As a biological anthropologist, my primary interest has always been the reconstruction of primate evolution, extending across the entire spectrum of extant and fossil species. This broad-ranging approach stems from a firm conviction that confident interpretation of human evolution depends on recognition of general principles that apply across the entire order Primates, sometimes across the class Mammalia and perhaps even across the subphylum Vertebrata. Because humans have so many unusual features, special-case arguments based on limited comparisons — confined, for instance, to just great apes and humans — have poor explanatory power. It is virtually impossible to avoid special pleading with a small sample size, and the door is left wide open to various kinds of bias.

One crucial general principle that applies to all multicellular organisms is adjustment (scaling) of individual features to fit overall body size. In most cases, scaling is allometric. That is to say, the relationship between the chosen feature and body size is not simply proportional but curvilinear. Simple proportional scaling, known as isometry, is relatively rare in biology. There are a few notable examples of isometric scaling among mammals, including simple proportionality of heart size, lung volume and skeleton mass to body mass. Predominantly, however, scaling to body size is non-linear, making appropriate allometric analysis essential. Prominent examples include many quantitative features of the brain, notably its overall size, and numerous quantitative aspects of reproductive biology. As it happens, two of my main interests in the field of primate evolution have, from the outset, been reproduction and brain size, and allometric analysis in both areas has played a prominent part in my research.

In fact, my long-standing combination of interests in reproduction and brain size proved to be a fortunate conjunction as many clues gradually emerged indicating that they are intimately connected in the realm of human evolution. For me, an early hint that such a connection existed was provided by a 1974 paper in *American Naturalist* co-authored by G.A. Sacher and E.F. Staffeldt. Their broad analysis of data for newborn mammals showed that gestation period shows a far tighter correlation with neonatal brain size than with overall body size of the infant at birth. Indeed, they went so far as to suggest that the brain serve as a pacemaker for development in the womb. Sacher later expanded this finding by showing that primates are unique among mammals in the relationship between brain size and body size throughout fetal development. The outcome of this is that in primates the newborn’s brain is approximately twice as big as in other mammals, once neonatal body size has been taken into account.

But thinking about the implications of the Sacher/Staffeldt findings also led me to an early appreciation of the fundamental distinction between correlation and causation. In a standard bivariate allometric plot — for example showing the scaling relationship between brain size and body size among mammals — a visually striking correlation may be seen. However, that does not necessarily mean that there is a direct causal connection between the two variables examined (brain size and body size in this case). In biology, individual variables are often connected by networks of interactions, and teasing
out the causal relationships involved can be a very challenging process. In many cases, the two variables in a standard allometric plot may actually be connected through an unrepresented third variable, known to statisticians as a confounding factor. My favourite example has been taught to generations of statistics students since the pioneering days of George Udny Yule: A report from Alsace in eastern France revealed a striking correlation between numbers of babies born in each village and numbers of storks nesting locally. To my chagrin, this does not reveal that storks do actually deliver newborn babies. Correlation is not the same as causation. The confounding factor here is village size. On average, larger villages have more chimneys for storks to nest on, and they also have more births each year.

Unfortunately, many interpretations of brain:body size relationships in humans, nonhuman primates and other mammals give inadequate attention to that fundamental distinction between correlation and causation. One initially appealing notion was the Expensive Tissue Hypothesis, which postulates that both brains and guts require a considerable amount of energy and that some kind of direct trade-off between them must occur. A prime prediction from this hypothesis is that species with large guts should have small brains and that only species with relatively simple digestive tracts can have large brains. This expectation was seemingly confirmed for primates by a plot of relative brain size against relative gut size, which showed a negative correlation. But little attempt was made to consider potential confounding variables. As a comparative biologist, my first rough-and-ready test of validity is to determine whether a finding reported for primates can be replicated with other groups of mammals. I knew that a study of bats had revealed that, once body size has been into account, fruit-eating bats are found to have brains twice as big as insect-eating bats. Yet fruit-eating bats also have relatively larger guts than insect-eating bats. So in this case there is a positive correlation between relative brain size and relative gut size, the opposite of what is predicted by the expensive tissue hypothesis. Admittedly, it can be (and has been) argued that primates are a special case. It is hence preferable to conduct a sophisticated analysis of data across mammals that takes into account numerous variables and seeks to pinpoint underlying causal relationships. Eventually, such a penetrating study was conducted and revealed no evidence of a trade-off between gut size and brain size. The bottom line is this: While it is true that humans have relatively large brains and relatively small guts, there is no convincing evidence that these two things are directly connected.

