CHAPTER 5

Growing a Large Brain

In my youth, whenever I did well on a test my mother would tell me: "You get your brains from your father." This always seemed unlikely to me, as half of my genes came from her and the other half from my father. But later in life my research into brain evolution eventually revealed that she had modestly disowned the vital contribution to brain development that all women make. Mammals owe their brains to their mothers, at least with respect to investment of resources.

The brain is the body's command center, and one of our most vital organs. Brain evolution in mammals, in particular regarding the outstanding size of the human brain, has been much studied. Yet despite all the attention, the strong connection between reproduction and brain development has often passed unmentioned. The brain's high energy needs make it one of the most expensive organs in the body. In adult mammals, the energy needed to operate one ounce of brain tissue is about ten times as much as the average consumption of other living tissues. Although it accounts for only a fiftieth of body weight, the three-pound brain of an average adult human consumes around a fifth of the body's energy turnover.

For a developing brain, energy costs are even greater. Put simply, construction costs are added to basic running costs, increasing the heavy demand for resources. Like any operating system (other than regional governments), the body must achieve a balanced budget to be successful. Thus the higher resource costs for developing and operating a larger brain must be offset in some way. This adjustment can be achieved by some combination of using stored resources (drawing on reserves), increasing energy intake (augmenting income), or reducing costs for other parts of the body (downsizing in other departments). Balancing the budget commonly leads to some kind of trade-off between costs of the brain and other expenditures, notably those needed for reproduction.

As luck would have it, from the outset my research into primate evolution fostered an unusual combination of interests in reproductive biology and brain evolution. This mix of topics alerted me to cross-connections between these two areas. In particular, it drew my attention to the investment any mother makes in her developing offspring. As a general rule, evolutionary biologists tend to ask why any mammal species *needs* a large brain. Taking a different tack, I asked how any mammal is able to *afford* a large brain.

Biologically speaking, the crucial point is that in all mammals the mother provides most of the resources that her offspring needs for brain development. At first, during pregnancy, those resources are delivered across the placenta. Then, following birth, the mother nurses her offspring, providing further resources in her breast milk until weaning. In addition to being a conspicuous energy guzzler, the brain stands out in another respect compared to other organs: It grows rapidly early on and quickly reaches its target size. This course of development is understandable because the brain—the body's online computer—must be up and running once the offspring starts to move around independently. In mammals, most of brain growth, at least in size, has typically taken place by the time of weaning. Rapid early brain growth is followed by relative stagnation. This explains why the head of a newborn mammal is disproportionately large compared to the rest of the body and then becomes less prominent by adulthood.

In contrast to the brain, other major organ systems—heart, lungs, liver, kidney, digestive tract, muscles, and skeleton—grow fairly steadily and continuously from birth to maturity. In humans, for example, the brain has virtually reached its adult size by the age of seven, but the rest of the body continues to grow for another fourteen years or so. During later development, other organs increasingly outpace the brain. In a newborn human, the brain accounts for about a tenth of body weight, but by adulthood it is only a fiftieth. Because it has high energy demands and makes up 10 percent of body weight, a newborn human baby's brain actually consumes about 60 percent of total energy turnover. Such heavy consumption then gradually declines until it reaches the typical adult level of about 20 percent.

My comparisons among mammals revealed that adult brain size is significantly associated not only with energy consumption but also with pregnancy length. This discovery confirmed my gut feeling that brain development is closely tied to reproduction. The first clear clue to such a connection came from biologists George Sacher and Everett Staffeldt in 1974. They analyzed data for a representative set of mammals and showed that pregnancy length is more consistently associated with the brain size of a newborn infant than with its body size. Indeed, Sacher and Staffeldt concluded from this finding that the brain might serve as a pacemaker for the developing fetus. This proposal still awaits proper exploration, but brain size at birth is evidently tightly linked to pregnancy length.

The brain continues to grow after birth, fueled by resources delivered in the mother's milk. This means that suckling duration is also connected with the ultimate size of the brain. Yet the completed size of the adult brain is still significantly related to pregnancy length alone. Across mammals generally, the brain typically reaches about nine-tenths of its adult size by the time suckling stops. Therefore there can be no doubt that the mother is the provider of most of the resources needed for brain development.

In addition to its connection with pregnancy length, brain size in mammals also shows a clear statistical association with energy turnover. Recognition of the links between brain size, gestation period, and energy costs ultimately spawned my "maternal energy hypothesis." This hypothesis proposes that a mother's energy turnover during pregnancy directly influences the size of her newborn infant's brain. Other things being equal, the longer the pregnancy or the higher a mother's energy turnover, the more resources she can transfer across the placenta to promote brain development in her fetus. Similarly, the mother's energy turnover continues to influence her contribution to her infant's brain growth after birth, while she suckles the offspring. As the combined duration of pregnancy and suckling increases, the amount of time available for a mother to deliver resources for infant brain growth increases as well. In a real sense, then, when the offspring eventually reaches adulthood its completed brain size is largely attributable to maternal resources.

Primates obey this general rule, but they also show a unique relationship between brain growth and the development of the rest of the body. Throughout fetal development, primates consistently differ from all other mammals. George Sacher—this time in 1982— again made a seminal contribution to our understanding of brain development, discovering an important principle now known as "Sacher's rule." At all stages of pregnancy, a primate fetus consistently has about twice as much brain tissue as a similar-sized fetus of any other mammal. In other words, brain development is specifically privileged in primates.

However, the information available for Sacher's study was severely limited, as brain and body size have seldom been measured during fetal development, either in primates or in other mammals. Fortunately, there is an indirect way to test Sacher's rule. Because the difference between primates and nonprimates applies to all stages of fetal development, it is still present at birth. In contrast to fetal stages, data for brain and body size in newborn mammals are relatively abundant. Sure enough, when I assembled a large data set, analysis revealed that, for any given newborn weight, a primate has about twice as much brain tissue as a nonprimate. Sacher's rule was resoundingly confirmed.

