1.08 The Evolution of Encephalization

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Glossary

allometry	The scaling relationship between two characters A and B (e.g., brain mass and body mass), where changes in A and B are not proportional. (Proportional change in A and B is termed isometry.) Allometry is thought to reflect design constraints, so predictions on the effects of directional selection are usually conducted on residual trait variance after removal of allometric scaling.
altricial	A relatively slow mode of juvenile development, where offspring are usually not mobile and are strongly dependent on parental care. The term can be opposed to 'precocial.'
behavioral drive hypothesis	The idea that generalism, exploration, opportunism, social learning, and behavioral flexibility can have accelerating effects on evolutionary rate, by increasing the range and frequency of selective contexts in which randomly occurring mutations can confer higher fitness.
behavioral flexibility	A general term describing the capacity to modify behavior. Often used as blanket term that encompasses learning (a change in behavior contingent on an association with a stimulus and/or a reward), opportunism (exploitation of a temporarily abundant resource not part of the usual diet of a species), or innovation (see definition below).
ecological intelligence	Cognitive complexity selected in the context of interactions with the physical environment. Usually contrasted with Machiavellian (or social) intelligence, which is selected in the context of social interactions.
encephalization	In comparative biology, the term describes the difference between animals in the amount of neurons available beyond the average determined by allometric body design. In paleoanthropology, it designates the observed increase over evolutionary time in the absolute and relative size of the brain in hominids. In neuroanatomy, it describes the increased importance that higher brain structures play over lower ones in birds and mammals compared to other vertebrates and to invertebrates.

generalism	One extreme of a continuum where the other extreme is specialization, generalism refers to the use of a relatively broad range of foods or habitats by a taxonomic group or an individual.
independent contrasts	The most widely used procedure for removing the effects of common ancestry on taxonomic similarities or differences between traits. The technique measures 'differences' between related taxonomic groups in the values of biological traits, rather than actual trait values on extant taxa. Relatedness between groups is usually measured through mitochondrial or nuclear DNA data.
innovation	A behavior pattern performed for the first time by an animal and that is not the result of a genetic change or a pathology. The novel behavior is an attempt to solve a problem (feeding, social) that the standard repertoire cannot resolve. Also defined as a new or modified learned behavior not previously found in the population (Reader and Laland, 2003, p. 14).
specialized cognitive skills	Cognitive abilities that are specific to a restricted selective context (e.g., spatial memory, learned song) and whose neural substrate is often a restricted brain area (e.g., hippocampus, nucleus HVC). The terms 'adaptive specialization' (implying adaptation to a particular selective context, e.g., food caching, brood parasitism) or 'module' (implying that information relevant to one specialized context or domain is not available in other contexts) embody related ideas. The term can be opposed to general process skills, where cognitive differences between taxonomic groups are thought to reflect broad, unspecialized abilities based on large and/or diffuse neural substrates.

1.08.1 Introduction

The term 'encephalization' expresses different ideas in different scientific disciplines. In comparative biology, it describes the difference between animals in the amount of neurons available beyond the average determined by allometric body design (e.g., Jerison, 1991; Schoenemann, 2004). Porpoises, for example, are said to be more encephalized than tenrecs because they are far above the regression line of log brain size plotted against log body size for all mammals, while tenrecs are far below. In paleoanthropology, encephalization designates the observed increase over evolutionary time in the absolute and relative size of the brain in hominids (e.g., McHenry, 1994; Bruner *et al.*, 2003; Rightmire, 2004; Stedman *et al.*, 2004). The brain of *Homo erectus*, at *c.* 1000 g, is thus considered to be more encephalized than the brain of *Australopithecus*, at *c.* 500 g. In neuroanatomy, encephalization describes the increased importance that higher brain structures play over lower ones in birds and mammals compared to other vertebrates and to invertebrates (Reiner *et al.*, 2004). In this view, the average mammal brain is more encephalized than the average fish brain.

Despite their differences, all three usages share one common assumption: the information-processing advantage provided by extra neurons, increased size, and increased forebrain involvement should normally be the major evolutionary driving force behind encephalization. Extra neurons in the forebrain, whether they evolve in a hominid, a cuttlefish, a capuchin monkey, or a crow, should provide faster and/or more complex and/or a greater amount of information processing and information storage about changing environmental conditions. Natural selection can lead to efficient genetically biased responses to conditions that are stable over long periods of time. But when relationships between events change rapidly, neuronal storage allows animals to respond faster than information stored only in the genome. The main functional and evolutionary hypothesis on encephalization is thus that something about extra neurons, increased size, and increased forebrain involvement is associated with the speed, complexity, and amount of information processing in these structures.

It is useful to envision variation between animals in information-processing capacity as a cognitive continuum. A corvid, for example, seems to learn more items faster (Wilson *et al.*, 1985) and with more complex processes (e.g., episodic memory, prospection; Emery and Clayton, 2004) than a columbiforme does. Its higher brain centers (the meso- and nidopallium) are eight times larger than that of a columbiforme of the equivalent body size (Rehkämper *et al.*, 1991a; Boire, 1989). The whole brain of a corvid is more than 1.5 standard deviations above that of the average bird, while a columbiform brain is 1.5 standard deviations below. This kind of organ–function correlation is not very controversial when it involves wings and flight or beaks and feeding. When the correlation involves brains and cognition, however, this is often a different story. Critics plead that cognitive complexity is difficult to assess in a way that is fair to all species (Macphail, 1982). They say that brains have many contradictory functions unlikely to lead to directional selection for an overall size increase (Shettleworth, 1998). Others claim that a correlation between morphology and function does not necessarily imply adaptation (Gould and Lewontin, 1979) and point out that adaptationist accounts of brain–cognition co-evolution in humans have often been politically tainted (Gould, 1981; see Human Cognitive Specializations).

Such qualms are legitimate and must be addressed, but they do not invalidate a critical empirical examination of brain–cognition questions. How is brain size variation distributed among taxa? Is the distribution continuous or patchy? Is it whole brain variation that we should be concerned with or variation in some specific structures? Is it relative rather than absolute size of neural structures that matters and if the former, relative to what? Can we reliably show that brain size variation is associated with variation in cognition? How did the variation evolve? What are the costs and benefits of larger versus smaller brains, and in what ecological contexts do these costs and benefits apply? These are the who, what, and why questions we will examine in this article.

1.08.2 How Is Encephalization Distributed Among Taxa?

1.08.2.1 Variation Between Classes

Size and structure of the central part of the nervous system differ clearly between the major animal taxa. From the nerve ring of nematodes to the cerebral ganglion of insects to the brains of cephalopods, birds and mammals, there are major discontinuities in the size and organization of the central organs. If we were to statistically partition the variance in nervous system characteristics over all animals, we would likely find that most of it lies at very high taxonomic levels. Neurons themselves are highly conserved in all animals, as are synaptic processes. For example, memory appears to be based on similar rules of long-term potentiation via glutaminergic synapses from Aplysia (Bailey *et al.*, 2000; Pittinger and Kandel, 2003) and cephalopods (Hochner *et al.*, 2003) to humans. The basic building blocks of learning and cognition might thus show a strong constancy throughout evolution.

The way these neurons are organized in the brain and how many of them are available for more complex information processing also appear to be conserved within major taxa. A mammalian brain is, on average, larger than an avian brain and features a laminar cortex, while avian brains are organized in discrete nuclei (Karten, 1997). In turn, bird brains are larger than cephalopod brains, which are organized in supra- and subesophagal lobes. These average differences have sometimes led to a *scala naturae* vision of brain evolution, where more recent lineages are seen as more encephalized on average than older ones. At least two hypothetical mechanisms could produce such a trend. The first is the possibility of an evolutionary arms race. The oldest animals on earth had no nervous system at all. These were followed by animals with neurons that are linked by a central chain, then by animals with neurons linked to a central organ. Odontocetes and apes have the largest brains and are relatively recent (23 and 34 My respectively; Marino, 2002; Marino *et al.*, 2004). The assumption here is that the bigger the brain, the more information it can store, the faster it can change behavior in response to environmental contingencies (Sol, 2003), and the more complex a behavioral repertoire it can program (Changizi, 2003). Animals that can do more of all this are assumed to have an advantage over those that can do less, once the costs of an enlarged brain are taken into account. A further positive feedback effect of the behavioral flexibility associated with larger brains may add extra pressures for encephalization via social channels. The more flexible the behavior, the trickier it is for other animals to predict and the more useful is a large brain to make such predictions and change behavior quickly in response to the rapid change of others (Byrne and Whiten, 1988). The consequence of these mechanisms is that a competitive arms race might then follow, as it does for sexual selection, limited by the costs of increasing the size of the organ.

