

COMPARATIVE STUDIES OF THE BRAIN AND ITS COMPONENTS

by

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ABSTRACT

The weight of the adult brain and its component parts in mammals and birds are correlated with body weight, and with lifestyle independently of body weight. It is not clear that any particular exponent relating brain weight to body weight is characteristic of either mammalian or avian taxa, which means that most explanations for particular values of exponents lack empirical foundation. Dietary differences within different orders of mammals seem to be correlated with encephalisation (brain weight after body weight effects have been statistically controlled for), as do differences in patterns of development in birds. Strangely, dietary differences among birds and developmental differences among mammals are not correlated with encephalisation. There is no firm evidence that the exponent relating brain to body weight differs with taxonomic level in mammals—earlier claims that there was such a relationship were founded on inappropriate statistics and failure to control for differences in diet. Recently, evidence has started to accumulate which relates the size of brain components to differences in lifestyle. Links are beginning to be forged between evolutionary, ecological, behavioural, and neuro-anatomical studies of the brain.

KEY WORDS: brain size, hippocampus size, comparative method.

INTRODUCTION

We do not yet know why, as a general rule, adults of larger-bodied species have larger brains. Nor do we yet know why animals of the same size can have markedly differently sized brains. It has sometimes been argued that allometric relationships, such as that between brain and body weight, are non-adaptive with a common growth mechanism (e.g. a growth hormone) causing selection for increased body weight to result in heavier brains as well as heavier bodies. At the other extreme, the form of the allometric relationship between brain and body weight has frequently been used to generate adaptive explanations to explain why brain and body weight covary. For example, the suggestion that brain weight increases with the $2/3$ power of body weight generated the idea that brain weight and body surface areas are functionally related because body surface areas increase with the $2/3$ power of body weight. Similarly, recent indications that brain

weight increases with the $3/4$ power of body weight have led to the suggestion that brain weight is constrained by energetic demands because basal metabolic rate increases with the $3/4$ power of body weight. But body weight is not the only factor that we must consider when assessing the costs versus the benefits of larger brains. Lifestyles, including behavioural and ecological habits, seem to be related to variation in brain size in both mammals and in birds.

Here we shall review the relationship between brain and body weight in mammals and birds, before asking how brain weight (or volume) correlates with lifestyle variables independently of body weight and of taxonomic affinity. Finally, we shall illustrate how some of the selective forces influencing the size of brain components are becoming more clearly understood.

THE ALLOMETRIC EXPONENT AND ITS INTERPRETATION

Brain weight increases with body weight according to the allometric equation:

$$\text{brain weight} = a (\text{body weight})^b$$

where a is the allometric coefficient and b is the allometric exponent. There has long been interest in both the value of b and its interpretation (see GOULD, 1966). Although DUBOIS (1897) computed allometric exponents of 0.55, which he claimed as a universal constant, most early studies found that brain weight “generally scales to the two-thirds power of body weight (an immense number of sources ranging from Snell 1891... JERISON 1973)” (GOULD, 1975). LAPICQUE (1907) was the first to show that the value of two-thirds was not itself universal; for example, he found that among adults of a species the value was near 0.25. Subsequent authors agreed on a range from 0.2-0.4 as being appropriate when comparing species within genera or adults within a single population.

The concept of an optimal scaling principle was advanced by JERISON (1973), who suggested that the value of the allometric exponent increased from the intraspecific level to that of the “true” value of 0.67. GOULD (1975) suggested that the exponent of 0.67 could be explained if the amount of information (especially sensory information) being processed by the brain is more likely to be related to body surface area than to body volume. However, as GOULD (1975) pointed out “a relationship between brain weight and body surfaces... has never been satisfactorily explained”, nor had there been advanced a complete explanation of the smaller exponent values at lower taxonomic levels.