Human infants are like other primates in this respect. Average brain weight of a newborn human baby can be accurately predicted from average body weight at birth using a scaling formula calculated for primates. A typical human baby weighing seven and a half pounds at birth has a twelve-ounce brain, pretty much what is expected in comparison to other primates. By contrast, a nonprimate mammal weighing seven and a half pounds at birth will usually have a brain weighing only six ounces or so. Because the brain is privileged throughout fetal development in all primates, their newborns are literally given a head start in life. Moreover, because this feature is universal among living primates, it must have been present in their common ancestor. The initial impetus for human brain expansion, and its connection with reproduction, are deeply rooted in our evolutionary past.

TO UNDERSTAND BRAIN GROWTH after birth, we need to take account of the brain's state of development in the newborn. The previous chapter already introduced the fundamental distinction between poorly developed (altricial) and well-developed (precocial) offspring. Altricial mammals—such as mice, hamsters, hedgehogs, treeshrews, rabbits, and cats—have relatively short pregnancies. As expected, altricial newborns are small relative to the mother's body size and have small brains. Accordingly, a greater proportion of brain growth must take place after birth, typically while the infant develops in a nest.

As a general rule, in altricial mammals brain size increases approximately fivefold between birth and adulthood. Rapid brain growth continues approximately up until the eyes and ears open and the body is covered in fur. This developmental state roughly corresponds to birth in precocial mammals. After the eyes and ears have opened in altricial mammals the rate of brain growth is greatly reduced. The slower pace then continues until the brain reaches its adult size.

By contrast, newborn precocial mammals—primates, hoofed mammals, dolphins, and elephants—are relatively big and already have quite large brains, so less brain growth occurs after birth. The general rule for precocial mammals is that the brain approximately doubles in size between birth and adulthood. This degree of growth is far less than the typical fivefold increase for altricial mammals. Moreover, in precocial mammals, including nonhuman primates, the switch from rapid to slower growth of the brain typically occurs around the time of birth.

In this respect, however, humans are unique among mammals. As already noted, the relationship between brain and body size in a human fetus or newborn fits the general primate pattern. But after birth the pattern of human brain growth differs sharply from that of any other primate and any other mammal. Strikingly, human brain size increases almost fourfold after birth, rather than merely doubling as in other primates. This marked increase in human brain size after birth is combined with another unique feature: The rate of brain growth does not slow down around the time of birth, as it does in nonhuman primates and in other precocial mammals. Nor does the rate of brain growth slow down a few weeks after birth, as it does in altricial mammals. Human brain growth does not switch to a slower pace until about a year after birth.

To put it another way, the human brain continues to show a rate of growth as fast as that of a fetus for a year after birth. Continuation of a fetal pattern of brain growth for so long after birth explains why a newborn human infant is particularly helpless compared to other newborn primates. Zoologist Adolf Portmann fittingly noted that the length of human pregnancy should really be reckoned as twenty-one months: nine months inside the womb followed by another twelve months outside it. Anthropologist Ashley Montagu put it slightly differently, writing that in humans a nine-month period of normal pregnancy in the womb ("uterogestation") is followed by another nine months of fetus-like development in the outside world ("exterogestation").

It is clear that in a human newborn the brain and allied anatomical structures are immature compared to nonhuman primates and to other precocial mammals in general. This fact has several medical implications. One is an increased incidence of conditions affecting the ear, nose, and throat. Many of these conditions improve or are completely resolved during the first year of life. A prime example is inflammation of the middle ear (otitis) in human infants, which in severe cases can lead to hearing loss. Otitis is common in human infants because the Eustachian tube, which allows air to flow between the back of the throat and the middle ear cavity, is still relatively immature at birth.

Rapid brain growth during the first year of life is connected with another unusual feature of newborn human infants: their striking plumpness. In an average human newborn weighing some seven and a half pounds, fat tissue accounts for over a pound, around 14 percent. Our babies are among the plumpest found among mammals. Human babies at birth look markedly different from the scrawny newborns of other primates, such as chimpanzees and rhesus monkeys. The proportion of fat tissue in a newborn human matches that in mammals living under arctic conditions and actually exceeds the level found in baby seals. As anthropologist Christopher Kuzawa has shown, a newborn human has about four times as much fat as expected for a standard newborn mammal of the same body size. In fact, the proportion of body fat in a human baby increases further over the first nine months after birth, building up to about a quarter of body weight. During that period, around 70 percent of the energy allocated to growth is used to deposit fat. In short, healthy babies do not lose their baby fat after birth but consolidate it and maintain it for up to three years. A mother's investment in building up her infant's fat reserves continues long after birth, largely thanks to nursing.

A standard explanation for our plump babies has been that natural selection favored an increase in body fat to offset the loss of insulating body hair. It is known that the optimal temperature for a human infant kept in an incubator is about 90°F, so cooling could be a problem. Baby fat is distinctively distributed, being mainly located just beneath the skin. In contrast to adult fat stores, there is relatively little fat in the belly cavity. Anthropologist Bogusław Pawłowski supported this view, arguing that various features of the human newborn evolved in early *Homo* to counter excessive cooling during nights spent sleeping in open savannah. Those features include relatively large size as well as a greater proportion of subcutaneous fat. A sleeping human infant is also unusual in being able to actively regulate its own body temperature.

However, Kuzawa's studies yielded only weak evidence for the role of subcutaneous fat proposed by Pawłowski. Kuzawa went on to explore a more likely explanation for our exceptionally plump babies: increased fat reserves as a crucial energy buffer. This would be particularly advantageous during the period of rapid brain growth in the first year of life. It could offset any disruption in the flow of resources to the growing infant. Going a step further, a 2003 paper by two nutritionists, Stephen Cunnane and Michael Crawford, argued that plump babies are the key to evolution of the large human brain, and not only because of energy supply. About half of the brain consists of fat, and a baby's fat reserves contain special fats—long-chain polyunsaturated fatty acids (LCPUFAs)—that are essential for normal brain development. Calculations indicate that LCPUFAs present in baby fat at birth should be enough to fuel three months of brain growth. Cunnane expanded on this theme in his 2005 book *Survival of the Fattest*, in which he described the normal human newborn as "positively obese." Deposition of fat in the human fetus takes place only during the last third of pregnancy; almost no fat is present during the first six months. As a result, fat reserves are well below normal in premature babies. A baby born five weeks early has only half the usual amount of fat, and a baby born ten weeks early has less than a sixth. With such early preemies the ribs and chest muscles stand out because there is so little fat tissue beneath the skin. Insufficient fat deposits mean that preemies are not well buffered for the rapid brain growth that takes place after birth. Although normal brain growth can nevertheless occur given adequate nutrition, it is vital to recognize the special needs of premature babies. Cunnane aptly describes stored fat in the newborn human as "insurance."