Because of the question of energy consumption, the expensive tissue hypothesis in fact has something in common with my own research into brain size scaling. Initial scaling analyses suggested a potential link between basal metabolism and brain size across mammals. However, the connection is clearly not a direct one. For instance, whereas there is considerable scatter in a plot of brain size against body size for mammals, there is remarkably little scatter in a plot of basal metabolic rate against body size. In other words, much of the variation in brain size cannot be explained by variation in basal metabolic rate. It quickly became apparent to me that reproductive biology is also intimately involved, particularly because of the links between fetal brain development, neonatal brain size and gestation period identified by Sacher and Staffeldt.
Eventually, I was led to formulate the Maternal Energy Hypothesis, which explicitly states that the relationship between adult brain size and energy turnover across mammals is mediated by resources provided by the mother during pregnancy and suckling. Unlike most other body organs, the brain is unusual in that growth is initially rapid and subsequently contrastingly slow. So most of brain growth occurs during gestation and lactation and is hence dependent on maternal resources. By the time of weaning, the brain is typically quite close to its completed adult size. In statistical terms, when we consider relationships among brain size, body size and energy turnover in adults, reproductive variables such as gestation and lactation periods are intervening (and potentially confounding) variables that must be taken into account.

One outcome of my combination of interests in reproduction and brain development was that I was prompted to ask a different question about the evolution of the human brain. Whereas investigators have generally asked why we need such a large brain, I began to ask how we can afford to have such an expensive organ. In a nutshell, my interpretation is that brains are generally useful and that every mammal has the largest brain that its mother was able to afford. This different perspective also leads to a different focus when considering human evolution. For instance, one key question that emerges regarding our evolutionary past is how dietary changes over time provided the progressively increasing resources needed to support enlargement of the brain.

Numerous comparative studies have been conducted in which brain size has been associated with specific aspects of behaviour on the basis of scaling studies. However, these studies have generally relied on a small number of empirical correlations, and little serious consideration has generally been given to potential confounding variables. It has, for example, been proposed that the evolution of brain size in primates is connected to social complexity, foraging skills or mating arrangements. But there is a fundamental problem that has scarcely been addressed: If a particular behavioural propensity leads to natural selection favouring increased brain size, it should be possible to demonstrate within a species that variation in brain size is positively associated with that behaviour. I know of no convincing evidence that variation in brain size among modern humans is directly associated with any measurable behavioural capacity. Indeed, none of the tests that I have conducted has yielded any evidence to support that expectation, once potential confounding variables were taken into account.

Fortunately, fossil evidence allows us to trace the evolution of brain size over the course of human evolution, from *Sahelanthropus* some 7 million years ago (mya) to modern *Homo sapiens*. Absolute brain size indicates that in our evolutionary trajectory brain size began to increase detectably only after the advent of the genus *Homo* around 2.5 mya. However, consideration of body size effects indicates that relative brain size began to expand over 4 mya. Strangely, however, available evidence indicates that the absolute size of the brain in *Homo sapiens* has actually decreased by about 10% over the past 30,000 years. It has often been noted that average brain size in *Homo neanderthalensis* was larger than in modern humans, but it is far less widely known that 30,000 years ago brain size was notably larger in *Homo sapiens* than it is today. The decrease in brain size within our own species has been correlated with an inferred decline in body mass. But we
are left with a major problem: If brain size is meaningfully connected with behavioural capacity, how is it that our brains were declining in size when cultural developments (notably over the last 10,000 years) were accelerating?

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