The second evolutionary phenomenon that would lead to encephalization over time is behavioral drive (Wyles *et al.*, 1983; Wilson, 1985). All other things being equal, animals that come into more frequent contact with environmental conditions likely to provide a selective context for randomly occurring mutations should be characterized by faster evolutionary rates. Opportunism, generalism, and invasiveness are three traits that will increase the rate of contact with new selective pressures. If these traits are associated with larger brains (see below), then encephalization should also correlate positively with rate of evolution. Because generalism and invasiveness also make animals more likely to range farther, they should also increase the probability of allopatric speciation. If larger-brained taxa beget more descendant species than smaller brained ones, then the average size of the brain should increase over time. The fact that individuals from larger-brained species tend to have fewer descendants per unit time than those from smaller-brained taxa will, to a certain degree, counteract the positive effects of an arms race and behavioral drive.

Discontinuities in encephalization over major clades prompted comparative psychologists in the 1960s to ask whether certain learning differences paralleled neuroanatomical trends. Overall, the results of these programs tended to show that there are quantitative differences in learning performance in the direction predicted by encephalization differences. Some researchers however, have questioned the heuristic value of these findings. One comparative learning researcher, Riddell (1979, p. 95), ironically summarized his experience:

> The comparative psychologist often appears to know little more than a grade school child who would rather have a pet dog than bird, or bird than fish, or fish than worm, simply because they make better friends, as they can be taught more.

Beyond these problems, there are two other limits to comparisons between classes: small sample sizes and the overlap between the encephalization distributions of the taxa. Because each class is $n = 1$, comparative statistics cannot be used to test predictions about the costs, benefits, evolutionary history, ecological associations, and behavioral correlates of encephalization. Comparing the average fish to the average bird to the average mammal has a sample size of 3. Some birds are as or more encephalized than some mammals. If a crow has a larger brain and more complex cognition than does a tenrec, is it useful to think of an average mammal versus an average bird? Intraclass variance might be biologically as important as interclass variance and the question of whether similar patterns govern intraclass or order variation in different taxa might be the more useful one to ask.

1.08.2.2 Variation Within Classes

The study of intraclass variation solves the statistical problem mentioned above (classes Aves vs. Mammalia: $n = 2$; variation between avian species: $n = 10000$). It also increases the validity of cognitive comparisons by measuring animals with more similar sensorimotor worlds. Comparing the results of several within-class or within-order analyses might thus be a good way of finding general patterns in encephalization.

The taxonomic distribution of a trait as well as its co-occurrence with other traits can be due to two types of processes: ancestral descent and repeated independent evolution. Ancestral descent may represent simple inertia or it may be the source of an important adaptive radiation. To separate ancestral descent and repeated independent evolution, we must know something about the phylogeny of the taxon and control for its effects on the distribution of apparently co-evolved traits. Most phylogenies today are based on differences in molecular sequences of either nucleic or mitochondrial DNA. When a well-resolved (a complete, well-differentiated tree at all levels) and robust (different parts of the genome lead to similar phyletic conclusions) molecular phylogeny is not available for a given taxon, a classical taxonomy, based either on Linnean characters or cladistics is still useful, but some degree of resolution will be sacrificed, usually yielding nonbranching elements and/or equal branch lengths (i.e., with no known genetic distance or estimated time of divergence).

Evolutionary biologists have long been concerned that interpreting correlations between traits in extant species as adaptive consequences of co-evolution might be biased by two sources of type 1 error (Felsenstein, 1985; Harvey and Pagel, 1991). First, two species might show similar values on two traits because they are closely related, not because of independent evolutionary events. This violates the assumption of data point independence for correlations and inflates the sample size via pseudoreplication. The similar values might thus be the result of inertia from an ancestral state, and cannot be considered the result of adaptive co-evolution. Techniques such as independent contrasts have since been routinely applied to trait correlations to deal with such problems. Contrasts are nodal differences between estimated ancestral values of the traits we are interested in. The nodes represent hypothetical ancestors, whose values are assumed to be averages of the trait values for the two branches descending from the node, often weighted for genetic distance. While the trait values of a given pair of taxa may not be independent, the difference between them can be assumed to represent independent evolution. Imagine that we have data for relative brain size and for diet breadth on 100 species and that the independent contrasts yield a nonsignificant correlation between the two traits. Comparative biologists will usually conclude that the null hypothesis for adaptive co-evolution has not been rejected. Imagine now that you examine the taxonomic distribution of your two traits and find that of the two subgroups in your taxon, one contains 85 large-brained species whose diet varies from three to ten food types, and a second one contains 15 small-brained species whose diet varies from one to four food types. What can we conclude?

That there has been no repeated co-evolution of generalist diets and large brains in this order? In all likelihood, yes. That diet and brain size cannot be proven to have had a selective effect on each other in this group? Yes. However, if we run a normal regression (nonphyletically corrected) on the 100 extant species and find a highly significant brain–diet correlation, we would run the risk of type 2 error if the nonsignificant contrast analysis leads us to conclude that the observed pattern contains nothing of evolutionary interest. Clearly, species that combine large brains and a generalist diet are or have been in the recent past quite successful. How they got the combination of the two traits is what a nonsignificant regression on the independent contrasts tells you: they inherited it from their ancestors and the combination did not appear through repeated independent evolution.

Despite its difficulties, the phylogenetic approach has two advantages: the occurrence of repeated independent events is a much more stringent test for adaptative co-evolution than is a single ancestral event. Phyletic trees, combined with molecular clocks, can also generate hypotheses on evolutionary sequences and timescales. If the large-brained generalist combination occurs in six widely separated clades and there is more brain size variance at older phyletic levels, (corresponding, say, to 100 My BP) and more diet breadth variance at more recent levels (say, 20 My BP), then we can hypothesize that large brains in general allow the evolution of broader diets, because variation in brain size precedes variation in diet. For example, most of the variance in avian brain size is at high phyletic levels like the parvorder. The molecular data of Hedges *et al.* (1996) suggests that divergence of extant birds at this level is 100–125 My old and may coincide with episodes of continental splitting. In contrast, the variance in avian innovative feeding (see below) is highest at much more recent levels of divergence, e.g., the species. The hypothesis that brain size divergence preceded feeding divergence thus follows and can be tested with statistical techniques such as path analysis.

1.08.3 What Is Encephalized?

1.08.3.1 Relative Brain Size

As recently as the 1960s, some researchers had a logic based on uncorrected absolute size for their evolutionary and/or ecological hypotheses on encephalization. Most researchers today (although see Byrne and Corp, 2004, for discussion) assume that encephalization should be studied after some kind of complete or partial control for allometry, often assessed by body size (see Scaling the Brain and Its Connections, Encephalization: Comparative Studies of Brain Size and Structure Volume in Mammals, Principles of Brain Scaling).

Usually, body size allometry is considered a confounding variable and is removed from most analyses of relative brain size. The assumption here is that as a body gets bigger, it takes more brain cells to analyze the information coming from more skin, a bigger retina, larger ears, a bigger nose, as well as to program more motoneurons for bigger and more numerous muscles. It also takes more interneurons to mediate all this added sensory and motor machinery. The brain–body relationship is not 1 to 1. As bodies get bigger, the increase in brain size follows at a slower pace. Not all organs follow this trend; the heart/body relationship, for example, is linear even when the data are not log transformed. The brain is thus a peculiar organ and its relationship with body size may differ from that of other organs. The decreasing slope of the brain–body relationship might mean that ever-larger bodies require proportionally fewer and fewer extra neurons in the brain or that the cost of enlarging the brain increases faster than the cost of enlarging the body. However, metabolic costs, one of the best known costs of encephalization (and the interpretation often cited for the slope of the log-log brain–body line; Martin, 1981; see however, Symonds and Elgar, 2002), decrease with body size. As animals get bigger, there is less surface-to-volume heat loss, body temperatures decrease, and it takes proportionally less energy to fuel a large body compared to a small one.