As previously discussed, aside from brain development, newborn human infants are in most other respects like other precocial offspring. Human babies are "altricial" only in a special sense: The brain is underdeveloped at birth, compared to its completed adult size, and continues to grow rapidly after birth. Portmann's description of the condition of the human newborn as "secondarily altricial" is fitting. It is the mismatch between brain development and other aspects of their condition at birth that makes our babies special. One reflection of this is that the bones of the skull are not fully developed at birth, leaving gaps known as fontanelles on the crown and on the sides. In human babies, these gaps, which have closed by birth in monkeys and are quite small in newborn apes, usually do not close until eighteen months to two years after birth.

Extension of a fetal pattern of rapid brain growth into the first year of life has some important implications. In the first place, the switch from fast to slow brain growth in the human infant is not associated with opening of the eyes and ears, as is otherwise typical for mammals. Human infants are unusual in having open eyes and ears during a yearlong period of fetal-type brain growth after birth. This extraordinary feature allows a human baby to interact with the environment with a relatively immature brain. As all parents know, human infants learn a great deal during the first year of life and already engage in sophisticated social exchanges. This feature was hugely influential in the gradual emergence of greater adaptability and behavioral flexibility during human evolution.

In this connection, it is no coincidence that the species-typical way in which human beings move around—walking upright—does not develop until about a year after birth. For a few months before striding develops, a human baby moves around in a distinct way, such as crawling on hands and knees or scooting. Here is another feature in which we stand out, since other primates move around in a species-typical fashion from the outset. It is also notable that active use of language does not begin until a human baby's second year of life, although infants busily learn many basic rules of communication during their first year. In sum, while human infants continue a fetal pattern of brain growth for a whole year after birth, they are able to interact actively with their surroundings.

But this uniqueness leads us to an important question: Why did this special human pattern of brain development evolve? The answer is quite straightforward. After nine months of development inside the womb, the brain size of the human fetus reaches the upper limit for safe passage through the pelvic birth canal. If the birth canal did not impose a size constraint, pregnancy might last about twenty-one months, continuing for a year or so beyond the usual time of birth to ensure full brain development.

It is far more efficient to develop brain tissue by transferring resources directly across a placenta. After birth, the mother must first convert her resources into milk, which is then transferred to the infant for digestion. This to some extent explains why human development in the womb is pushed right up to the limit allowed by the dimensions of the birth canal. Dimensions of newborn baby heads reflect this. As a general rule in biology, variation in any dimension within a species fits a typical bell curve or normal distribution. The central peak of the bell curve is the average value and smaller or larger values decrease progressively in a mirror-image fashion on either side of the average. The head circumference of a human newborn is a striking exception to this typical distribution. Head dimensions that are below the average decrease in the expected way, but above the average there is an abrupt decline in the largest head sizes. This reduction in upper-end variation is a sure sign of the filtering action of natural selection, eliminating head sizes that are too big for a safe birth.

Comparison with great apes, our closest zoological relatives, reinforces this conclusion. They all have shorter gestation periods: thirty-five weeks in orangutans, thirty-seven weeks in gorillas, and only thirty-three weeks in common chimpanzees. Female chimpanzees and orangutans are generally smaller than women, while female gorillas are somewhat bigger. Our true gestation period of thirty-eight weeks is between one and five weeks longer than in great apes. Body size does not explain this difference. And it certainly does not account for the dramatic difference in size at birth: Newborn orangutans and chimpanzees weigh approximately four pounds and baby gorillas about four and a half pounds, compared to an average of seven and a half pounds for newborn human infants. To put it another way, newborn body size is around 3 percent of mother's body mass in monkeys and apes and almost 6 percent in humans.

Thus a human baby weighs almost twice as much as a great ape infant at birth. Remember Sacher's rule: Brain and body size at birth fit a standard relationship across primates. As a human newborn is about twice as big as any great ape at birth, its brain size is correspondingly almost twice as big as well. This disparity tells us two important things. First, women must invest considerably more in fetal development than any great ape to produce our larger-bodied, larger-brained newborns. Second, it shows that humans really do push right up against the limits as regards brain and body size at birth. This explains why human birth is such a drawn-out, hazardous process.

Unusual challenges in human birth are also reflected by the difference between men and women in the shape of the pelvis. In monkeys and apes males and females do not obviously differ in pelvis shape. By contrast, a woman's pelvis is quite different from a man's. The width of the pelvis is about the same in the two sexes, but it is relatively wider in women because they have smaller bodies. Think of body shape. In women, the hips are generally wider than the shoulders, whereas the opposite is true for men. Internally, the lower end of the spine is shifted backward in women so that it does not bulge into the pelvic canal, which is smoothly rounded. In men, such a backward shift of the spine is unnecessary and the pelvic opening is heart-shaped. In addition, the joint between the left and right halves of the pelvis at the front, in the pubic region, is shorter in women than in men and the angle below is wider. There are numerous other differences, making it easy to tell whether a human pelvis is male or female. Biological anthropologists who investigate human skeletons from archaeological sites or crime scenes—skeleton detectives—will look at the pelvis first if they need to identify an individual's sex. Sex differences in the pelvis also result in different walking styles. When women walk, their hips sway because the pelvis is tilted more toward the front and moves up and down more obliquely. Movements at the hip and knee joints also differ.