Subsequent studies involving more mammal species (BAUCHOT, 1978; MARTIN, 1981; EISENBERG, 1981; HOFMAN, 1983) seem to demonstrate the value of the allometric exponent to be close to 0.75. MARTIN (1981) also showed that the interspecific exponents for birds and reptiles were close to 0.56. Neither the mammalian value nor the 0.56 value for birds and reptiles agreed with the previously commonly held value of 0.67, and on these grounds the explanations involving body and brain surfaces were largely rejected (but see JERISON, 1985). MARTIN (1981) went on to suggest an association between brain weight and basal metabolic rate both of which, in mammals, at least, scale on body weight with an exponent of 0.75. His hypothesis was that maternal metabolic rate sets constraints on the development of the foetal brain and that, because mammals are viviparous, the relationship between maternal metabolic rate and neonatal brain weight is a direct one. An alternative explanation was offered by HOFMAN (1983) who suggested that rather than directly constraining neonatal brain size, maternal metabolic rate influences gestation length and thereby indirectly affects neonatal brain weight.

MARTIN's hypothesis was designed to incorporate the 0.56 exponent of birds and reptiles by suggesting that, because the egg provides for development of the embryonic brain, the variables egg weight and the metabolic needs of the egg should be included in his equations. (a) Egg weight scales on maternal body weight with an exponent of 0.75 because egg weight is limited by maternal metabolic rate which scales on maternal body weight with a factor of 0.75; (b) metabolic rate of the egg scales on egg weight with an exponent of 0.75 and, since the metabolic rate of the egg determines hatchling brain size, hatchling brain size also scales on egg weight with an exponent of 1.0 because there is little or no neuronal division after hatching. The product of the three exponents 0.75, 0.75 and 1.0 gives the 0.56 exponent linking adult brain weight to maternal body weight. (It is not clear to us why the exponent (b) linking the metabolic rate of the egg to egg weight should be the same as that linking hatchling brain size to egg weight. The hatchling brain must grow in the egg as well as be nourished by the nutrients in the egg immediately prior to hatching, and the amount of energy required for brain and body growth within the egg is not estimated in MARTIN's formulation).

Neither MARTIN's nor HOFMAN's explanation holds up under further comparative scrutiny. For example, MARTIN's explanation would predict that, after controlling for body weight, species with high metabolic rates would give birth to larger-brained neonates, which they do not (PAGEL & HARVEY, 1988a). Species with longer gestation lengths do give birth to large-brained young as HOFMAN would predict

but, contrary to HOFMAN's theory, those young do not go on to have larger brains as adults (PAGEL & HARVEY, 1988a). Additional problems for both theories are discussed by BENNETT & HARVEY (1985a) and by PAGEL & HARVEY (1988a). As we shall mention below, there remains considerable doubt about whether any "universal" exponent is applicable to either mammals or birds.

THE CHANGE IN ALLOMETRIC EXPONENT WITH TAXONOMIC LEVEL

Developmental and population-genetic models incorporating evolutionary constraints and the influences of natural selection have been used to explain the apparent pattern of increasing exponent with taxonomic level (i.e. that the exponent linking brain and body size is lower among more closely related species). Both groups of models are based on the assumption that selection will act predominantly to change body weight, and brain weight will be dragged along with it.

LANDE (1979) proposed that selective forces acting to differentiate closely related forms operated largely on body weight and that initial changes in brain weight were a correlated response. This correlated response would result in the shallow slope characteristic of closely related species within a genus but, over evolutionary time, natural selection would be able to adjust brain weight to accumulated changes in body weight. Lande argued that there was a greater net directional selection on brain weight than on body weight involved in the greater diversification in brain and body weights at higher taxonomic levels.

GOULD (1975) and RISKA & ATCHLEY (1985) have separately proposed a different scenario, but again one that assumes selection for increased body size. They suggest that a larger exponent would be expected if selection acted to prolong the period of early ontogenetic brain and body growth. The reason is that, during early development, brain and body weight are related by an exponent which is often very close to 1.0 and therefore selection acting to prolong this period in descendant species would result in these descendants having not only larger bodies but also nearly proportionately larger brains. If closely related forms diverge through selection acting to prolong the period of juvenile growth, by which time the exponent linking brain to body weight increased has decreased considerably, then closely related species would differ by a low exponent. Selection on body weight causing differences between more distantly related forms would, therefore, result in growth changes during early development.