Another problem with using body size as an allometric control is that selection, both natural and sexual, operates on it and that a seemingly small brain relative to a large body may simply mean that there has been stronger selection on an enlarged body than on an enlarged brain. When sexual selection for enlarged bodies leads to gender dimorphism, this presents a further problem, though one possible solution is to take only the brain and body measurements of the gender under the lowest sexual selection pressure. Selection for specific organs that make up a large proportion of the body could also affect total size estimates. Herbivores and folivores have a large digestive system because the low digestibility and nutrient quality of their food requires larger amounts of food and longer digestion. Gorillas and ruminants may thus have a spuriously small relative brain size if allometry controlled via body size is biased by selection on a large digestive system. Some estimates of size (e.g., body length) may be less sensitive to this problem than others (e.g., mass), but the general problem remains. An alternative explanation for small brains in herbivores and folivores would argue that the demands of eating leaves and grass do not select for a large brain relative to body size because these foods are abundant and predictable, but the point is that both explanations are logical.

A third problem with body size is that large bodies are associated with longer generation times. When environments change, there are two ways an animal can modify its response. First, natural selection can increase the frequency over successive generations of alleles (mutated or already appearing in low frequencies) coding for traits that lead to higher fitness in the changed conditions. Alternatively, phenotypic plasticity such as innovation, individual learning, or social learning may allow animals to track the changed conditions. If large brains favor behavioral flexibility and large bodies (and brains; see below) decrease the rate of natural selection via long generation times, then bodies again will not have a neutral effect on brain size. Encephalization might thus follow evolution of enlarged body size, as Nealen and Ricklefs's (2001) analysis of birds suggests (but see Deaner and Nunn, 1999 on primates).

One proposed solution to the problems posed by body size allometry is to use a part of the nervous system itself as a control. This solution also reduces the measurement error inherent to estimates such as body mass, which can change rapidly as a result of food conditions. Harvey and Krebs (1990), Barton (1999), and Deaner *et al.* (2003) have pointed out that such measurement errors can create spurious positive correlations between relative brain size and other allometrically corrected variables such as life history traits. For example, correcting absolute brain size and longevity by the same erroneous body mass estimate will create a similarly high residual of the two traits in a species whose correct mass is underestimated by the erroneous estimate, and a similarly low residual for the species whose mass is overestimated. These correlated errors may create artificially correlated traits.

When a part of the nervous system is used to remove allometry, we need to specify the higher level centers that are assumed to be more closely involved with cognitively driven encephalization and the lower brain areas that can be used as the control. For this, we depend on neuroanatomy and neuropsychology. The encephalized areas can be very broad, such as the telencephalon in birds and mammals or the supraesophagal lobes in cephalopods. The areas chosen for the allometric control could, for example, be the brainstem in birds and mammals and the subesophagal lobes in cephalopods. The lower brain structure could be either that of the species itself or of a primitive evolutionary baseline. Portmann (1946, 1947a, 1947b) pioneered the use of these methods, which were later applied to mammals and cephalopods by Wirz (1950, 1959) and primates, bats, and insectivores by Stephan and collaborators (Stephan *et al.*, 1988, 1991; Baron *et al.*, 1996). In birds, the primitive reference group is usually galliformes, while in mammals, it is insectivores. For this method of removing allometry, there are thus three assumptions: the upper brain structure is the one most closely involved in encephalization, the lower brain structure has been subject only to the allometrically driven selection, and encephalization can best be understood by comparing primitive taxa to more recently encephalized ones. All these assumptions can be questioned.

Whether one uses whole bodies or lower brain structures as controls, there are in essence two statistical approaches to the removal of allometry: residuals and ratios. Residuals use the deviation from the best fit log-log regression as the measure of relative size, often transformed to a standardized scale so that all distributions are comparable from one analysis to another and normalized for parametric statistics. A problem with residuals is that they all change when you add only one new species. If this species has unusual weighting in the data point cloud, this will have a strong effect on all residuals. For example, if you add Rehkämper *et al.*'s (1991b) 23 hummingbird species to Portmann's (1947a) 140-species database, you tip the best-fit line counterclockwise due to the small body and brain size of hummingbirds. This might introduce an artifact due to the particular flight mode of hummingbirds, which might constrain both brain and body size evolution. You would thus be allowing a taxon that is a special case to influence every single residual.

In analyses that use ratios, the numerator is the brain part predicted to be most closely involved in cognitively driven encephalization (e.g., the neocortex of mammals, the mesopallium–nidopallium complex of birds, the vertical lobe system of cephalopods, and the mushroom bodies of insects; see below). The denominator is either a structure that encompasses the one in the numerator (e.g., whole brain or telencephalon or supraesophagal lobes or cerebral ganglia) or the lower brain structure not thought to control cognition (e.g., the brainstem, the subesophagal lobes, and the spinal ganglia). Allometric effects are assumed to be (wholly or partly; see below) controlled in ratios, because they apply to both the numerator and denominator.

One problem with ratios is that they are not normally distributed and thus present a statistical problem for parametric statistics. Large ratios tend to get larger faster than do small ratios. For example, parrots and corvids may easily reach values of 20 in a Portmann ratio, while ducks vary only around 1.6. Log transformations of the ratios can solve the problem by compressing the skewed high values (Lefebvre *et al.*, 1997). A second, more important, problem is that ratios may not entirely remove the confounding effect of body mass (Deacon, 1993). If we conclude, for example, that carnivory is associated with large brains and our estimate of relative brain size is confounded with body mass, there is a risk of type 1 error if carnivores also have larger bodies. In this case, the apparent brain–diet relationship could be a spurious effect of the brain–body and diet–body associations.

A third problem is that ratios of variables whose relationship is not 1 to 1 will overestimate one end of the continuum and underestimate the other. The lower the slope is below 1, the more neural structure size (normally plotted on the y axis) of animals that are at low values of the x axis will be overestimated. When the slope is above 1, the reverse will hold, with larger x values being overestimated. It is well known, for example, that expressing relative brain size as the proportion of total body mass represented by the brain will result in higher ratios in chickadees than parrots simply because chickadees are much smaller (Packard and Boardman, 1999). The brain-to-body-size ratio is often used in human paleoanthropology. The same problem may occur if the telencephalon is expressed as a proportion of the whole brain or the neocortex as a proportion of either the brain or the telencephalon (Clark *et al.*, 2001; Burish *et al.*, 2004). If the structures are thought to be progressive, the slopes of the y–x relationship are likely to be higher than 1. This will overestimate the larger-brained species (Barton, 2002), potentially favoring type 1 error of any prediction associating relative brain structure size and cognition.

It may be noted that one quantitative expression of encephalization, Jerison's (1973) encephalization quotient (EQ), combines the advantages and disadvantages of residuals and ratios. EQ expresses relative brain size as the ratio of the observed (unlogged) y value of a given species on a log-log body–brain graph, divided by the unlogged y value of the best fit regression for the x value of the species. If a species has a brain size of 20 g and the y value of the brain–body regression for an equivalently sized animal is 5, then $\text{EQ} = 4$. If the brain mass of a small-brained species of equivalent body size is 2.5, then $\text{EQ} = 0.5$. Given that EQ is based on a log-log regression, it is statistically better to calculate standardized residuals from this regression, which by definition will be normally distributed, instead of using ratios, which are not. If EQ was intended as a reference to IQ, it is puzzling that Jerison did not express his results as standardized residuals fitted to a mean of 100 and a standard deviation of 16. On this scale, parrots would score around 130, while quail would score around 75. Another problem with EQ is that values calculated from a regression line at one taxonomic level may be biased when they are used to test a hypothesis at another taxonomic level. For example, the EQ values of cetaceans (see Cetacean Brain Evolution) are routinely calculated with respect to the log-log regression line for all mammals. If one then tests a hypothesis on variation within cetaceans only, EQ may hide a confounding negative correlation with body size; small-bodied cetaceans tend to have larger EQs than large-bodied ones (Marino *et al.*, 2006). Allometry can thus still be present in EQ, even if the calculation was initially designed to remove it.

