How Did Humans Evolve Big Brains?

The growth of big brains is energetically expensive and so their evolution can occur only under certain favorable ecological circumstances

When the human brain is contemplated as a product of evolution, the question most frequently asked is, what were the selection pressures that made it so large? In an adventurous departure from this well-trodden path, Robert Martin of University College, London, is exploring the question of how, in energetic terms, humans can afford such a big brain. Martin discussed the energetic constraints on brain evolution when he delivered the 52nd annual James Arthur Lecture recently at the American Museum of Natural History, New York.

Martin, a primatologist, adopted a broad, comparative approach from which he derived some very specific questions. In addition to outlining some constraints under which human brain evolution must have taken place—such as a stable environment and a high energy feeding strategy—Martin's analysis points to the postnatal growth period in humans as something unique among primates. The use of substitutes for human milk might influence postnatal brain growth in ways of which we are yet unaware, he speculates.

"The range in body size in living primates is very big," says Martin, "going from the mouse lemur at about 60 grams to the 120-kilogram male gorilla. You therefore have to ask, to what extent are differences in brain size due to differences in body size and to what extent are they the result of significant biological differences?"

Studies on the relation between brain and body size have a long history, stretching back into the 19th century. With the help of his assistant, Ann MacLarnon, Martin has drawn on this resource and on more recent literature relating to, among other things, metabolism and body size. From it Martin has produced an original synthesis, which highlights maternal energy flow as a key constraint in the brain evolution.

The first step in the argument is to look at the relation between metabolic rate and body size (plotting data on logarithmic coordinates). "When you do this for basal metabolic rate you get a slope of 3/4. In other words, larger animals are more energy efficient than small ones," says Martin. This is consistent with the observation that large primates can subsist on leaves, which are relatively low in energy content, medium-sized primates are often fruit eaters, and the smallest primates live on energy-rich insects and seeds. "The same pattern applies in comparing active metabolic rates," reports Martin. "The slope of the line is again 3/4, but is set at a higher level."

The next consideration is the relation between brain and body, a relation that Harry Jerison of the University of California at Los Angeles has set out in his influential book *Evolution of the Brain and Intelligence*. Jerison derived a slope of 2/3 for the brain to body ratio, which implies that the increase in size of the brain in larger animals follows the increase in the surface area of the body. This might seem reasonable, says Martin, because innervation of sensory structures and muscles would be a surface area, not volume, phenomenon.

But Jerison's calculations were based on a relatively small sample, and so Martin repeated the operation with 309 placental mammals. The result in this case was a slope of 3/4, the same as that between metabolic rate and body size. The fact that the slope is the same in the two cases—the comparison of body weight with metabolic rate and body weight with brain weight—made Martin consider that there might be a link between them. "There is a good deal of evidence that might link the mother's metabolism with the developing brain of the fetus," adds Martin.

Roughly speaking, Martin is suggesting that the upper limit of brain development is determined while an infant is in its mother's womb. "It is the mother's energetic potential that determines the brain size of the developing fetus," he says. After birth the brain growth then follows a trajectory already set. In primates this typically involves a doubling of weight, except in humans where the brain quadruples in size.

With this possible relationship between maternal energetics and fetal brain growth established, Martin then looked at other factors that impinge on the equation. One obvious factor is the length of time a fetus stays in the womb. Broadly speaking, mammals can be divided into those that produce altricial infants, born after a short gestation with eyes and ears closed, no fur, and the jaw still in the reptilian condition, and precocial infants, whose longer gestation may account for their relative independence at birth. The difference in gestation times apparently has consequences for potential brain growth because on average precocial mammals' brains are 44 percent bigger than altricial mammals'.

With Martin's comparative approach, it was important to go beyond the immediate impact of the precocial and altricial "strategies" and look at the ecological background to these different life-styles. Altricial mammals generally produce large litters, sometimes with as many as 24 offspring whereas most precocials typically produce one infant, and none more than three infants, at a time. These reproductive strategies—the shotgun approach as against the single well-aimed shot—are known respectively as *r*-selection and *K*-selection.