The proposal that pelvic dimensions limit head size in the human newborn is quite logical and can be independently verified by an indirect test. All we need is to find a mammal that produces a large-bodied, large-brained newborn comparable to a human baby yet has no constraint on its birth canal because it has no bony pelvis. Thanks to the wonders of biological diversity, such mammals do exist. The ancestors of dolphins and whales secondarily returned to life in water. As a result, the entire hindlimb girdle—including the pelvis—became redundant and a few bony splints are all that is now left. And some dolphins happen to be reasonably close to humans in body weight, pregnancy length, and adult brain size. A dolphin with no pelvis can give birth to a particularly large baby with a brain more than twice as big as the twelve-ounce brain of a human newborn. But the brain of a dolphin merely doubles in size between birth and adulthood, rather than quadrupling as it does in humans. Water-living, pelvis-less dolphins have no need to extend fetal brain development into postnatal life.

Because the head of a newborn human is already so big compared to the size of the birth canal, its passage through the pelvis is fraught with difficulty. Birth is eased to some extent by specific action of the hormone relaxin. Production of relaxin, an insulin-like hormone produced by the ovaries, placenta, and breast, peaks late in pregnancy. Among other things, the hormone softens up the ligament that binds the left and right halves of the pelvis together at the front. It also relaxes the pelvic musculature, rendering the pelvic canal a little more flexible. The fontanelles between the main bones of the skull play a part in easing birth as well, allowing flexibility in the shape of the newborn's head. Nevertheless, passage of the human infant through the pelvic canal during birth is still a remarkably tight squeeze. Some kind of physical obstruction arises during about one in five human births.

Difficulties in the human birth process have been remarked upon through the ages. In the Bible, for instance, the following divine punishment for original sin was meted out to Eve and every woman thereafter (Genesis 3:16): "I will greatly multiply your pain in childbirth. In pain you will bring forth children." This biblical connection between eating forbidden fruit from the Tree of Knowledge and painful childbirth is intriguing in view of the clear link between large brain size and challenging human births.

To pass through the pelvic canal, the human newborn undergoes a complex pattern of rotation that is highly unusual among primates. The tortuous pathway followed is not only due to the newborn infant's relatively large head and broad shoulders. It also reflects changes in shape and orientation of the adult human pelvis for upright two-legged walking. These two factors combined in evolution to produce a veritable obstacle course for the human infant during birth.

Problems caused by a relatively large newborn head are not confined to humans. As anatomist Adolph Schultz originally noted, newborn head size can also create difficulties at birth for certain nonhuman primates. Once again, body size is a key factor that must be taken into account. As is to be expected, across primate species average newborn body size increases with average mother body size. But, as for many other biological features, scaling is not simply proportional. Across species, newborn size increases at a slower pace than mother's body size. In other words, as the mother's body size increases, the size of her newborn represents a smaller and smaller fraction of her weight. In comparison to mother's size, small-bodied monkeys have large infants, medium-sized monkeys and gibbons have moderate-sized infants, and great apes have small infants. For instance, squirrel monkeys—large-brained, small-bodied New World monkeys—have relatively large newborns that fit tightly in the birth canal. But the monkey pelvis, unlike that of humans, has not been radically modified for upright walking. So birth is relatively straightforward despite the snug fit.

In humans, birth of a large-headed newborn takes place through a pelvis reconfigured for two-legged striding. Moreover, the birth canal is tortuous because the inlet into a woman's pelvic canal is largest from side to side, while the outlet is largest from back to front. As a result, a two-stage turning sequence is needed for the newborn to pass safely through the pelvis. Anthropologist Karen Rosenberg described the special features of human birth in a 1992 paper, showing that as the human newborn's head enters the inlet of the pelvic canal, it is already rotated so that its long axis is oriented from side to side rather than from back to front, as is typical for nonhuman primates. Then, during its passage through the pelvis, the infant's head is rotated even more to fit the front-to-back orientation of the long axis of the pelvic outlet. Its face is usually pointing toward the mother's rear as it emerges. In other primates, the baby's face is typically directed forward as it passes through the pelvis, and there is no rotation at all.

The human newborn's large head is not the only thing that makes birth problematic. The infant's shoulders are also quite wide relative to the birth canal, so additional juggling is needed for them to pass through. This is why the head is turned to one side as the shoulders pass through the birth canal. The shoulders, too, make a tight fit, so jamming is an additional hazard during human birth, occurring in up to one in a hundred cases.

The distinctiveness of the human birth process has perhaps been somewhat exaggerated. In 2011, primatologist Satoshi Hirata reported that in a captive colony of chimpanzees close-up video recordings showed that the head was rotated to face backward in all three births that were monitored. The head and body of the newborn rotated to face forward after the head had emerged. As Hirata and his coauthors noted, the actual birthing process has been little studied in nonhuman primates, so rotation in the birth canal may occur in other species. However, if birth with the newborn's head facing backward occurred regularly in standard laboratory primates such as rhesus monkeys, squirrel monkeys, and common marmosets, surely it would have been noticed. Moreover, the uniqueness of human birth is not limited to rotation but also has to do with head size and adaptations for upright striding. For these reasons, two-stage rotation is obligatory.

All of these special features combine to make human birth a drawn-out and difficult process, and it is hardly surprising that medical professionals call it "labor." One multicultural study, published in 1999 by gynecologist Leah Albers, analyzed the duration of labor for more than 2,500 full-term births. All cases involved low-risk mothers who gave birth without medical intervention under the care of nurse-midwives in hospitals. Birth took an average of almost nine hours for first-time mothers and around six hours for mothers with previous births. In extreme cases, birth took as long as twenty hours.

By contrast, in nonhuman primates birth is relatively rapid and straightforward. Anthropologist Wenda Trevathan reviewed birth duration in primates in her 1987 book *Human Birth: An Evolutionary Perspective* and found that, as expected from the small size of newborns compared to the girth of the mother's pelvis, birth is usually relatively uncomplicated in great apes. Orangutans, chimpanzees, and gorillas all give birth in a couple of hours. The unexpected backward-facing births of chimpanzees reported by Hirata and colleagues do not entail prolonged birth duration, as in humans; to the contrary, they may well be the outcome of a loose fit within the birth canal. As in great apes, birth usually takes a couple of hours in monkeys as well. But with small-bodied mothers labor can be more difficult because of a tighter fit between the baby and the birth canal. Certain small-bodied, large-brained monkeys—notably squirrel monkeys—have been reported to have relatively difficult births, although they also last only a couple of hours. In any event, humans are the only primates that have such protracted, difficult births at such a large body size.