1.08.3.2 Whole Brains or Parts Thereof?

Are larger whole brains the consequence of selection for increased size of some of its components only or is enlargement of the whole brain the means by which larger specific structures evolve? Do these components vary independently of others or are there functional links between anatomically distant areas that cause change in them to occur together? The answer to these questions will depend in part on how much room the components occupy in the brain. The higher the proportion of the whole brain a component structure occupies, the more its enlargement will have a consequence for the size of the whole brain. For example, the mesopallium–nidopallium complex of a crow represents 72% of its telencephalon, which represents 78% of its whole brain. When we say a crow has a large brain, we might really only be saying that it has a large mesopallium. Selection for an enlarged high vocal center (HVC) or hippocampus in a chickadee will not have that effect, because these are small structures compared to the whole brain.

1.08.4 Why Be Encephalized?

1.08.4.1 Costs

Encephalization should normally only occur if the benefits of enlarged brains exceed its costs. These benefits and costs will operate in specific lifestyles, which need to be specified in any evolutionary account (Johnston, 1982). The two major costs to encephalization appear to be developmental and metabolic (Bennett and Harvey, 1985b). All other factors being equal, bigger brains require a longer time to develop and are energetically more expensive to maintain. The metabolic cost of brains is particularly high in humans and other primates (Aiello and Wheeler, 1995; Aiello and Wells, 2002; Fish and Lockwood, 2003), but less clear in other taxa (e.g., bats; Jones and MacLarnon, 2004). It is important to note that both metabolism and development are related to body size and diet and that their relationship to brain size is thus likely to be complicated by these interactions. If slower development means fewer offspring per unit time and is an allometric correlate of large body size, then the relative importance of natural selection and behavioral flexibility as alternative mechanisms to track environmental change will be affected. If high metabolic rate is associated with the higher surface-to-volume mechanism of heat loss in small-bodied animals, then this might affect the amount of energy available for encephalization. If herbivores are on average characterized by precocial development, low metabolic rates due to low nutrient quality, large ranges required to collect large amounts of low-quality food and large body size due to selection for an enlarged digestive system as well as defense against predators, then all these factors are also likely to affect brain size.

The brain develops slowly and some researchers have proposed that it is the major developmental constraint on time to reproduction (Sacher, 1978). Apart from parental behavior, four life history traits will affect the number of descendants per unit time, which affects the selection probability of a mutation favoring adaptation to environmental change: length of the reproductive period (reproductive longevity, time to sexual maturity), number of offspring per reproductive event, time to sexual maturity of the offspring, and time intervals between successive reproductive events. An animal that lives for 25 years, takes 5 years to mature sexually, and has one offspring every 2 years will have far fewer descendants at the end of 100 years than an animal that has three offspring per yearly reproductive event, lives for 5 years and takes 1 year to mature. Changes due to selection will occur much more slowly in the first species because fewer generations per century mean both fewer mutations and less differential reproduction, thereby increasing the value of behavioral flexibility as a mechanism for change.

1.08.4.2 Benefits

The major hypothesis for the explanation of encephalization is that bigger brains allow enhanced cognitive abilities, abilities useful in certain lifestyles. The problem then becomes the definition of enhanced cognitive abilities and the lifestyles they could be useful in. This hypothesis can be tested by specifying the lifestyles that could benefit from more complex cognition, operationalizing the complexity of cognition, then looking for a statistical association between lifestyle, brain size, and cognitive complexity. General cognitive complexity can be opposed to specialized cognitive skills associated with specific lifestyles in a restricted set of taxa. The spatial memory associated with food caching in corvids and parids or brood parasitism in cowbirds is thought to be one example of the latter, as is the acoustic memory associated with song repertoire size in oscines (DeVoogd *et al.*, 1993). In these cases, specialized neural structures are studied and the cognitive variation is relatively easy to operationalize: memory for more cache locations or acoustic memory for more songs. The small size of the structures (HVC, RA, hippocampus) implies that they are unlikely to form the basis of encephalization. What we are looking for instead is variation in unspecialized cognition over potentially all species, based on the involvement of a large enough part of the brain that can address the issue of whole brain encephalization.

The difficulty is operationalizing unspecialized cognition in all species. Researchers usually look to abilities associated with complex cognition in humans. If we want to include as many taxa as possible in our tests, we have to look outside of tests that only a few nonhuman species can solve, such as learned sign language, episodic memory, fast-mapping, or understanding of the mental states of others (theory of mind). Associative learning is one obvious possibility. If we define the continuum of cognitive complexity as the latency of or the number of errors in learning, however, we face the problem of confounding variables and ecological validity. If a crow solves a learning test in the lab faster than does a kiwi, this might be because that the crow is tamer and less neophobic in the lab, the task favors visual rather than olfactory cues, or the task resembles situations crows encounter often in the field but kiwis do not. What we need is cognition that occurs spontaneously in the field, without the confounding variables of tests in captivity and in a situation that is natural to each animal. Tool use, play, and presumed deception and social learning are possible choices. We can also look to innovative behavior.

We then plot the taxonomic distribution of our cognitive measure from the field and see if, as predicted by encephalization theory, the distributions correlate positively with relative brain size, taking out as many confounding variables as possible. If the results of field and laboratory tests are positively correlated, this would support the assumption that they are both valid estimates of cognition. Research on birds and primates, based on re-analyses of published data as well as new tests (Webster and Lefebvre, 2001; Reader and MacDonald, 2003; Lefebvre *et al.*, 2004), suggests that tests in captivity are indeed positively correlated with field measures. We can further test our assumption that unspecialized cognition exists by predicting positive correlations between the distribution of the different cognitive measures. All of these relationships have been tested in birds and primates (see below). Overall, the analyses conducted up to now on the two taxa suggest convergent evolution of interspecific variation in cognitive abilities (see also Emery and Clayton, 2004). Similar positive correlations between innovation rate, tool use rate, and reversal learning performance have been found in birds and primates, perhaps suggesting that these cognitive abilities are nonmodular (Lefebvre *et al.*, 2004). The only exception for the moment seems to be the relationship between food storing and innovation in 22 species of birds; a negative relationship is found in New World corvids and Old World parids, suggesting a (possibly modular; Lefebvre and Bolhuis, 2003) trade-off between storing and innovativeness.

It is important to note that correlations between brain size and cognitive variables do not demonstrate the survival value of having a large brain, nor are they evidence for natural selection on enlarged brains. The correlations suggest that large brains are on average present in tool using, innovative, playful, social taxa that develop slowly, but they also suggest that small-brained taxa can do well, provided their lifestyles do not include these attributes. A survey of long-term population trends (1968–95) in 40 British bird species provides evidence for selection on large over small brains, with larger declines observed in small-brained species than in large-brained ones (Schultz *et al.*, 2005). Sol *et al.* (2002, 2005) examined colonization success of introduced birds in different parts of the world; some species succeed almost everywhere (e.g., sparrows and blackbirds), while others are extinct after only a few years. Relative brain size (and innovation rate in the zone of origin) significantly predicts variance in colonization success. Contrary to natural invasions, where unsuccessful cases are seldom documented, introductions allow good coverage of the entire spectrum of responses. If introductions are an unbiased estimate of all invasions, then establishment in new areas might be one of the key selective forces that affect encephalization trends (Sol *et al.*, 2005) and the allopatric divergence that often follows invasion, a key mechanism in the association between speciosity and relative brain size in birds (Nicolakakis *et al.*, 2003).

1.08.4.3 Ecology and Lifestyles

To express ecological theory in a very simplified way, the distribution of abiotic factors drives the distribution of vegetation, which in turn drives the distribution of animals. Lifestyles (diet, sociality, and sexual selection) are then driven by the distribution of animals and plants. If biotic and abiotic resources are spatially and temporally predictable and in relatively low-density clumps, a specialized, conservative, territorial polygynist with monoparental care may do better than a generalist, opportunistic, invasive, gregarious monogamist with biparental care. The reverse would apply to spatially and temporally unpredictable resources found in abundant patches. We would then expect selection to act on cognition to provide the information-processing capacity that best suits each lifestyle, with accompanying selection on encephalization (Bennett and Harvey, 1985a). Testing the idea that omnivory should be associated with brain size is thus not an ecological prediction on cognition, but a dietary prediction on encephalization with two missing links: how does resource distribution favor omnivory and how does omnivory require more complex cognition or lift dietary constraints on brain size? The use of an ecological framework is all the more important because the same resource distribution may lead to similar predictions on lifestyle differences that are sometimes viewed as independent pressures for complex cognition and encephalization. For example, social and diet breadth pressures on the evolution of cognition and brains are often seen as alternatives (see Forebrain Size and Social Intelligence in Birds). If, however, one type of resource distribution favors gregarious generalists and another favors territorial specialists, then the two pressures go in the same direction. Whether or not the lifestyle differences are independent is a matter of empirical test (with multivariate techniques, for instance), not a logical *a priori*.

