Evolving ideas of brain evolution

Jon H. Kaas and Christine E. Collins

Recent analyses of an old data set are starting to reveal patterns in the evolution of mammalian brains. The latest study shows that mammalian groups are characterized by basic similarities in brain proportions.

The brains of mammals vary greatly in size, shape, internal organization and functional capabilities. The human brain is much larger than that of a mouse lemur, for example (Fig. 1), and includes subdivisions and connections not found in a lemur. Those of us who are interested in how these differences evolved have only a few sources of information. A useful, if fragmentary, historical record is available from 'endocasts' of fossilized skulls: occasionally, during fossilization, the space inside the skull fills with silt which then hardens, producing a cast of the internal structures. This record can be very accurate, but it mainly shows us the sizes and shapes of brains and the locations of large brain features such as fissures (grooves). It provides few clues to internal organization. So theories about brain evolution have also depended on comparative studies of the brains of living mammals, and Clark, Mitra and Wang[1] describe one such analysis on page 189 of this issue.

The general premise of comparative studies is that physical features that are found in several species have been retained from their common ancestor, and that features that are shared only by closely related species must have evolved recently. The challenge for those using this approach is to get reliable and comparable observations from the brains of a suitable range of living species. So it is perhaps not surprising that, although it is 20 years old, one of the most extensive studies[2] of the sizes of brain parts in mammals still forms the basis for many comparative analyses of mammalian brain evolution. In this paper[2], Stephan *et al.* published the volumes of easily identified brain structures for an impressive number of insectivore, bat and primate species.

In one analysis[3] of these data, Finlay and Darlington concluded that most of the differences among mammalian brains result from the disproportionately greater growth in larger brains of the later-maturing structures of the forebrain. Their theory emphasized the overriding importance of a basic plan for brain development that had been modified during evolution according to the size of the brain. More recently, Barton and Harvey[4] reconsidered the data[2] and argued that, in general, the sizes of brain parts evolve independently of each other, although some functionally related parts grow larger together. In primates, such related brain parts include the cerebellum (involved in processing sensory information to coordinate movements) and the neocortex (also involved in processing sensory information). Soon afterwards, de Winter and Oxnard[5] used multivariate statistical methods to provide evidence for other patterns of brain evolution, including the evolution of similar brain proportions in distantly related species — such as woolly monkeys and apes — that behave similarly.

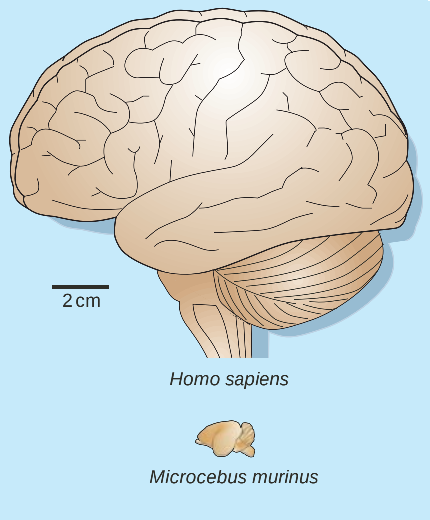

Figure 1 **Side-on views of the brains of a human and a small prosimian primate, the mouse lemur (*Microcebus murinus*). Although these brains are very different in size, their proportions are similar, and group together with those of other primates, as Clark *et al.* show[1].**

Clark *et al.*[1] have now compared the sizes of different brain parts to total brain size, by using multidimensional comparisons of brain proportions. They define what they call 'cerebrotypes' for the species they have examined. So, for example, in tree shrews the fraction of the brain occupied by the telencephalon is about 61%, and that taken up by the cerebellum is about 13%. The combination of such proportions makes up the cerebrotype for this species. One of the authors' findings[1] is that different taxonomic groups have distinct cerebrotypes. So insectivores, which are now thought to have evolved from several ancestors rather than just one[6], contain separate taxonomic groups, and these groups have different cerebrotypes. In addition, the cerebrotypes of tree shrews clearly do not group with those of primates, fitting with the fact that tree shrews are no longer considered to be primates[6].

Furthermore, the cerebrotypes for primate groups can be divided into largely separate subtypes for prosimians (such as lemurs), New World monkeys, Old World monkeys and hominoids (apes and humans). The overlap in the cerebrotypes of some species of Old and New World monkeys suggests that these species have similar lifestyles, and that their brains have therefore evolved in similar ways. Overall, the presumed length of time since diverging from a common ancestor correlates well with differences in cerebrotype for primate groups. Observations of the proportional size of the cerebellum also lead to the interesting conclusion that its size, and therefore functions, relate broadly to the rest of the brain. However, in animals with certain specialized functions — such as echolocation in dolphins, whales and small bats — the cerebellum is disproportionately large compared with that in other species.

The differing conclusions that have been reached[1,3–5] from analysis of the same data[2] are not necessarily contradictory, as they reflect different approaches and emphasize different aspects of the data set. Indeed, the outlines of patterns of brain evolution are starting to emerge. It seems fair to conclude that mammals have a characteristic pattern of brain development, which has been distorted during evolution as brains became larger. It also seems reasonable that the size of one brain structure in relation to another varies from species to species, and that these variations occur in ways that should reflect the importance of the function of that structure. Finally, groups that share a common ancestor are characterized by basic similarities in brain organization.

But we are far from a complete understanding of brain evolution. We need to know more about the details of brain organization (the sizes, numbers, identities and interconnections of subcortical nuclei and cortical areas) for more species, and what these differences might mean for function. We already know, for example, that two mammal groups — carnivores and primates — have different patterns of layers in part of the visual thalamus, but we don't fully understand how these two patterns relate to visual abilities.