Wenda Trevathan and Karen Rosenberg also noted that complex human births, with their associated risks, make some kind of assistance almost obligatory. Birth of a backward-facing newborn and the danger of jamming present major challenges. In addition to providing general assistance during birth, a midwife can intervene to avoid problems that may arise. In about a third of human births the umbilical cord becomes wrapped around the baby's neck because of the complex pattern of rotation. In most cases this is not life-threatening, but occasionally the cord tightly constricts the baby's neck. If corrective action is not taken quickly, the infant can be strangled. Surveillance and prompt intervention by a midwife can ensure that the umbilical cord does not create a serious threat during birth.

As brain size gradually expanded over the course of human evolution, it must have posed an ever-increasing challenge for the birth process. Over the past 4 million years, the size of the brain approximately tripled, increasing from about a pound in *Australopithecus* to roughly three pounds in modern humans. Modern great apes and humans have quite similar pregnancy lengths, so we can reasonably assume that their common ancestor had a relatively long pregnancy as well, about eight months. As brain size increased in the hominid line, pregnancy gradually increased to reach the nine months typical for humans today.

In the earliest stages of hominid evolution, as in modern great apes, dimensions of the pelvic canal probably imposed little constraint on birth. When the switch to upright, two-legged striding in human evolution occurred, it changed both the size and the shape of the pelvic canal. As brains became bigger, the pelvis increasingly constrained the size of the newborn's head. At some point it became necessary to postpone part of fetal brain growth until life after birth. This was the only way to bridge an expanding gap between the largest newborn brain size permitted by pelvis dimensions and the completed size of the adult brain.

Australopithecus, the earliest well-documented hominid, existed between 4 million and 2 million years ago. At about a pound, average adult brain size was still relatively small. In modern nonhuman primates, the brain at birth is generally about half the size of the adult brain, and if *Australopithecus* still fitted this pattern, the newborn would have had an eight-ounce brain. It is unlikely that its size would have posed a major problem. However, various studies have indicated that the pelvis of *Australopithecus* had perhaps already begun to constrain the birth process because adaptations for upright two-legged walking were already under way. In particular, the pelvis had become relatively broad and low-slung, contrasting with the tall, narrow pelvis of great apes. Remodeling of the pelvis changed the shape of the bony birth canal in *Australopithecus*, making it wider from side to side and narrower from front to back. Perhaps this change in shape prevented the newborn's head from passing straight through the birth canal in the typical nonhuman primate fashion. Instead, some obligatory rotation of the baby's head may have been needed to align its long axis with the largest dimension of the entry into the pelvic canal, as in the first-stage rotation seen in humans. Some authors have even suggested that birth in *Australopithecus* was as complex as in modern humans, although that is unlikely. Additional rotation of the newborn's head during birth was probably unnecessary.

Unfortunately, the size of the brain and body in newborn *Australopithecus* is not documented by fossil evidence. Instead, various estimations have been made using comparisons with living species. To roughly assess brain size at birth, for example, we might take a graph for monkeys and apes showing the size of the newborn's brain in relation to the mother's body size. The same approach could be taken to estimate newborn body size. Yet we are faced with a tricky problem. As mentioned, compared to monkeys and apes modern human babies are far larger than expected, with appreciably larger brains. Thus human newborn brain and body size would be greatly underestimated if calculated from such a graph. This would not matter if *Australopithecus* did not differ from modern monkeys and apes. On the other hand, if *Australopithecus* had already started to evolve toward the modern human condition, its newborn brain and body sizes would be underestimated similarly. The whole point of the calculations is to find out whether *Australopithecus* was ape-like or human-like, so we are locked in a vicious circle.

In an attempt to break that circularity, anthropologist Jeremy DeSilva came up with an ingenious suggestion. Although human newborn brain and body sizes are larger than expected in comparison to monkeys and apes, the relationship between adult brain size and newborn brain size is more consistent across species. Therefore we can estimate newborn brain size for *Australopithecus* from adult brain size, which is well documented in the fossil record. Sacher's rule reflects a consistent relationship between brain size and body size in newborns, so once we have an estimate of newborn brain size we can use it to calculate newborn body size. Taking this approach, DeSilva concluded that *Australopithecus* had larger-brained, bigger-bodied babies than a modern ape of comparable adult size. This, in turn, indicates that birthing difficulties indeed might have begun to emerge even in *Australopithecus*.

Yet DeSilva's approach does not entirely avoid circularity, although it does reduce it. Between birth and maturity, human brain size almost quadruples, whereas brain size merely doubles in an average nonhuman primate. Because of this, if we try to calculate newborn brain size from adult brain size in humans, using a graph for monkeys and apes, there will be some overestimation. Nevertheless, the fact remains that *Australopithecus*, which is actually somewhat smaller than a chimpanzee in body size, ends up with estimates for neonatal brain and body size that differ from those of chimpanzees.

Although there is no fossil evidence to indicate brain size in newborns, fairly complete skulls of two three-year-old *Australopithecus afarensis* from Ethiopia and of a four-year-old *Australopithecus africanus* from South Africa have been discovered. The brain sizes of these immature australopithecines are similar to those of chimpanzees of the same age. But adult chimpanzees have smaller brains than adult *Australopithecus*, about thirteen ounces instead of a pound. This means that a smaller proportion of brain growth was achieved in three-year-old and four-year-old *Australopithecus* than in chimpanzees of the same age. So there is indirect evidence that more brain growth occurred after birth in *Australopithecus* than in chimpanzees, hinting at the beginnings of a pelvic constraint.