Diet (Eisenberg and Wilson, 1978), sociality (Dunbar, 1992; Dunbar and Bever, 1998), sexual selection (Madden, 2001), and parental care (Gittleman, 1994) have all been shown to be associated with encephalization. In some of these tests, we do not know to what extent the apparent co-evolution of the traits is due to common ancestry or repeated independent events, given that independent contrasts have not been conducted. Larger brains have been found in omnivorous and frugivorous groups (Allman *et al.*, 1993) compared to folivorous or herbivorous animals. For sexual selection, there is interspecific evidence for an association between brain size and bower building (Madden, 2001) and intraspecific evidence for an association between telencephalon size and song repertoire size in zebra finches (Airey and DeVoogd, 2000). Monoparental versus biparental care, which is a consequence of sexually selected mating systems, has also been implicated in brain size differences (Gittleman, 1994).

1.08.5 Mammals

Mammalian encephalization has received considerable scientific attention, probably because the class contains two of the most encephalized orders, primates and cetaceans, and because we humans number among the 5000 or so mammal species (see Encephalization: Comparative Studies of Brain Size and Structure Volume in Mammals). Mammals thus provide a valuable case study for understanding the selection pressures favoring evolutionary changes in brain size, with many hypotheses regarding brain evolution originally applied to mammals and relatively large databases of whole brain and brain component volumes available (for extensive discussion, see the articles on brain evolution in mammals, various mammalian orders, and humans, this volume, e.g., Primate Brain Evolution in Phylogenetic Context, The Evolution of Hemispheric Specializations of the Human Brain, The Evolution of Human Brain and Body Growth Patterns, Mosaic Evolution of Brain Structure in Mammals, Encephalization: Comparative Studies of Brain Size and Structure Volume in Mammals, Evolution of the Cerebellum, Evolution of the Hippocampus). This has made possible large-scale comparative studies. Moreover, experimental data have been combined with comparative studies of brain evolution, and breeding experiments have also addressed the evolution of larger brains.

Mammalian encephalization, like encephalization in all animals, is generally assumed to result from the selective benefits of enhanced cognitive, perceptual, or motor abilities, with most research focusing on cognition (Macphail, 1982; Barton, 1999). Evidence regarding the assumed link between brain volume and cognitive capacity has come from two sources: correlations of behavioral demonstrations of cognitive ability and brain size, and from associations between enlarged brains and lifestyles thought to require increased cognitive demands. The behavioral data provide a more direct test of the assumption that cognitive capacity and brain size are linked, and so are key in this respect (Macphail, 1982; Deaner *et al.*, 2000). Several lines of evidence in mammals have pointed to a correlation between a species' relative brain volume and its cognitive capacity. First, laboratory learning data collated from a variety of sources has been shown to correlate with relative whole brain size, although the number of species tested is small (Riddell and Corl, 1977). Second, various measures assumed to indicate general cognitive capacities correlate with relative neocortex size: the frequency of reports of tactical deception, innovation, social learning, and tool use all correlate with relative neocortex volume in primates (Reader and Laland, 2002; Byrne and Corp, 2004). These latter measures have the advantage of covering a larger number of species. Third, it has been proposed that the ability to perform apparently complex cognitive acts such as imitation and understanding the intentions of others are associated with brain enlargement (Byrne, 1992). For example, among mammals, the consensus view is that true imitation has only been experimentally demonstrated in large-brained apes and dolphins, while the smaller-brained mammals tested present equivocal evidence of imitation (Mitchell *et al.*, 1999; Caldwell and Whiten, 2002). However, tests of complex cognition have been the subject of much controversy (e.g., Tomasello and Call, 1997). Moreover, because research has tended to focus on only a few, typically large-brained mammal species, it is difficult to know the true phylogenetic distribution of such traits and to conduct proper comparative analyses.

Problems with comparative studies can be solved by experimental studies of evolution. Studies on rhesus macaques and mice have demonstrated that brain size is heritable (Jensen, 1979; Atchley *et al.*, 1984; Cheverud *et al.*, 1990; Markina *et al.*, 2001), which indicates that it is open to modification by selection. Moreover, selection experiments in mice have bred large- and small-brained lines and have found differences between the lines in performance on learning tasks (Markina *et al.*, 2001). Interpretation of these findings is controversial, not least because learning ability is inferred from performance and a number of other behavioral changes are observed in the selection lines, such as changes in anxiety or exploratory behavior (Jensen, 1979; Johnston, 1982; Markina *et al.*, 2001). A further problem is that selection on learning performance has tended to result in selection for task-specific abilities (Jensen, 1979). Moreover, the critical test of whether selection on learning capacities can lead to evolutionary changes in brain size would be to select for cognitive ability and to examine the effect on brain size (Johnston, 1982). As far as we are aware, such experiments have not been done, although one study reports a decrease in size of a hippocampus area in mice lines exposed to environmental stressors (such as natural predators; Poletaeva *et al.*, 2001).

The vast majority of work on encephalization has focused on identifying the selection pressures associated with brain enlargement. Hypotheses have tended to fall into two camps, social and ecological explanations for brain enlargement. Social (or Machiavellian) intelligence hypotheses argue that enlarged brains evolved as an adaptation to living in large, complex social groups (Jolly, 1966; Humphrey, 1976; Byrne and Whiten, 1988; Flinn, 1997; Whiten and Byrne, 1997). Byrne and Whiten (1997) distinguish the term "narrow Machiavellianism," the idea that it is selection for strategies of social manipulation or deception that has driven brain evolution, from their own broader use of the term "Machiavellian intelligence," which includes all forms of social intelligence such as social learning. Ecological explanations for the evolution of large brains are also common and include the extractive foraging (Parker and Gibson, 1977) and cognitive/spatiotemporal mapping hypotheses (Milton, 1988; Deaner *et al.*, 2000). Unpredictability and patchiness of resources are often cited as key ecological factors favoring brain enlargement (Eisenberg and Wilson, 1978). For example, fruit is likely to be distributed more patchily in space and time than are leaves, and so a fruiteating diet may be expected to have more cognitive demands than a leaf-eating one. Technical intelligence hypotheses that argue that technology or technical skills drove brain evolution can be considered with the ecological intelligence hypotheses, because they tend to focus on foraging or antipredator tool use (Passingham, 1982; Byrne, 1997a, 1997b).

What evidence is there in support of these hypotheses? Relative neocortex or brain size is positively correlated with social group size in nonhuman primates, carnivores, cetaceans, bats, and some insectivores, consistent with social intelligence hypotheses (Worthy and Hickie, 1986; Sawaguchi and Kudo, 1990; Dunbar, 1992; Marino, 1996; Barton, 1999; but see Connor *et al.*, 1998; van Schaik and Deaner, 2003 on cetaceans). In ungulates, social species tend to have larger relative brain and neocortex sizes than do nonsocial species, (Schultz and Dunbar, 2006). Barton (1993) finds a correlation between group size and neocortex size in haplorhine primates, but not strepsirhines, which may indicate that group living favored brain size evolution among haplorhines only. Adding support to Machiavellian intelligence hypotheses, the frequency of reports of deceptive behavior has been found to correlate with relative neocortex size (Byrne and Corp, 2004). The findings that human and other primates tend to have superior abilities in problems involving social knowledge versus those involving nonsocial knowledge has also been taken as evidence that cognitive abilities developed as a response to social pressures (Cheney and Seyfarth, 1988; see also Baron-Cohen *et al.*, 1999).

