Living in the Fast Track Makes for Small Brains

Some species have brains larger than would be predicted from their body size, a puzzle that has biologists seeking answers that have turned from metabolic rate to life history factors

BIOLOGISTS have long been interested in the precise biological constraints that might limit how big a species' brain can be. In recent years the maternal metabolic rate has been seen as an important determining factor. But two researchers at Oxford University now suggest that more influential is the life history strategy of the species: that is, does it "opt" to be long-lived and to produce offspring individually and at infrequent intervals; or does it instead produce many offspring within a short life-span?

The way to be a large-brained species, conclude Mark Pagel and Paul Harvey, is to go with the first of these two options. And the key factor is having a long gestation period, at the end of which time the single neonate will be relatively generously endowed mentally.

Brain size varies enormously across mammals as a whole, going from barely a gram in some rodents to many kilograms in the blue whale. Body size is the key variable here, of course. The relationship between brain size and body size is not linear however, and scales with a 0.75 exponent: as a result a shrew's brain accounts for about 3% of its body weight whereas the blue whale's brain represents only one-hundredth of 1% of its body weight. What biologists are interested in, therefore, is whether a species has a large brain for its body size.

Now, it happens that some groups of mammals are generally brainier than others: carnivores have bigger brains than insectivores, for instance, and primates are the biggest brained species of the lot. Within each group the same 0.75 scaling of brain on body size still holds. So, again, the question is, why do some species within the group have bigger brains than would be predicted?

In the early 1980s Robert Martin, now of the Anthropological Institute in Zurich, identified maternal metabolic rate as possibly the key factor in the brain equation. One reason for his doing this was that, like brain size, metabolic rate also scales to the 0.75 power of body weight. Was this just a coincidence, or did it mean that brain size and metabolic rate were linked directly, with body size just tagging along as a related variable? If the latter were true, then a species with a metabolic rate that was high for its body size would be able to produce offspring with larger brains.

A related idea, advanced by M. A. Hofman in 1983, was that metabolic rate constrains gestation time, which is then the ultimate determinant of brain size. Like Martin, Hofman based his argument on information on body size variation.

One factor that complicates the issue is that some mammals produce helpless offspring (altricial) while others give birth to neonates that, apart from the need to suckle, can immediately fend for themselves (precocial). Although altricial neonates usually have brains about one half to one third the size of precocial neonate brains, there is no overall difference among adults of the species, given a similar body size.

"Thus, there is large variation in neonatal brain size that cannot be explained solely on the basis of maternal size and, by implication, maternal basal metabolic rate," say Pagel and Harvey. "But if species that give birth to precocial offspring also have higher metabolic rates and longer gestation times for their body size, then Martin's and Hofman's predictions would be supported."

Pagel and Harvey undertook a survey of their own, collecting data on 116 mammalian species from 13 orders. One key difference in their approach, however, was that instead of measuring neonatal brain size they determined total brain weight produced during a litter. This is crucial, because although precocial species typically produce one offspring per litter, altricial species commonly drop several. "Litter brain mass does not increase proportionately with metabolic rate," conclude Pagel and Harvey. In other words, the metabolic constraint argument fails.

"Precocial mammals produce offspring with large neonatal brain sizes without the benefit of higher relative energy turnover," say the Oxford researchers. Pagel and Harvey did discover, however, that "the two- to threefold differences in relative neonatal brain size between precocial and altricial species could be accounted for almost entirely by differences between the two groups in gestation length and litter size, independent-

Baboons and the big-brain secret. *Primates as a group have the largest brains of all mammals; and monkeys and apes are even better endowed than prosimians. Primate mothers therefore have to divert a lot more energy to the developing fetus than do other mammals.*

ly of metabolic rate or maternal size." Therefore, claim Pagel and Harvey, not only does Martin's metabolic constraint fail, but so too does Hofman's suggested link between metabolic rate and gestation time.

