become engrossed in a realistic novel, we experience the realities of the characters as vividly as if we were living their lives. This verifies the fact that when we communicate with language we share experiences, and this is an unusual way for animals to communicate.

It is as if we could communicate by having others see what we see and hear what we hear. The role of language in communication is very close to fictional accounts of communication by extrasensory means and may explain the attractiveness of ideas of such psychic powers. These imagined powers are not far removed from what we do in everyday life when we use ordinary language. But the penalty for our exotic method of communication is uncertainty about the information, misunderstanding and false understanding.

Normal animal communication, we have learned from the ethologists, is direct and certain. It is with commands that are usually obeyed: *sign stimuli* and *releasers* and *fixed action patterns*. We can use elements of human language to train other animals, and there is some suggestion that when this has been done with great apes and with dolphins, cognitive activity becomes involved in the communication (Premack & Woodruff 1978; Herman 1980; Herman *et al.* 1984). But there is as yet no evidence that the communication is in any sense like human communication with shared consciousness. Rather the homologue for animal communication in the human species may be the important communication with 'natural' gestures, such as unrehearsed facial expressions, which might be described as communicating directly without the intervention of consciousness or a sense of identification. It is also sometimes described as limbic language (Myers 1976), and it has some of the characteristics of animal communication in its universality and lack of ambiguity.

I have tried in these remarks to suggest the nature of the evolution of intelligence as an aspect of the evolution of encephalization. This has led to a definition of intelligence as processing capacity beyond that required for routine bodily functions. It led also to the assertion that the 'excess' capacity (in Lashley's words) is used primarily for the construction of reality: the representation of a world that is the reality of each species. In my final example I indicated that human reality is deeply associated with human language. It is reasonable to extend this implication to the specialized correlates of encephalization in other species, and to suggest that their adaptations may be as unusual as language. The correct view is surely that in the evolution of excess processing capacity, that is, in the evolution of encephalization, a variety of intelligences evolved. Human intelligence, deeply associated with human language, is one kind of intelligence. The evolutionary message about intelligence, like the message about so many other dimensions in biology, is a message about pluralism and diversity, about the variety of intelligences in the biological world.

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Discussion

H. B. Barlow, F.R.S. (*University of Cambridge, U.K.*). If, as you suggest, the encephalization index is related to information processing capacity or intelligence, then the following curious paradox arises. In a heavy brain weighing hundreds of grams a high index might correspond to the addition of many grams of brain tissue, and a correspondingly large number of brain cells, whereas in a light brain of, say, 10 g the same increase of the index would correspond to the addition of a comparatively small number of cells. Why does the heavy brain require many times as many extra cells as the light brain to confer the same increase in intelligence?

H. J. Jerison. The question is fundamental. To answer we must review the units to be used in assessing neural information processing and how these would measure encephalization. The implicit premise in the question is that the unit is the nerve cell. In that case, encephalization could be measured by the number of 'extra neurons' after accounting for the number of neurons encumbered by routine body functions. A large animal species requires a larger brain than a small animal species for handling routine body functions (much as it requires a larger heart or liver), but when the larger-bodied species is encephalized to the same extent as the smaller one, it should have the same number of 'extra neurons' as the smaller species. The fractional enlargement of the brain due to encephalization (beyond the 'allometric enlargement associated with body size) would have to be greater in the larger species because there are fewer neurons per unit volume in larger than in smaller brains. The nonparadoxical answer is, thus, that the increase in brain size related to intelligence could be based on the same number of nerve cells in large and small brained species, and that size differences despite equal encephalization in large and small brains are due to the way nerve cells are packed in brains (for quantitative examples, see Jerison 1963).

An alternative processing 'unit' might be a brain map of a peripheral sensory or motor surface. Equally encephalized species should then have comparably extensive mappings in their brains, but to maintain constant ratios of central brain cells to peripheral body cells the brain maps in larger species would have to contain more neurons. (This is one explanation for brain–body allometry.) Advances to higher grades of encephalization would be by increasing the number or complexity of the maps. Such increments would require multiplication rather than addition of cells, and *more* neurons for equal encephalization in larger relative to smaller brains. Both an additive 'extra neurons' factor and a multiplicative mapping factor have to be considered in a complete analysis of encephalization (see Jerison 1977).

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