In support of ecological intelligence ideas, diets presumed to require increased cognitive demands have been shown to correlate with relative brain volume in several mammalian groups. For example, primate relative whole brain size and neocortex size correlate with frugivory (Barton, 1999) and diet breadth and relative neocortex volume are correlated in African anthropoid primates (Reader and MacDonald, 2003). Similar associations with diet, albeit not based on independent contrasts, have been found in bats (aerial insectivores have smaller brains for their body size than frugivores and nectarivores, with piscivores, foliage gleaners, carnivores, and sanguivores falling between the two extremes; Eisenberg and Wilson, 1978), small mammals (in rodents and lagomorphs, folivores and insectivores have small brains relative to their body mass and body length compared with those of other dietary categories; Harvey *et al.*, 1980), and the Carnivora (carnivorous and omnivorous species have larger relative brains, though not significantly so, than insectivorous carnivora; Gittleman, 1986). In a phylogenetically controlled study of 59 bat species, Ratcliffe *et al.* (2006) have recently reported a larger relative brain size in species that use a flexible combination of gleaning and hawking techniques, compared to those that are specialized on either of the hunting modes. Home range correlates with relative brain size in primates, in support of spatiotemporal mapping ideas (Clutton-Brock and Harvey, 1980; Deaner *et al.*, 2000). Consistent with technical intelligence hypotheses, tool use frequencies correlate with relative neocortex volume in primates (Reader and Laland, 2002; Lefebvre *et al.*, 2004). However, the fact that few primates appear to make regular use of tools in the wild questions the idea that technical intelligence was a driving force for primate brain enlargement (van Schaik *et al.*, 1999).

A number of other lifestyle correlates of relative brain size have been described. For example, in didelphid marsupials, preference for arboreal activity is associated with relative brain volume (Eisenberg and Wilson, 1981). Cerebellum volume has also been linked to locomotion mode in primates, bats, and cetaceans (Stephan and Pirlot, 1970; Rilling and Insel, 1998; Marino *et al.*, 2000). Females of carnivore species where the females provide the sole parental care have larger brains than those of biparental or communal species (Gittleman, 1994). Neocortex volume has also been linked to sexual selection, being correlated with mating competition in frugivorous primates (Sawaguchi, 1997).

Potential costs and constraints of mammalian encephalization have received less attention, though there is support for the idea that brain enlargement carries metabolic and developmental costs, with brain size negatively correlated with litter size in marsupials (Eisenberg and Wilson, 1981), and positively correlated with the age of sexual maturity and life span, but not gestation length, in primates (Barton, 1999; Allman *et al.*, 1993; Kaplan and Robson, 2002; van Schaik and Deaner, 2003). In odontocetes, relative brain size is also associated with relative time to sexual maturity and life span. Within life span, however, length of the adult period is more closely correlated with relative brain size than is length of the juvenile period, suggesting that the temporal costs of delayed maturity might be compensated by a longer time as a reproducing adult (Lefebvre *et al.*, 2006). Primate brain size is not correlated with basal metabolic rate, and comparative analysis indicates that improved diet quality, by allowing reduction in gut mass relative to body size, is one possible mechanism allowing the energetic constraints on the evolution of the metabolically expensive large brain to be lifted (Aiello and Wheeler, 1995; Barton, 1999; Fish and Lockwood, 2003).

Given that there is support for a number of hypotheses regarding mammalian encephalization, can any consensus be formed? The findings described above are consistent with the idea that several selective pressures are responsible for the evolution of encephalization. An alternative view is that one factor is driving brain evolution, but that the cognitive abilities afforded by a large brain are applied to other domains. Determining causation is difficult since most comparative studies are based on correlational evidence. Moreover, the divisions between social and ecological intelligence may be fuzzy and social and ecological demands on cognition may evolve together, making it difficult to consider social and ecological intelligence hypotheses as alternatives (Barton, 1999; Deaner *et al.*, 2000; Reader and Laland, 2002; Seyfarth and Cheney, 2002). It is also difficult to separate perception from cognitive demands. For example, primate brain size variation is associated with visual specialization. Visual processing may be critically involved in the treatment of both social and ecological information; relative expansion of parts of the visual system is correlated with both frugivory and group size (Barton, 1999). What is clear, however, is that evolution has shaped mammalian brains in response to the demands of their lifestyles, with convergent evolution of brain structures in several groups (De Winter and Oxnard, 2001; Kaas, 2002).

1.08.6 Birds

It was long believed that the avian forebrain was composed of hypertrophied basal ganglia with only meager pallial derivatives, whereas in mammals, the pallium had grown into a highly parcellated laminar neocortex (Ariens-Kappers *et al.*, 1936). The recent revised nomenclature of the avian telencephalon (Reiner *et al.*, 2004) recognizes many anatomical and functional similarities between the avian and mammalian forebrains. In particular, the newly named avian nidopallium, mesopallium, and arcopallium are considered homologous to mammalian pallial derivatives, the neocortex, claustrum, and pallial amygdala (Karten, 1969, 1991; Güntürkün, 1991; Wild *et al.*, 1993; Butler, 1994; Veenman *et al.*, 1995; Striedter, 1997; Reiner *et al.*, 1998; Smith-Fernandez *et al.*, 1998; Medina and Reiner, 2000; Puelles *et al.*, 2000).

A large amount of variance in the size of both adult and hatchling avian brains can be explained by the altricial versus precocial dichotomy in development mode. Birds that develop slowly and require extensive parental care are born with relatively smaller brains than birds that are mobile only a few minutes or hours after birth. The reverse applies to adult brain size, where altricial birds have larger brains than do precocial ones (Portmann, 1946; Bennett and Harvey, 1985a, 1985b). In Bennett and Harvey's study, most of the ecological variables (e.g., diet, habitat) that showed a relationship with relative forebrain size in univariate analyses became nonsignificant when development mode was included in multivariate statistics. Only mating system (monogamous → polygynous) and mode of prey capture (moving from a perch vs. other categories) remained significant predictors of relative size of the brain and forebrain. All large-brained avian clades develop slowly, but the reverse is not true. The altricial Columbiformes (pigeons and doves) and Caprimulgi (nightjars) are, in relative terms, not much more encephalized that the precocial Galliformes and ratites. On average, growing a large brain may impose some limits on incubation energetics, as well as the length of intrauterine growth. It might not be possible for birds to stock sufficient energy in the egg for extensive brain growth. Stark (1993) offers some interesting observations of the comparison of brain growth in altricial and precocial birds. He found that in the freshly hatched buttonquail, a precocial species, all telencephalic areas and fiber pathways have undergone differentiation and started myelinization. There are no more areas of cell proliferation in the hatchling, indicating that the number of neurons is definite and that postnatal volume increase can be exclusively attributed to growth. Similarly, the optic tectum of the hatchling muscovy duck has almost reached adult size and differentiation level. In contrast, the three altricial species that Stark (1993) studied have a significant posthatch cell proliferation in the periventricular zone. In the budgerigar and Java sparrow, cell proliferation continues until the 10th postnatal day. Stark suggests that a large postnatal increase in the volume of the brain depends on a persistence of this large periventricular proliferation zone, which can be maintained as long as there are no functional demands on the developing systems. This is possible in altricial hatchlings freed from the need for a functional forebrain by extended parental care. Stark (1993) proposed that to arrive at a larger brain volume, more cells have to divide during the proliferation phase. Theoretically, the increase in cell numbers can be achieved in three ways: increasing the rate of periventricular cell division, increasing the area of cell proliferation, or lengthening the proliferation period. There is no empirical support for the first two options in birds; the third option is possible only in altricial species where parental care compensates for the lack of functional independence by the chicks. Stark (1993) also suggests that nutritional constraints on the hatchlings affect the options: precocial species tend to eat foods that can be easily obtained, while altricial ones eat foods that are widely dispersed or difficult to find. In a recent study, Iwaniuk and Nelson (2003) corroborate the conclusions of Stark (1993) using continuous development time measures in addition to the dichotomous precocial/altricial classification. They divide development into four periods: incubation, fledging, postfledging parental care, and total period of parental care. All developmental periods except time to fledging are significantly correlated with brain size, once common allometric correlates are removed. The relationships vary with development mode, and Iwaniuk and Nelson (2003) suggest that factors such as diet and foraging techniques interact with development in determining brain size.