"Twenty-three of the families in our data set had offspring with brains larger than expected from maternal size," says Pagel and Harvey. "Of these, 20 have gestations longer than that predicted for their size, and 18 have litters of one." This tells you, they explain, that building bigger brains is reproductively expensive. But it also has crucial consequences for a species' evolutionary ecology. For a start, selection for increased brain size—or its associated precociality—must be intense in those species that move in this direction. More significant, such a move is part of a package of life history characteristics.

Crudely put, some species live fast lives, some live slow lives. Fast-living species have short life-spans, mature early, have large litters after a short gestation, and wean early. By contrast, slow-living species have a greater longevity, mature late, give birth to single offspring after a long gestation, and wean late. In the first case, the potential reproductive output over a lifetime is large, but is usually much reduced by loss of offspring to predation and so on. In the second case, potential reproductive output is low, but offspring survival is high.

These two life history strategies are known as r and K selection, respectively, and are usually associated with particular environmental circumstances. For instance, r selection is favored under conditions of fluctuating availability of resources, K selection under stable conditions.

Small species live fast lives, large species slow lives. But, again, one is interested in variation for species of a given size: some live faster than would be predicted, some slower. Harvey, in collaboration with another Oxford colleague Daniel Promislow, has found that mortality rate drives this variability: species that experience a high mortality rate live faster than would be predicted from their body size, whereas a low mortality rate is associated with slower than predicted lives. So, building bigger brains demands that a species inhabit a stable environment and experiences low mortality.

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ADDITIONAL READING

R. D. Martin, "Human brain evolution in an ecological context," Fifty-second James Arthur Lecture (American Museum of Natural History, New York, 1983).
M. D. Pagel and P. H. Harvey, "How mammals produce large-brained offspring," Evolution 42, 948 (1988).
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Trees from Genes and Tongues

Drawing large, elaborate trees that purport to chart the path of some period of human history has become commonplace these days, particularly since DNA mapping and sequencing techniques are now so tractable. The latest such tree, however, goes back to the classical system of sorting various protein markers—but it comes with an interesting twist: this tree, which covers perhaps the last 100,000 years of human history, also integrates information about linguistic groupings. The authors of the work, Luigi Luca Cavalli-Sforza, of Stanford University, and three colleagues from Italy, note that the results show a remarkable match between genetic and linguistic groupings, "indicating considerable parallelism between genetic and linguistic evolution."

Just as molecular biologists debate whether or not genetic change is constant enough to be used as an evolutionary clock, so too do linguists clash over how language changes through time. Some linguists, for instance, use genetic mutation and long-term genetic change as a direct analogy for language evolution, and thereby seek indications of prehistoric relatedness, sometimes stretching back 50 millennia and more. Others, while recognizing obvious groups among modern languages stemming from common origins, argue that the analogy is limited and origins are lost forever in the mists of time. The results of Cavalli-Sforza and his colleagues will certainly contribute to this debate by giving a biological framework on which to hang the linguistic information. Not least are indications from this new genetic work that some language groups are rather older than many linguists currently allow.

Cavalli-Sforza and his colleagues analyzed 120 non-DNA polymorphisms in 42 indigenous populations around the world. In common with the recently published data on mitochondrial DNA, this new analysis shows that the first split separates African from non-African populations. The abundance of the classical marker data of Cavalli-Sforza and his colleagues, however, allows the analysis to go into much more detail than has been typical. For instance, the next split occurs between northern Eurasians and populations in Southeast Asia. These major clusters are further divided, producing a complex but internally consistent tree, as shown in the diagram. The genetic pattern is echoed not only by the linguistic data, but also by the fossil evidence of recent human evolution, note Cavalli-Sforza and his colleagues. ■ ROGER LEWIN

ADDITIONAL READING

L. L. Cavalli-Sforza et al. "Reconstruction of human evolution: Bringing together genetic, archaeological, and linguistic data," Proc. Natl. Acad. Sci. U.S.A. 85, 6002 (1988).