MARTIN & HARVEY (1985) pointed out that differences in body

weight among adults of a species are often not associated with differences in brain weight, so that the exponent is less than 0.2-0.4. But they also found that adults of closely related species differed by a much higher exponent than had previously been realised, not 0.2-0.4 but usually above 0.5. Part of the reason for the discrepancy between MARTIN and HARVEY's and earlier findings was the fact that they did not base their analyses on model 1 regression but on major axis analysis. The problem with model 1 regression is that it gives an artificially low exponent for species of similar body weight (because the ratio of error variance to real variance is high), but a more accurate estimate when body weight differences are greater. Closely related species tend to have similar body weights and, perhaps, part of the pattern of increased exponent with taxonomic level was a result of the use of inappropriate statistical procedures?

PAGEL & HARVEY (1988b, 1989) looked against the problem of changing exponent with taxonomic level in mammals using a more suitable statistical model, the structural relations model of SPRENT (1969). First, they noted that major axis analysis as well as model 1 regression was likely to give an artifactual pattern of increased exponent with taxonomic level when no such pattern existed in the data. Second, using the more appropriate analysis, they found that the increased exponent with taxonomic level occurred in only the primates, bats and rodents. These were orders in which encephalisation had been shown previously to vary with diet (as we shall see below) and, when the effects of diet were held constant using a multiple regression analysis, little if any evidence remained for the increased exponent with taxonomic level. Third, exponents within some orders were very much lower than in others, varying from below 0.5 in cetaceans to above 0.90 in primates—there was, in fact, no evidence for a "general" slope of 0.67, 0.75 or any other particular value in the mammals as a whole.

BENNETT & HARVEY (1985a), studying birds, had already found that there were differences in exponents among taxa, and that exponents did not show a general increase with taxonomic level. They also found that the exponent relating brain to body weight differed among components of the avian brain with an increase from the optic lobes through the brain stem, the cerebellum and the hemispheres. Not only did their study fail to support the notion of an increasing exponent with taxonomic level it also provided evidence that in birds, as well as in mammals, the exponent can be much greater than MARTIN's 0.56 level. The exponents relating cerebellum and the hemispheres weight to body weight did not incorporate 0.56 within their 95% confidence limits.

ECOLOGICAL CORRELATES OF WHOLE BRAIN WEIGHT

Over the past decade, explanations for variation in brain weight, particularly in mammals, have focussed increasingly on the idea that natural selection might be acting directly on the brain itself, rather than its weight being solely a consequence of changing body weight. This has led to studies in which variation in species' ecology has been shown to correlate with variation in brain weight. Studies by CLUTTON-BROCK, HARVEY & MACE (summarised in HARVEY, CLUTTON-BROCK & MACE (1980) showed that, in several rodent and primate families, variation in brain weight was correlated with differences in diet. Leaf-eating primates and rodents have small brains for their body weight. Why this should be so is as yet not known, although it was postulated that frugivorous (fruit eating) primates have more spatially complex foraging needs which might select for an increased brain weight. EISENBERG & WILSON (1978) invoked a similar line of reasoning when they found a relationship in bats between diet and variation in brain weight. Again, fruit eating species were shown to have the largest relative brain weight which EISENBERG & WILSON believed is due to an enlarged neocortex. An enlarged neocortex would be selected for in animals whose foraging strategy involved location of energy-rich food that had a clumped distribution, both in time and in space, as this complex information would require increased levels of processing and integration.

The idea that selection would bring about changes in brain size as a response to particular problems posed by the species' environment was applied to a further study by EISENBERG & WILSON (1981), this time on didelphid marsupials. Arboreal species were found to have relatively larger brains than terrestrial species because, it was claimed, they are faced with increased demands on motor coordination which would select for increased brain size. This pattern has not been replicated in any other mammalian taxon, such as the primates (CLUTTON-BROCK & HARVEY, 1980) and bears further investigation within the didelphid marsupials. For example, it is not clear that the association exists independently within or among different didelphid genera.