If the relationship between ecology and encephalization appears to be confounded by developmental constraints, this is not the case for more direct measures of cognition. Lefebvre and collaborators have quantified avian cognition in the field by measuring the frequency of novel, unusual, or rare feeding behavior in over 800 species in five areas of the world (see Lefebvre *et al.*, 1997, 1998 for examples). They have collated over 2300 cases of innovative feeding and 130 cases of tool use and shown that both measures of cognition show taxonomic distributions that are positively correlated with relative size of the brain and forebrain (Lefebvre *et al.*, 1997, 1998, 2001, 2002, 2004; Nicolakakis and Lefebvre, 2000). Nine potential confounding variables have been included in these analyses, to ensure that biases inherent to the quantification of anecdotal judgments on novelty and cognitive complexity do not affect the biological trends. One of these confounding variables was development mode, which does not account for the correlation between encephalization and either innovation rate or tool use frequency.

Using the detailed brain data on 32 species from 17 parvorders gathered by Boire (1989) and Rehkämper *et al.* (1991a), and the innovation and tool use rates from previous papers, Timmermans *et al.* (2000) and Lefebvre *et al.* (2002) were able to pinpoint the avian telencephalic areas most closely associated with cognition. Rehkämper and Zilles (1991) and Boire and Baron (1994) have suggested that it is the disproportionate increase of the size of the nidopallium and mesopallium that drove the enlargement of the avian telencephalon. Consistent with these predictions, Timmermans *et al.* (2000) showed that it is the relative size of the mesopallium that correlates most closely with innovation rate. In simple regressions, the nidopallium, hyperpallium (Wulst), and components of the striatopallidal complex were also all correlated with innovation rate, with or without phylogenetic corrections. In multiple regressions, however, these structures dropped out of the model because of their strong correlations with the size of the mesopallium, which explains a larger proportion of the common variance. Lefebvre *et al.* (2002) repeated a similar analysis with two types of tool use, true tools and proto-tools, which are described in over 100 avian species (see also Boswall, 1977, 1978, 1983a, 1983b for comprehensive reviews). Proto-tools involve the use of objects that are part of a substrate, e.g., anvils on which prey are battered or dropped, or wedges and thorns with which food is held. True tools are detached from the substrate, e.g., hammers, probes, scoops, sponges, and levers held directly in the beak or foot;

their use is presumed to require more complex cognition that that of proto-tools. Lefebvre *et al.* (2002) confirmed that true tool users have larger brains than do proto-tools users and that, within the forebrain, relative size of the nidopallium and mesopallium are the best predictors of avian tool use frequency. The mesopallium comprises higher-order, multimodal processing areas. The nidopallium features tertiary areas of this type, but also includes primary projection fields from both somatosensory and visual pathways, as well as secondary areas that receive input from these primary fields (Rehkämper *et al.*, 1985). The nidopallium thus has the necessary features for both the cognitive and sensorimotor aspects of tool use, in particular the integration of visual and somatosensory information involved in the fine manipulation of objects.

Beyond these comparative studies of the whole avian spectrum, a few authors have concentrated on encephalization patterns within particular orders such as Anseriformes, Trochiliformes, and Psittaciformes. Iwaniuk and Nelson (2001) recently examined a large number of waterfowl. This group is of particular interest because it is precocial, keeping constant the main confounding variable identified by Bennett and Harvey (1985a). Iwaniuk and Nelson worked from endocasts of museum specimens of 354 individuals representing 55 species. Their analysis did not show any significant relationship between foraging mode or diet and relative brain size in Anseriformes, which does not preclude that further analyses on finer brain structures might not reveal clearer trends. One interesting species in their sample is the musk duck, *Biziura lobata*. It has a large brain compared to its sister species and also shows a much more altricial mode of development than do other Anseriformes, raising only one or two offspring that do not feed themselves right after hatching, but rely instead on the mother and slowly become independent. Trochiliformes (hummingbirds) were studied by Rehkämper *et al.*, (1991b); they show a level of encephalization intermediate between that of Galliformes and Passeriformes. It is not clear if hummingbirds' encephalization level is a product of relative brain enlargement or selection for small bodies. Boire (1989) and Boire and Baron (1994) suggest that it is cerebellum size that might be the main component of brain enlargement in this order, in line with the complex motor control required for hovering. Terns and swifts, which have more complex flight behavior than other birds, also show an enlarged cerebellum (Boire, 1989; Boire and Baron, 1994). Psittaciformes have recently been examined by Iwaniuk *et al.* (2005), who measured whole brain size in 180 species, as well as the size of brain regions in 19 species. Their study confirms previous work (Portmann, 1946, 1947a; Boire, 1989, Boire and Baron, 1994) showing that this order, which shows complex cognitive abilities (Pepperberg, 1999, 2002; Borsari and Ottoni, 2005), has a larger telencephalon than other nonpasserine birds, while subtelencephalic brain components show a much smaller range of variation. Psittaciformes are among the birds showing transactional social behavior in the classification proposed by Burish *et al.* (2004). This complex form of sociality is associated with larger ratios of telencephalon to total brain size.

Besides the avian equivalents of the mammalian neocortex, the mesopallium and nidopallium, areas such as the olfactory bulb and the hippocampus have also been subject to comparative studies. In general, birds are considered microsmatic, but there is increasing evidence that many of them use smell in foraging, orientation, and homing, as well as site and individual recognition (see references in Healy and Guilford, 1990). There is a large database on the size of avian olfactory bulbs (Bang and Cobb, 1968) showing considerable taxonomic variation; unfortunately, these data are not actual volumes, but the ratio between the largest diameter of the olfactory bulb and that of the longest length of the cerebral hemispheres. This measure is not independent of the size and shape of the cerebral hemispheres, and the data should therefore be interpreted with care. Initial interpretations of these data led to the conclusion that large olfactory bulbs are associated with aquatic habitats (Bang and Cobb, 1968; Bang, 1971). A more careful statistical analysis suggested that nocturnal birds have larger olfactory bulbs (Healy and Guilford, 1990). The hypothesis was that olfaction might be useful for birds in low-light conditions for tasks such as site recognition and location of predators and slow-moving or stationary prey. For the moment, this proposed association between activity pattern and olfactory bulb size is interesting, but awaits a more reliable database. It should be noted that large olfactory bulbs in birds are not generally associated with the enlargement of the telencephalon. However, it has been suggested that in Anseriformes, the increased telencephalization is in part correlated with enlarged olfactory structures (see Rehkämper *et al.*, 2001). This is shown by the considerable expansion of telencephalic targets of olfactory projections (Ebinger *et al.*, 1992). For example, the olfactory structures in Anseriformes are twice the size of those in the pigeon (Ebinger *et al.*, 1992).

In absolute size, the avian hippocampus is quite small compared to that of mammals, but several studies suggest a correlation between the size of this structure and lifestyles implying more spatial cognition. The hippocampus is larger in food-storing birds than in nonstorers (Krebs *et al.*, 1989; Sherry *et al.*, 1989; Healy and Krebs, 1992, 1996; Healy *et al.*, 1994; Hampton *et al.*, 1995; Basil *et al.*, 1996; Volman *et al.*, 1997). Spatial cognition is not only relevant to food gathering, but also to homing abilities (Rehkämper *et al.*, 1988) and spatial abilities in finding host nests in brood-parasitic cowbirds (Sherry *et al.*, 1993; Reboreda *et al.*, 1996). Some authors (e.g., Bolhuis and Macphail, 2001) have criticized this literature, but Lucas *et al.* (2004) have recently shown that despite differences between species from North America and Europe (Brodin and Lundborg, 2003), there is a clear correlation between the degree of food-caching specialization and hippocampus size in Corvidae and Paridae. In pigeons, breeds that were artificially selected for homing have a larger telencephalon than nonhoming breeds, and this seems to be the result of an enlarged hippocampus (Rehkämper *et al.*, 1988). In food-caching birds, most studies conducted at the species level report no correlation between the size of the hippocampus and that of the telencephalon (Healy and Krebs, 1992, 1996; Healy *et al.*, 1994; Hampton *et al.*, 1995; Basil *et al.*, 1996), but others have found a correlation at the level of the subfamily and family within Passerines (Sherry *et al.*, 1989). It is interesting to note that food-caching experience leads to neurogenesis both in the hippocampus of young marsh tits and in the mesopallium (Patel *et al.*, 1997). This could mean that the more specialized, hippocampal, component of spatial memory may be linked to more generalized problem-solving processes in the mesopallium. This might explain the fact that species differences in food caching in the field are often stronger than those seen in spatial memory tests in captivity. Lefebvre and Bolhuis (2003) report a negative or zero correlation between innovation rate and reliance on food caching in corvids and parids. If the captive tests solicit both specialized spatial memory and more general problem-solving ability, interspecifc differences would be magnified by a positive correlation between the two processes, but dampened by a negative or zero correlation. More research is clearly needed on this point. In the other intensively studied avian specialization, imitated song (Jarvis *et al.*, 2000), correlated evolution of small, specialized nuclei and larger telencephalic structures has been suggested by DeVoogd and coworkers. Airey *et al.* (2000) have shown that zebra finches have heritable variation in both the size of their song repertoire and the size of nucleus HVC, the control center for syllable organization (Yu and Margoliash, 1996). HVC size is positively correlated with whole telencephalon size in zebra finches, leading DeVoogd (2004) to suggest that song repertoire might be an honest signal for general cognitive ability.