Advanced hominids belonging to the genus *Homo* first appear in the fossil record around 2 million years ago. Brain size steadily increased among successive *Homo* species, so challenges in the birth process would have increased in parallel. In *Homo habilis*, for example, average adult brain size had already increased by a third compared to the norm for *Australopithecus*, from a pound to about twenty-one ounces. If *Homo habilis* followed the typical pattern for nonhuman primates, newborn brain weight would have been about ten and a half ounces. This is only 15 percent less than the twelve-ounce newborn brain size of modern humans. Because *Homo habilis*, like *Australopithecus*, was relatively small-bodied, the larger head of the newborn was probably even more subject to limits imposed by the birth canal. Unfortunately, the skeleton of *Homo habilis* is poorly documented in the fossil record, so we must await further discoveries to assess the extent of difficulties at birth.

Like *Homo habilis*, *Homo erectus* dates back to around 2 million years ago, but the latter was closer to modern humans in body size. *Homo erectus* also had a bigger brain than *Homo habilis*, with adult brain size averaging about two pounds. If *Homo erectus* followed the general rule for nonhuman primates, brain size in the newborn would have been about a pound—four ounces more than the twelve-ounce brain of a modern human newborn. Pelvic dimensions in *Homo erectus* are quite close to those in modern humans, so this hominid species doubtless showed some extension of a fetal pattern of brain growth into postnatal life. Development in the womb in *Homo erectus* was most likely pushed to the limit, as in modern humans. Therefore this species probably also gave birth to newborn infants with a twelve-ounce brain. If pregnancy lasted nine months, as in modern humans, prolongation of a fetal pattern of brain growth into the first three or four months of life after birth would have been needed. Accordingly, we can speculate that newborn *Homo erectus* already showed a partial version of the "secondarily altricial" state of newborn humans today. Increased helplessness of infants during the first few months after birth would have made intensive parental care obligatory. At the same time, birth of infants with a brain that was still relatively immature would have begun to open up opportunities for increased behavioral flexibility and early social learning.

Limitations of the fossil record once again constrain our interpretations. Thus far, only a single fossil specimen indicates brain size in a young individual at this stage of evolution: a partial skull of a *Homo erectus* infant discovered in 1936 at the 1.8-million-year-old Mojokerto site in Java, Indonesia. Making matters worse, the specimen preserves only the braincase and lacks the face and teeth, making it difficult to estimate the infant's age at death. However, in 2004 anthropologist Hélène Coqueugniot and colleagues performed a detailed study of the Mojokerto braincase using CT scanning. Combining results from three different age indicators, they concluded that the infant was about a year old. Its brain weight came out at a little over twenty-three ounces, roughly three-quarters of the average brain size of slightly more recent adult *Homo erectus* from Java. Coqueugniot and her team concluded that brain growth was already well advanced in the Mojokerto infant and that there had been little evolution toward a "secondarily altricial" condition. Two years later, though, anthropologist Steven Leigh came to a different conclusion. He noted that, for a one-year-old, the brain size of the Mojokerto infant fell within the lower end of the modern human range rather than into the range of chimpanzees. Moreover, one of the age indicators used by Coqueugniot was recent closure of the fontanelle on the skull roof. In fact, closure of that fontanelle at an age of about a year itself indicates that the brain of the Mojokerto infant must have been relatively immature at birth. So the limited and uncertain evidence that is available does suggest that *Homo erectus* was moving toward the modern human condition.

Neanderthals (*Homo neanderthalensis*) and *Homo sapiens* both descended from *Homo erectus*. The lineages leading to these two advanced sister species diverged at least half a million years ago and perhaps even earlier. Brain size increased from two pounds to three pounds in both Neanderthals and modern humans after they diverged from *Homo erectus*. Most of that one-pound increase in brain size occurred independently in the two lineages, as is reflected by marked differences in brain shape between *Homo neanderthalensis* and *Homo sapiens*. Any further extension of a fetal pattern of brain growth into life after birth, beyond the condition present in *Homo erectus*, would have taken place separately in the two species as well. This means that the need for more intensive parental care would have increased as a parallel development in Neanderthals and modern humans. By the same token, the scope for greater behavioral flexibility and early social learning in young infants must have increased independently in the two lineages.

Because closely related mammal species belonging to the same genus consistently have similar gestation periods, it is safe to assume that pregnancy in Neanderthals lasted nine months, just as in modern humans. Moreover, it now seems that the bony pelvic canal of female Neanderthals was quite similar to that of modern women. Fragments of an adult female

Neanderthal pelvis were discovered at the Tabun site in Israel more than eighty years ago, but its overall shape remained uncertain until computerized techniques became sophisticated enough to carry out virtual reconstructions. Using this approach, anthropologists Timothy Weaver and Jean-Jacques Hublin found that areas of the pelvic inlet and outlet are actually quite similar to those of *Homo sapiens*. Nevertheless, the shape of the birth canal is distinctly different. The inlet and, particularly, the outlet are wider in the Tabun pelvis as compared to the modern human one. Because of this, a second-stage rotation of the head for exit from the birth canal would have been unnecessary in the Neanderthal, and the baby would have emerged with its head facing sideways. A marked shift to the modern birth pattern, with the baby's head undergoing a second rotation to face backward at emergence, seemingly occurred after Neanderthals and humans diverged.

The fossil record for Neanderthals is considerably better than for earlier hominids, and two fairly complete skeletons of newborn individuals have been discovered. The first is from the Le Moustier cave site in Dordogne, France. In 2010, anthropologist Philipp Gunz and colleagues included the Le Moustier newborn in a detailed study of brain development after birth. The analyses showed that Neanderthals and modern humans are quite similar with respect to brain development at birth, but they follow quite different trajectories thereafter. Whereas the brain of Neanderthals takes on an elongated form as it develops, the brain of *Homo sapiens* becomes globular in shape. The second newborn Neanderthal specimen, found in 1999, was discovered in Mezmaiskaya Cave in Russia. In 2008, anthropologist Marcia Ponce de León and colleagues performed virtual reconstructions of the Mezmaiskaya newborn, concluding that brain size at birth was similar in Neanderthals and modern humans. In fact, in both the Mezmaiskaya and the Le Moustier specimens, the newborn's brain was similar in size, at about fourteen ounces. This weight is somewhat above the average for modern humans, so it seems that female Neanderthals did not have an easier time at birth.

AT BIRTH, all primates have larger brains for their body size than all other mammals. Yet by the time adulthood is reached, the distinction between primates and other mammals is fuzzier because of development after birth.

