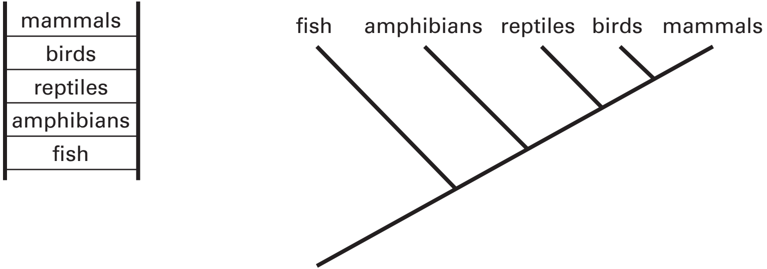


Figure 1.1

Simplified version of nature's ladder for vertebrate animals (*left*), and the same scale now stretched over evolutionary time as it became understood that life evolved, that is, changed over time (not drawn to scale). The merging lines (*right*) indicate that modern birds and mammals (aligned at the top) shared a common ancestor, and their common ancestor shared a common ancestor with modern reptiles, and their common ancestor shared a common ancestor with modern amphibians, and so on, back to the first life-form on the planet. This particular "genealogical tree" of vertebrates is wrong, though; see figure 1.4.

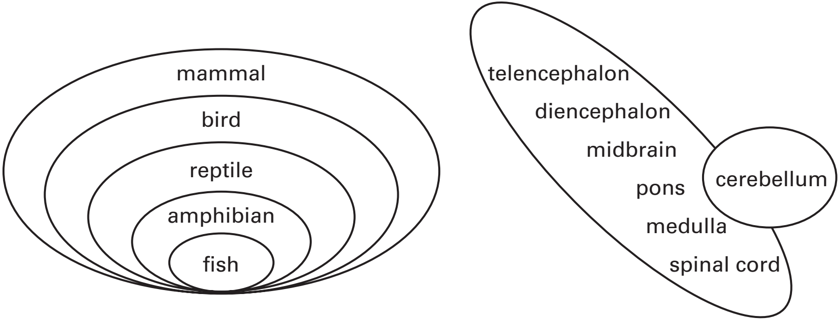


Figure 1.2

In Edinger's view, just as mammals would have evolved by progressing past a bird-like stage, and birds in turn would have progressed past a reptile-like stage, the brain of each vertebrate group would have acquired new structures on top of those in preexisting species (*left*). The resultant layering of structures was reminiscent of the sequence of structures along the vertebrate brain and spinal cord (*right*), from top (telencephalon) to bottom (spinal cord).

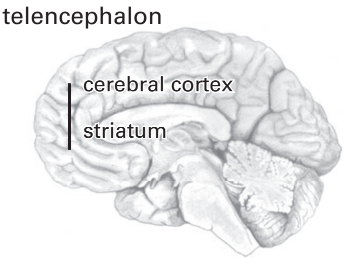


Figure 1.3
Although the human brain has the same subdivisions as all vertebrate brains, the human telencephalon (cerebral cortex + striatum) is several times larger than all other brain structures together.

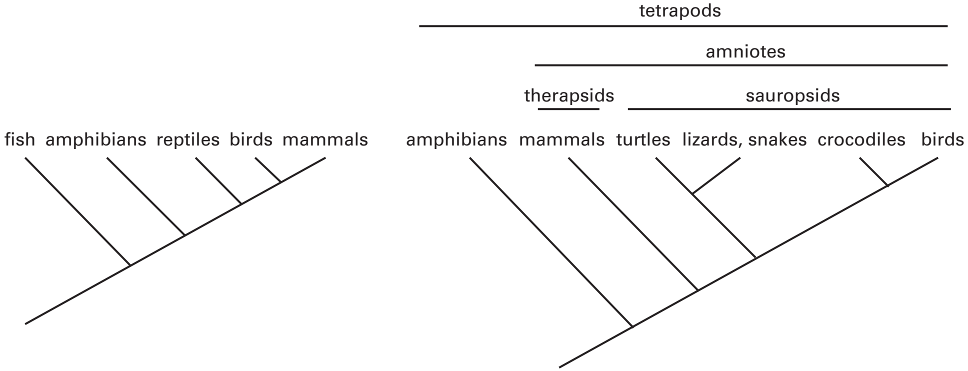


Figure 1.4
Modern rendition of fact-based evolutionary relationships among tetrapod vertebrates (*right*), in contrast to the initial view based on the stretching of nature's ladder over evolutionary time (*left*). Mammals (the modern therapsids) and reptiles (the modern sauropsids, which include birds) are sister groups. Mammals could therefore never have descended from reptiles.