1.08.7 Invertebrates

Encephalization has not been as well studied in invertebrates as in vertebrates. Some structures have, however, been thought to play equivalent roles to the ones that the forebrain plays in mammals and birds. Invertebrates often cited for their cognitive skills are the hymenoptera on the one hand and the octopus and cuttlefish on the other (see Cognition in Invertebrates). Hymenoptera have the most complex social behaviors of all insects. Octopus and cuttlefish are at the extremes of the habitat complexity distribution proposed by Hanlon and Messenger (1996, figure 3.9). The same intraclass logic we have applied earlier to birds and mammals can thus be applied to the groups that hymenoptera and octopus belong to, insects and cephalopods. In these classes, the mushroom bodies and vertical lobes, respectively, are the brain structures most often mentioned in studies of encephalization.

1.08.7.1 Insects

In insects, the mushroom bodies have long been seen as the higher centers that might be the substrate of cognition (see Strausfeld *et al.*, 1998, and Farris, 2005, for reviews). They control sensory integration, learning, and memory, and, according to Farris (2005), are convergent equivalents of the mammalian cortex. Their crucial role in memory is evidenced by *Drosophila* mutants that lack both the vertical lobes of the mushroom bodies and long-term (but not short-term) memory (Pascual and Préat, 2001). The insect taxa (ants, honeybees, and wasps) that have evolved complex societies with division of labor, as well as altruistic reproduction and nest defense, have enlarged mushroom bodies (Howse, 1974; Gronenberg *et al.*, 1996; Ehmer and Hoy, 2000). Diet might be as important as social life in determining insect mushroom body size. Mares *et al.* (2005) found that honeybees (*Apis mellifera*) do not have larger mushroom bodies than does the bumblebee *Bombus impatiens*, as one would have predicted from the much more complex social life of honeybees. *B. impatiens* is a dietary generalist, however, which raises the intriguing possibility that specialized species of *Bombus* might have smaller mushroom bodies than either *B. impatiens* or *A. mellifera*. Farris and Roberts (2005) compared 11 generalist and specialist scarab beetle species and found sharp differences in mushroom body size and structure associated with dietary differences. Generalist (e.g., phytophagous) beetles have larger and more convoluted mushroom bodies featuring double calyces, whereas specialist species (e.g., dung beetles) have smaller mushroom bodies with single calyces. Ontogenetic changes, both natural and experimentally manipulated, that make honeybees switch from larval care to the much more complex task (e.g., learning and dance communication of flower patches, swarming; Seeley and Burhman, 1999) of foraging outside the hive are accompanied by an increase in the Kenyon cells of the mushroom bodies (Withers *et al.*, 1993). Similar results have also been reported for carpenter ants (Gronenberg *et al.*, 1996)

1.08.7.2 Cephalopods

Compared to other classes, the relative brain size of cephalopods is between that of fish and reptiles on the one hand and birds and mammals on the other (Packard, 1972). Within the 800 or so cephalopod species, there is a large degree of variation in learning performance, brain size, and vertical lobe size. The vertical lobe is the area of the cephalopod brain that Nixon and Young (2003) describe as the modulator for the systems that guide visual and tactile responses. Nixon and Young (2003) list the relative size of 14 brain areas in 63 species (see also Wirz, 1959). The data in their table 2.6 are expressed as fractions of total brain size. As Hanlon and Messenger (1996) point out, the two genera that are most often mentioned as intelligent, octopus and cuttlefish (*Sepia*), do not have the largest vertical lobes according to this fraction estimate. However, when we use the more usual technique of regressing either whole brain size or vertical lobe size against body size (in this case, mantle length, given for 49 of the species), the two species are 1.5 (octopus) and 2.5 (cuttlefish) standard deviations above the mean cephalopod regression line. The third cephalopod whose nervous system has been intensively studied, the squid *Loligo*, places around 2 standard deviations above the line.

Many studies have been conducted on associative learning in octopus by Young and his colleagues (Wells, 1966). Three features of avian and primate cognition, innovation, social learning, and improvement over successive learning reversals, have been described in the field by Norman (1999) and in the lab by Fiorito and Scotto (1992) and Mackintosh and Mackintosh (1964). Octopus in Indonesia forage for complimentary fragments of coconut shells thrown by humans in shallow water, using them as portable dens (Norman, 1999). Octopus (Fiorito *et al.*, 1998) can also solve the kind of innovative food-finding problem that passerines, but not doves, readily succeed at (Webster and Lefebvre, 2001; see however, Bouchard, 2002 for pigeons). Finally, octopus that observe a trained conspecific attack a white stimulus (instead of the normally preferred dark stimulus), will also attack the white stimulus when tested alone after the observation sessions (Fiorito and Scotto, 1992). Lesions of the vertical lobe, which are known to affect associative learning in octopus, also affect observational learning, but only over short time intervals (Fiorito and Chichery, 1995). The octopus vertical lobe seems to show evidence of convergent evolution with vertebrate learning mechanisms, with long-term potentiation of glutaminergic synaptic field potentials (Hochner *et al.*, 2003). In cuttlefish, the vertical lobe also appears to be involved in learning. In particular, Dickel *et al.* (2001) show a striking similarity between ontogenetic increases in the relative size of the vertical lobe (but not of other areas) and improvements in learning.

1.08.8 Conclusion

Studies of encephalization often focus on taxonomic differences in the size of whole brains or of forebrain areas. This does not necessarily mean that size is the key causal variable behind differences in cognitive performance. Many other features of nervous systems, e.g., synaptic networks, neuronal density, neurotransmitter facilitation, might be equally or more important. Comparative studies on brain size have often been justified by the ease with which broad data bases could be gathered on preserved brains (Portmann, 1946, 1947a, 1947b), endocasts (Mlikovski, 1989a, 1989b, 1989c, 1990; Iwaniuk and Nelson, 2002) and fossils (Burish *et al.*, 2004; see The Hominin Fossil Record and the Emergence of the Modern Human Central Nervous System). However, recent molecular work suggests that size may indeed be one of the crucial aspects of adaptive evolution of brains. Dorus *et al.* (2004) examined 214 genes in humans, macaques, mice, and rats and found that those with the highest rates of evolution in primates determine brain size. Genes not involved with the nervous system or involved in physiological rather than developmental aspects of the brain showed similar evolutionary rates in rodents and primates. This suggests that size differences may be more than easy proxies for subtler differences in anatomy and function. Disregarding for the moment the major interclass transitions in the way the nervous system is organized, comparisons within taxa suggest that differences in cognitive performance show convergent co-evolution with differences in the size of association areas and of whole brains. Within the constraints of a highly conserved neuronal and synaptic machinery, building an intelligence might be similar to moving an animal through the air. In the same manner that locusts, bats, and albatrosses have evolved convergent, independent solutions to similar problems posed by gravity and lift, honeybees, cuttlefish, crows, and chimpanzees might also have evolved convergent solutions to the common problem of flexible processing and storage of information.

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