Martin says that "*r*-selection is suited to unstable environments where for a lot of the time populations will be in a growth phase. You have selection for high reproductive output and little for efficiency of resource utilization in these circumstances. By contrast, *K*-selection is effective in stable environments in which populations are mostly close to carrying capacity. In this case, there is selection for high efficiency in use of resources and low reproductive output."

Humans, Martin points out, are the most extremely *K*-selective of all mammals, and this implies, he suggests, that human evolution occurred under very stable environmental conditions.

Stability of the environment is not the only factor that can influence potential brain development. The nature of the resources exploited in the environment are important too. "If you look at bats," says Martin, "you find that fruit-eating bats have bigger brains in relation to their body size than insect-eating bats." The reason typically given to explain the difference is that as fruit is more widely dispersed and difficult to find than insects, the fruit eaters need to be smarter to gather their food.

A similar pattern is to be seen in Old World monkeys. The leaf-eating monkeys have smaller brains than the fruit eaters. Fruit is more difficult to find and therefore frugivores need bigger brains, or so the usual explanation runs.

"I decided to ask a different question," says Martin. "Rather than, what is the brain needed for? I asked, how can certain bats and primates afford big brains?" He looked at data for metabolic rates in the bats and saw that they correlate with brain size: the small-brained insect eaters have lower metabolic rates than the big-brained fruit eaters. "I suggest, therefore, that insect eaters have small brains, not because they don't need big brains but because the lower energy throughput of the mothers doesn't allow for it."

Relevant data on primates are sparse, and therefore the same type of comparison cannot be done on the Old World monkeys. One New World monkey, the owl monkey, is known to have a metabolic rate about half of what would be expected for its body size, and it has a small brain. Another energy-poor animal of South America, the sloth, also has a tiny brain. "I would predict," says Martin, "that when metabolic rates for Old World monkeys are measured, it will turn out that leaf eaters will be lower than the fruit eaters."

The lessons for students of human evolution are twofold. First that our ancestors evolved under a *K*-selective environment, that is, a stable environment. And second, that they followed a high energy feeding strategy that would have sustained the development of a large brain.

Modern humans have brains that are three times as large as for a modern ape of the same body size. This tremendous expansion in brain capacity has occurred mostly in the last 2 million years, but, suggests Martin, the process has a much longer history than most paleoanthropologists allow. "The mistake people make is to compare the australopithecines with modern apes, which are similar in brain size, and they forget that the brains of modern apes are certainly bigger than that of the common ancestor shared by apes and humans. So, brain expansion must have started earlier in the human line than is generally acknowledged." Martin points out that brain expansion is a typical development through evolutionary time in all mammalian groups, perhaps through a steady honing of metabolic efficiency, but that the process in hominids is particularly exaggerated.

The expansion of brain size in human evolution has involved an acceleration in fetal development of both brain and body. "Human infants have brains and bodies twice as big as you'd expect, given the length of gestation," says Martin. "This must be extremely costly energetically. A high energy feeding strategy was essential for its development." In addition to the accelerated fetal development, the human brain expands four times from the neonatal size to adult status, compared with the doubling typical of primates. In all primates, however, human and nonhuman, the number of nerve cells in the brain is established at birth. Postnatal growth occurs in nerve connections and supporting tissue.