It is often claimed, even in academic texts, that adult primates have bigger brains than other adult mammals. This claim is misleading. It is, of course, untrue for absolute brain size. An adult elephant has a brain four times bigger than the average human brain, and a sperm whale's brain is, at sixteen pounds, the largest of any mammal. Reliable conclusions are possible only if we scale brain size to body size across mammals. Eugène Dubois, the discoverer of *Homo erectus*, was among the first to recognize this at the end of the nineteenth century. Since then, the relationship between brain size and body size has been much discussed. Two works that broke ground in this area were Harry Jerison's 1973 compendium *Evolution of the Brain and Intelligence* and John Allman's 1999 book *Evolving Brains*.

A rudimentary measure to compensate for size effects when comparing brain size between species is a simple ratio of brain size to body size. For instance, my brain is 2 percent of my body weight. However, ratios are just as misleading as absolute brain sizes, for a basic reason: Across species, brain size increases at a slower rate than body size. Across mammals, when body size triples, brain size barely doubles. Hence, other things being equal, the ratio between brain size and body size will gradually decline as overall body size increases. Small-bodied mammals generally have higher ratios than large-bodied mammals. Primitive mouse lemurs provide a useful example among primates. With a body weight of two ounces, a lesser mouse lemur is one of the smallest living primates. Yet an adult's brain makes up 3 percent of its body weight, leaving my 2 percent brain-to-body ratio in the dust.

Thus both absolute brain size and ratios between brain size and body size are misleading. Reliable comparisons of brain size between mammal species require special analyses that allow for the fact that the relationship between brain size and body size follows a decelerating curve. Only such analyses, first proposed by Dubois and embedded in a convincing overall framework by Jerison, permit meaningful interpretation of brain size in mammals.

If appropriate scaling analyses are used to take body size into account, relative brain sizes can be compared across species. Comfortingly, when body size is appropriately taken into account, we humans turn out to have the largest brain size among modern mammals. But what about that oft-repeated claim that primates have larger brains than other mammals? Well, this notion is still misleading, for two reasons. First, although *average* relative brain size is indeed larger for primates than for other mammal groups, individual primate species vary widely and overlap extensively with other mammals. In fact, a few lower primates have relative brain sizes below the overall average for mammals. Second, although humans do have the largest relative brain size found among mammals, most primates have distinctly smaller values. Relative brain size in humans is three times bigger than in great apes and twice as big as in the closest nonhuman primates, notably the New World capuchin monkeys. The yawning gap between human relative brain size and the highest values for nonhuman primates is occupied by dolphins and their relatives, which are members of an entirely different group of mammals. As regards relative brain size, some dolphins are remarkably, not to say uncomfortably, close to humans.

To sum up, it is simply wrong to imply that adult primates all have larger brains than other adult mammals. This is untrue in any sense—absolute, proportional, or appropriately scaled. It is crucial to recognize this because at birth primates do consistently have relatively larger brains than other mammals. While newborn primates have brains twice as big as in other newborn mammals at any given body size, this distinction between primates and nonprimates is far less obvious once adulthood is reached. Greater brain growth after birth allows some mammals to catch up with primates and even partially overtake them. For instance, once adult, many carnivores overlap with monkeys and apes in relative brain size. Carnivores have poorly developed, altricial newborns, so a large amount of brain growth occurs after birth. Mammals can evidently become large-brained adults in different ways. Although primates undoubtedly benefit from their head start at birth, that is not the end of the story.

Up to this point, brain size in humans and other primates has been discussed without reference to sex. Everything said thus far applies equally well to males and females. However, there exist some intriguing differences between males and females regarding the completed size of the brain. A developmental perspective is needed to tease apart some of the complex issues involved.

The first obvious feature, which has aroused some controversy, is a pronounced difference in brain size between adult men and women. On average, an adult woman has a brain size about 10 percent smaller than that of an adult man. This was first established soon after the Darwin/Wallace theory of evolution was announced. French anatomist Paul Broca, best known today for his discovery of Broca's area, a language area in the human brain, pioneered measurements of human brain size. His basic technique was to fill the braincases of human skulls with lead shot to measure their volumes. He noted the 10 percent average difference in braincase volume between men and women, triggering a debate that has continued ever since. Broca believed that brain volume is a meaningful indicator of intelligence, and much of his research was aimed in that direction.

There is a natural tendency to believe that brain size, as indicated by braincase volume, should tell us something useful about the owner's abilities. Partly for this reason, decades ago eminent men in Western society made arrangements for their brains to be removed and studied after death. It was simply assumed that outstanding men owed their abilities to larger brains and that the smaller average brain size in women reflected lesser intelligence. Paul Topinard—Paul Broca's leading disciple—published a paper early in 1882 in which he gave the following explanation for the observation that women have smaller brains: "A man, who must strive for two in the struggle for existence, bears all responsibilities and concerns for the future. He is constantly and actively challenged by the environment and by rival forces. So he needs a larger brain than the woman that he must protect and feed. She devotes herself to household tasks, and her role is to bring up the children, to love and to be passive." A few months later, he published another paper espousing the diametrically opposite view that the smaller size of the woman's brain is due to relative smallness of body size. He wrote, "I believe that I have been able to demonstrate that the sexes are equal as far as development of the brain is concerned. Indeed, it might even be claimed that women are more advanced in their evolution than men." Regretfully, I have not been able to find out what happened to change Topinard's mind over those few months. Perhaps he got married and had some sense beaten into him.

The oft-repeated conclusion that women are less intelligent because they have smaller brains is part of a larger picture in which human brain size is crudely equated with ability. Stephen Jay Gould effectively debunked this notion in his excellent book *The Mismeasure of Man*, but the pernicious tendency lingers on. In the first place, as in mammals generally, brain size is related to body size, so the fact that women generally have smaller bodies than men surely has something to do with their smaller brain sizes, as Gould correctly noted. Paul Harvey has commented that Gould—doubtless carried away by his enthusiasm for a just cause—removed the effect of body size twice over. Different body sizes, while they account for most of it, do not entirely explain the brain size difference between men and women.