BENNETT & HARVEY'S (1985b) study on birds attempted to detect differences in environmental complexity correlated with differences in encephalisation. Their initial results appeared to agree with the mammal analyses: diet and several other variables were significantly correlated with differences in brain size. But, in contrast to the mammalian pattern, subsequent analyses showed that the ecological correlates were not independent of each other and that mode of

development and method of prey capture were the main variables associated with variation in brain size. They added that there was a small, additional, correlation with mating system and that was that monogamous birds had larger brains than polygynous birds (the opposite result was obtained for primates by CLUTTON-BROCK & HARVEY (1980)—monogamous primates were found to have relatively larger brains than polygynous primates). Ecological correlates though to involve complex processing, for example, migration, habitat type and nesting patterns were not correlated with variation in brain weight.

The strongest effect obtained by BENNETT & HARVEY was between mode of development and encephalisation: birds which produce altricial young have larger relative brain sizes as adults than do birds producing precocial young (confirming a result of PORTMANN, 1946, 1947). This result, like that found between mating system and brain size, is the opposite of the relationship found between mode of development and adult brain size suggested by MARTIN (1981, 1983) for mammals. However, MARTIN's result turned out to have been a taxonomic artifact—nearly all his so-called precocial species had been primates, and when taxonomic affinity was controlled for the difference vanished (BENNETT & HARVEY, 1985a). Altricial and precocial mammals do not differ in relative brain size.

ECOLOGICAL CORRELATES OF THE SIZE OF BRAIN COMPONENTS

MACE *et al.* (1980) and EISENBERG & WILSON (1981) suggested that larger brains may have resulted from particular component parts increasing in size and others not, and that the variation in the size of those which did could be associated with relevant ecological variables. BENNETT & HARVEY's (1985b) study was the first to look at the possible association between ecological variables and parts of the brain. They analysed data on four parts of the avian brain: the hemispheres, the cerebellum, the optic lobes and the brain stem and found several correlations between the weight of component brain parts and ecological variables that were independent of body weight, but it was not obvious why many of the relationships should exist. There was, for example, a significant correlation between mating system and cerebellum size. It is not clear why monogamous and altricial birds should have relatively larger cerebella than polygynous or precocial birds. Conversely, other relationships which might have been expected, for example a correlation between nocturnality and optic lobe weight, were not found. Overall, the authors did not provide evidence in support of the 'sensory hypothesis' which had been discussed previously with reference to mammals.

Support, not specifically for a sensory hypothesis, but for the idea that selection can bring about variation in the size of particular component parts of the brain in response to species-specific environmental demands comes from two recent studies. The first considers avian olfaction and the large amount of variation found in the size of the olfactory bulb. Olfaction in birds has been shown experimentally to have a variety of functions (e.g. food finding, orientation, and homing). These functions are likely to be affected by reduced light conditions and thus HEALY & GUILFORD (1990) found that variation in the size of the avian olfactory bulb was associated with species' activity timing in many avian taxa. They showed that nocturnal birds have relatively larger olfactory bulbs than diurnal birds. No other ecological variables included in their analysis was significantly correlated with variation in olfactory bulb size independently of body weight (e.g. diet, nesting dispersion, migratory behaviour). Enhanced olfactory ability may thus be a rather generalised response to many of the problems brought about by living in the dark. It may be, however, that for particular activities performed by nocturnal birds (e.g. finding and capturing fast moving prey), we might expect to find enhancement of other sensory capacities (e.g. hearing in owls, KNUDSEN, 1981).

KREBS *et al.*'s (1989) study of passerine birds showed that the relative size of the hippocampal complex (dorsomedial forebrain) is associated with behavioural differences between species. Birds which hoard food are known to use memory for relocation of their food stores and it is thought that in order to do so successfully they require a large and an accurate spatial memory, perhaps larger than that required for the successful performance of other tasks, for example, foraging for food, or remembering the boundaries of a territory. The avian hippocampal complex, like the mammalian hippocampus, has been shown to play an important role in certain memory tasks, particularly those involved with spatial memory. SHERRY & VACCARINO (1989) showed that, following ablation of the hippocampus, black-capped chickadees (*Parus atricapillus*), members of a North American food storing passerine species, could not successfully retrieve their stored food whilst there was no disruption to other aspects of food storing behaviour. KREBS *et al.* (1989) found that the food storing species have relatively larger hippocampuses than birds which do not store food. Experimental evidence for differences between the spatial memory abilities of food storing birds and closely related non storers has, however, been both insubstantial and inconsistent (reviewed in KREBS *et al.*, 1990), although BALDA & KAMIL's (1989) study of three food stor-

ing corvid species which differ in their dependence on their food stores appear to show differences in their spatial memory abilities.