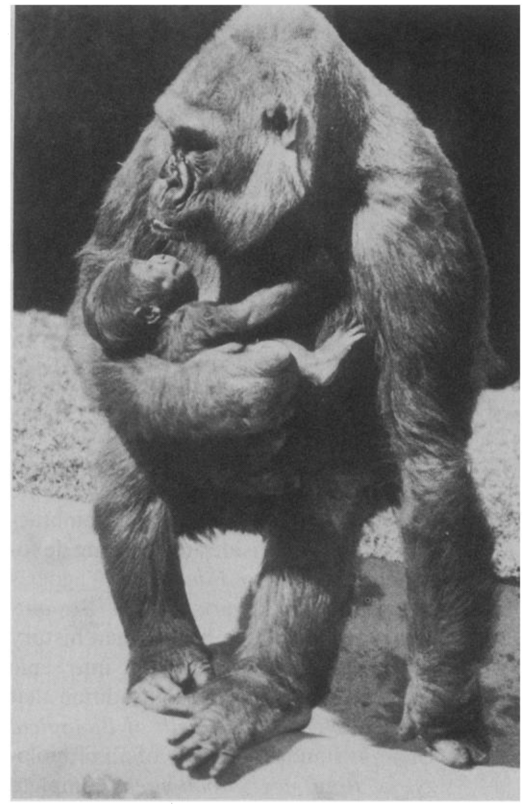
Parental care is a feature of primates, comments Martin, particularly in the higher primates. But human neonates are born essentially with a fetal brain, and are therefore much more helpless than infants of the other higher primates. This development demanded increased investment in parental care at some point in human history.

It is possible to work out when this extra care would have become necessary in human evolution, says Martin. If one assumes that the brains in modern infants are as large as pelvic engineering will allow, then this gives an upper limit of brain capacity of about 350 cubic centimeters at birth. The typical primate pattern of postnatal development, that is, doubling of brain size, would yield an adult figure of 700 cubic centimeters. So, once the adult brain got much beyond this level, any additional brain growth would have to be assigned to postnatal life, thus making the infant increasingly helpless at birth. Hence the rise of parental care in the human sense. This figure of 700 cubic centimeters fits neatly with *Homo habilis*, the first hominid to show accelerated brain expansion, some 2 million years ago.

Martin's analysis demands a stable environment and high energy feeding strategy for human ancestors, going right back to the split between humans and apes some 5 million years ago. This, he admits, is at odds with the simple savanna hypothesis that envisages a shift to the savanna as an important early stage in human evolution.

"I don't say that early hominids must have evolved in rainforests, which do provide a stable environment, but if they were living on the savanna they would have had to adopt cultural techniques with which to even out the erratic supply of food. The use of digging sticks to gain access to energy-rich tubers would be a good example." Martin points out that there is a correlation between brain size and generalized diet and he suggests that hominids would have benefited from expanding their dietary habits in as many directions as possible. The inclusion of substantial meat eating later in human evolution was probably important in this respect, he acknowledges.

The whole picture, Martin suggests, is still far from clear. "Given the fact that brain size, energy levels, and reproduction are so intimately tied together, I feel we have yet to find a satisfactory explanation for how the human brain reached the size it did during evolution. I need to have an explanation of where the stability and high energy came from."



Female energetics limit brain growth?

The search for some insights into human brain evolution by the comparative approach also highlights the unusual pattern of brain growth, both pre- and postnatally. "This has medical implications that have yet to be properly explored," contends Martin. "What are the special features in pregnancy that sustain this accelerated growth? And what in mother's milk supports the tremendous postnatal growth of the brain? What worries me is that when we take cow's milk and simply modify it in various ways for feeding to infants, do we really know what we are doing in terms of postnatal development of the brain?"

Martin plans to follow up this aspect of the work, an unusual departure from a project that began with examining the brains of the mouse lemur and the gorilla.—ROGER LEWIN

Additional Readings

1. H. J. Jerison, *Evolution of the Brain and Intelligence* (Academic Press, New York, 1973).
2. R. D. Martin, "Relative brain size and basal metabolic rate," *Nature (London)* **293**, 57 (1981).
3. B. K. McNab, "Food habits, energetics and the population biology of mammals," *American Naturalist* **116**, 106 (1980).
4. G. A. Sacher and E. F. Staffeldt, "Relation of gestation time to brain weight for placental mammals: Implications for the theory of vertebrate growth," *ibid.* **108**, 593 (1974).