In addition, we might productively consider theoretical problems and solutions to the evolutionary challenge of making brains bigger or smaller[7]. For other body organs, as well as for bridges and buildings, the problems of changes in scale have been investigated thoroughly[8]. It is now time to do the same for brains and to find out whether theory and evolution would cope with these problems in similar ways. ■

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Climate change

The Indonesian valve

James D. Wright

The behaviour of the North Atlantic is often invoked to explain the effects of climate change. But for certain episodes, including perhaps a period in human evolution, events elsewhere may have had a greater influence.

The climate of East Africa became drier between about 5 million and 2.5 million years ago, and that may have been the catalyst that forced our ancestors to adapt to a savannah environment as the forests dwindled[1,2]. At about the same time, the Earth entered a climate mode dominated by the waxing and waning of large continental ice sheets. The coincidental timing of global cooling, African aridity and human evolution invites speculation about a common link[3]. For that, we must look to the oceans — in redistributing heat and influencing greenhouse-gas concentrations globally, they are the main component in determining climate change. Marine records tell us that the transition to large-scale glacial cycles took at least a million years; and plate-tectonic motions that opened or closed ocean gateways are thought to have triggered these events[4].

On page 157 of this issue, Cane and Molnar[5] present an analysis of changes in surface-ocean circulation that they believe occurred as an oceanic gateway — the Indonesian seaway — narrowed over the past 5 million years. This gateway acts as a valve for water flowing from the Pacific into the Indian Ocean. Plate tectonics in the Indonesian region is complicated, but Cane and Molnar show that the passages regulating water flow from the Pacific to the Indian Ocean 5 million years ago were wider and deeper, and were located further to the south, than they are today. Surface water in the South Pacific is warmer and saltier than that in the North Pacific. Cane and Molnar argue that the more southerly position for the Indo-Pacific connection meant that the warmer South Pacific flowed into the Indian Ocean. The result was warmer sea surface temperatures in the Indian Ocean and high levels of evaporation and precipitation — and wet East African climates.

Over the past 5 million years, the constriction and northern movement of the Indonesian seaway have progressively shut off the South Pacific source of water, while increasing the influence of the colder North Pacific. These changes should have cooled the tropical Indian Ocean and reduced the precipitation, leading to a gradual drying of East Africa. Again, then, the idea is that the Indonesian seaway, controlled by the northern movement of New Guinea and smaller islands, has acted like a valve, regulating the relative amount of warm and cool water entering the Indian Ocean.

A more speculative aspect of Cane and Molnar's paper deals with the possible effects on global climate of this narrowing of the Indonesian seaway. The authors argue that, when the seaway was farther south, conditions in the tropical Pacific would have been more like those observed during modern El Niños (that is, both east–west and vertical thermal gradients in the ocean would have been weaker). This configuration would have promoted greater heat transport to the high northern latitudes than at present; and that higher heat flux would have inhibited the growth of large ice sheets in the Northern Hemisphere. In support of Cane and Molnar's speculation, palaeoceanographic reconstruction of the tropical Pacific between 5 million and 3 million years ago matches the prediction of smaller east–west and vertical temperature differences[6].

This speculation is especially provocative because it requires a new principle for understanding the glacial cycles that developed 3.5–2.5 million years ago. Existing models for large-scale Northern Hemisphere glaciation focus on increased circulation of the North Atlantic 'conveyor', which includes the Gulf Stream, as the cause of ice-sheet development[4,7–9]. The finer points in these models vary, but most of them begin with increased precipitation at high northern latitudes as a result of a more vigorous Gulf Stream. And going back one step, the closure of the Panamanian isthmus is seen as the trigger for initiating the more powerful Gulf Stream.

Recently, however, a fly in the ointment for these hypotheses has appeared[10]. An evaluation of North Atlantic circulation for between 5 million and 2 million years ago contradicts the enhanced Gulf Stream mechanism for Northern Hemisphere glaciation. The new data[10] indicate that the North Atlantic conveyor became considerably weaker, not stronger, 3.5–2.5 million years ago.

Cane and Molnar[5] propose a shift in thinking away from the North Atlantic to the Indonesian gateway as a factor governing global climate change. There are good reasons to take this idea seriously, speculative though it may be, because the Indonesian region is undoubtedly important in the redistribution of heat received at the Earth's surface and in moisture fluxes to the atmosphere. Moreover, Cane and Molnar make several predictions that can be tested.

The most obvious prediction is that sea surface temperatures in the Indian Ocean cooled between 5 million and 2 million years ago. This may be difficult to test, however. The change in temperature was probably 2–3 °C. Oxygen-isotope analysis of planktonic foraminifera, a useful tool for estimating past sea surface temperatures, can resolve this change. But because of evaporation, the South Pacific is saltier, as well as warmer, than the North Pacific. The evaporation that increases the salinity also increases the oxygen-isotope value of the surface water, offsetting the temperature effect. Advances in measuring the Mg/Ca ratios in foraminifera, and then using those ratios to estimate temperature, may solve the problem.

My own view is that Cane and Molnar are correct in their view that African aridity is linked to sea surface temperatures in the Indian Ocean, and that the most likely cause of cooling there was a narrowing of the Indonesian seaway. I am less confident that these changes had much to do with glaciation of the Northern Hemisphere, for one simple reason: from 10 million to 5.6 million years ago, cyclic glaciation was highly active in the Northern hemisphere and glaciation was suppressed between 5.5 million and 3.5 million years ago. Moreover, changes in the North Atlantic conveyor circulation cannot be ruled out in driving these glaciations. The conveyor delivers a substantial amount of heat to the high northern latitudes; the link with glaciation might have been through reduced heat fluxes as conveyor circulation decreased[11], rather than through precipitation. Nonetheless, Cane and Mol-