Experimental support for variation in the size of the mammalian hippocampus being correlated with differences in spatial memory comes from studies involving several strains of inbred mice, where genetic differences in the size of parts of the hippocampus have been shown to correlate with performance in behavioural problems involving spatial memory and exploratory behaviour. The size of a particular hippocampal synaptic field, the intra- and infra-pyramidal mossy fiber terminal fields (iip-MF) have been associated with differences in learning on water-mazes, Y-mazes, radial mazes, with open-field behaviour, habituation and two-way active-avoidance learning (CRUSIO *et al.*, 1989). The mice strains with larger hippocampal mossy fiber fields showed increased performances on these tasks. Within strain differences in spatial abilities were small and this seems to be because the hippocampus is influenced by environmental variables only during early development.

A large body of work on the size of brain components in Chiroptera, Insectivora and primates is strongly suggestive of relationships between species' lifestyles and the sizes of brain components (BARON & JOLICEUR, 1980; STEPHAN, 1983; JOLICEUR *et al.*, 1984; STEPHAN *et al.*, 1984; BARON *et al.*, 1988; BARON *et al.*, 1989). Relationships between structures for which the function is clearly delineated are particularly tantalising, for example within the prosimians there seems to be a trend between activity timing and the size of the visual structures, with diurnal species having relatively larger visual structural areas, whereas there is a trend for nocturnal species to have larger olfactory structures (STEPHAN *et al.*, 1988).

Both HEALY & GUILFORD (1990) and KREBS *et al.* (1989) show correlations between groups of birds in the size of parts of their brains and their behaviour or ecology. Whole brain size, however, was not shown to be different thus providing evidence that natural selection can act independently on parts of the brain without necessarily altering other parts. Flexibility of brain structure is obviously possible, therefore, but may not be to the same degree for all parts of the brain, and may also be different for different species. Weight considerations for flight in birds and bats, for example, may constrain the weight that various brain components can reach. Increasing the size of the olfactory bulb may be more expensive for a bird which flies than for one which does not and, depending on the selective forces involved, decreasing the size of one part might be necessary in order to increase the size of another.

INTRASEXUAL DIFFERENCES IN BRAIN COMPONENTS

Variation in the size of parts of the brain are thus beginning to be examined in terms of different species' environmental demands, both behavioural and ecological, and it is now clear that brain structure is much more flexible than has been generally believed. Brains have also been shown to be 'flexible' in the size of their components within species as well. The avian song system has received much attention in recent years and intraspecific variation in the size of the several different diencephalic and telencephalic areas involved in song production has been shown to be associated with several variables (NOTTEBOHM & ARNOLD, 1976; DEVOOGD, 1986). In the canary, for example, where song is primarily produced by the male, the song nuclei of the male are larger than those of the female. The size of the song nuclei also varies seasonally depending on when song production is required. The involvement of gonadal steroids in these size differences is being intensively studied and it has been shown that the song system is capable of substantial plasticity. The administration of hormones (e.g. testosterone) to female canaries has been shown to decrease the sex differences in the size of the song nuclei and also to induce behavioural changes (the female will produce song very like that of the male) but that the differences are not entirely removed by such treatments (DEVOOGD *et al.*, 1985).

CONCLUSIONS

In this short review we have concentrated on associations between the weight of the brain or its component parts and species differences in lifestyles that have evolved independently on several occasions. Such patterns of evolutionary convergence between different components of the phenotype provide one of the strongest lines of circumstantial evidence indicating the adaptive function of differences in morphology. In the future, it will be necessary to test ideas that are intended to explain these relationships. Some of those tests will be comparative, either at the behavioural or neuro-anatomical levels, and others, hopefully, will be experimental.

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