Regardless of any sex difference, body size is a significant factor influencing brain size even among men. It has often been noted that the French novelist Anatole France, recipient of the Nobel Prize for literature in 1921, had the smallest brain on record, just over two pounds. Recently it has emerged that Albert Einstein also had a very small brain, barely 10 percent bigger than that of Anatole France. In this case, Einstein himself did not request removal of his brain. Acting on his own initiative, a pathologist friend took this step at the postmortem examination. As Michael Paterniti amusingly recounts in *Driving Mr. Albert: A Trip Across America with Einstein's Brain*, retrieval of the brain and accompanying documentation was a close call. But the bottom line is that Anatole France and Albert Einstein were both notably small men. Their small brains clearly reflect this basic fact, rather than anything about their intellectual ability.

Brain size in humans varies widely, partly because body size is so variable. Although average brain weight in modern humans is about three pounds, the overall range in perfectly normal people extends from two to four pounds. The largest normal human brains are about twice as big as the smallest. Wide variation is also evident when men are compared to women. Although a male brain is on average about 10 percent bigger than a female brain, overlap is extensive. Moreover, the range of variation is greater in men than in women.

The notion that men are more intelligent than women has proven to be strangely resilient in the face of much contradictory evidence. An authoritative 1995 paper by education experts Larry Hedges and Amy Nowell reviewed numerous previous studies of sex differences and variation in mental test scores. They showed that, overall, average values in intelligence test scores hardly differ between men and women, although men show greater variation. The authors noted, however, that men and women diverge somewhat for particular skills. Women tend to do better on tests that require writing skills, while men tend to do better on tests calling for mechanical skills. The crucial point is that despite the 10 percent difference in brain size, there is no overall difference in intelligence between men and women.

It is worth noting that the inventor of the intelligence quotient (IQ), Frenchman Alfred Binet, originally developed his test to identify students in need of special help with schoolwork. His noble aim was to ensure that disadvantaged children would receive educational support. Unfortunately, IQ testing is now widely used more to discriminate, and the notion of IQ has a negative connotation in many people's minds. Moreover, it is clear that scores achieved on IQ tests are influenced by cultural context and can be improved by training. There is no such thing as a culture-free IQ test that measures inborn ability.

In fact, IQ test scores are sometimes subject to a peculiar but little-advertised form of manipulation. When I was growing up in England, stepping up from primary to secondary school in the state system was based on a widely feared examination known as the "Eleven Plus," usually taken by pupils between the ages of eleven and twelve. IQ testing was used to assess mathematical ability and literacy. The outcome decided whether a schoolchild could go on to a university-track grammar school or was relegated to a lower-level secondary modern school. I still remember fretting about the approaching Eleven Plus examination and rejoicing when I passed. A few years ago, I found out that the examination results were systematically adjusted. At an age of eleven to twelve, girls consistently perform better than boys on IQ tests, so the results for girls were adjusted downward to ensure that roughly equal numbers of boys and girls went on to grammar schools. So much for superior male intelligence!

Development sheds additional light on differences between male and female brains. Although it is true that men have brains about 10 percent bigger than those of women, there is little sex difference at birth. Indeed, large samples are needed for a statistically significant result. The average brain weight of a newborn boy is just over 3 percent greater than the average brain weight of a newborn girl. Consequently, a boy's brain must grow more after birth to result in the 10 percent difference in brain weight between adult men and women. It has long been accepted that division of nerve cells (neurons), the basic components of the brain, stops about halfway through human pregnancy. What this means is that, unless the brain of a newborn boy has a higher density of neurons, it cannot have many more neurons than a girl's brain. Although recent evidence indicates that some division of neurons does occur during the second half of pregnancy and after birth, this makes little contribution to overall brain size. Then why is a man's brain 10 percent bigger than a woman's? Perhaps more connections are formed in the male brain, requiring more nerve fibers.

But there is a curious sex difference in human brain growth after birth. A girl's body generally grows faster than a boy's, and as a result, eleven-year-old girls are somewhat bigger than eleven-year-old boys. Yet most brain growth takes place early in life—by the age of seven years, the brain has almost reached adult size. What this means is that a seven-year-old boy has a brain that is some 10 percent bigger than the brain of a seven-year-old girl. This has a major consequences for energy requirements. Brains are energy guzzlers, so the almost adult-sized brain of a seven-year-old boy requires more resources than the almost adult-sized brain of a seven-year-old girl. However, there is another interesting implication. An eleven-year-old boy has an almost adult-sized brain that is 10 percent larger than the brain of a girl of the same age. Yet at the age of eleven girls do better than boys on IQ tests.

Let me propose an alternative, slightly outrageous explanation of the brain size difference between boys and girls. Brains are not exclusively made up of neurons and nerve fibers. They also contain glial cells, which apparently play no direct role in nervous processing. Instead, glial cells seem to have a support function, providing nutrients and a structural scaffold. They may also have a packing function, rather like polystyrene peanuts. Human males need bigger skulls because they have bigger jaws, teeth, and jaw muscles and generally have a bigger body. Perhaps the male brain merely contains more glial cells for packing and support, and not more neurons and connections between them. This directly leads to a prediction that neurons and nerve fibers should be less dense in male brains than in female brains. Present evidence is equivocal. Some authors have reported that at least some parts of male brains have lower neuron densities, while others deny that there is a difference. The jury is still out, but I see no evidence that there is any fundamental difference between male and female brains that translates into any significant difference in ability.

Of course, the most striking sex difference concerning the brain is the unique role the mother plays in its development. Throughout pregnancy and lactation, maternal resources are crucial for the offspring's developing brain. We in fact get our brains from our mothers. And that maternal contribution goes even further than I originally thought. A fascinating study by radiologist Angela Oatridge and colleagues used a magnetic resonance scanner to study brain dimensions in nine pregnant women. They discovered that a woman's brain decreases in size by an average of about 4 percent over the course of pregnancy and then takes about six months after birth to regain its previous size. Seemingly a human mother goes above and beyond the call of duty, cannibalizing her own brain to nourish her developing fetus.