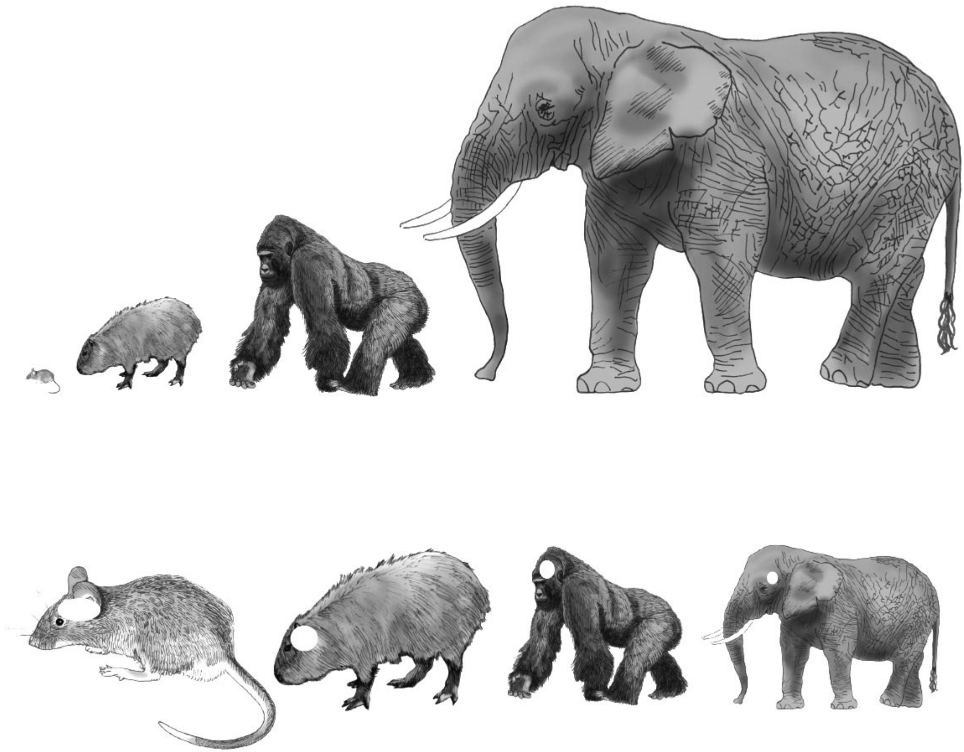


Figure 1.5

Larger animals usually have larger brains: a rat brain, at 2 grams (about 1/14 ounce), is much smaller than a capybara brain (75 grams; about 3 ounces), which is smaller than a gorilla brain (about 500 grams or 1.l pounds), which in turn is much smaller than an elephant brain (4,000–5,000 grams or 9–11 pounds). However, the relative size of the brain, that is, the fraction of body mass that it occupies, is smaller in larger animals, which becomes evident when these animals are drawn as if they had the same body size (*lower row*).

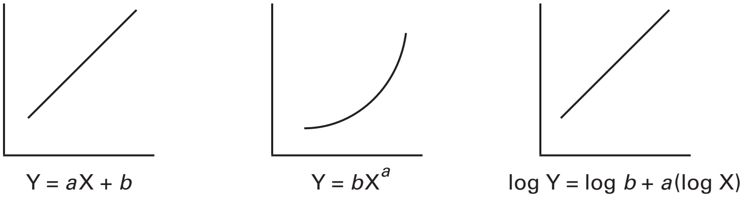


Figure 1.6

Linear function plotted on a linear scale (*left*), power function (where the allometric exponent $a > 1$) plotted on a linear scale (*center*), and relationship between log-transformed values plotted on a linear scale (*right*), which turns the power function into a linear function, much easier to calculate in the days before digital computers. In allometric functions, X is body mass, and Y is typically the mass, volume, or surface area of a body part.

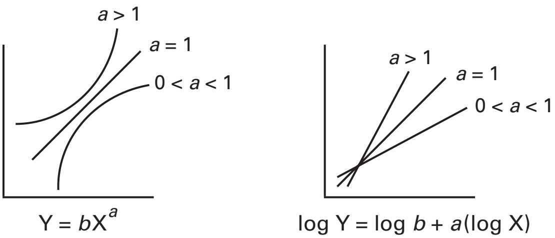


Figure 1.7

Power laws when plotted directly on a linear scale (*left*) and when plotted as the log-transformed values of X and Y on a linear scale (*right*), depending on the allometric exponent a of the function. When $a > 1$, Y increases faster than X (body mass), as with bone mass; when $a = 1$, Y increases proportionately to X, as with blood volume; and when $0 < a < 1$, Y still increases with X, but more slowly, as with brain mass.

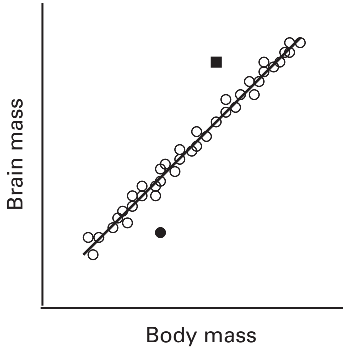


Figure 1.8

Plotted line is the allometric function brain mass = $b \times$ body mass^{a}, calculated for the data points shown, where each point represents one mammalian species. The line illustrates the predicted brain mass for an animal of any given body mass; knowing that body mass allows one to predict, by simply applying the formula, how large the brain of that animal should be. Occasionally, however, a species (filled circle) is found to have a much smaller brain, and another (filled square) is found to have a much larger brain, than it "should." Of course, whether a species with a larger-than-expected brain has a brain too large for its body or a body too small for its brain is a whole other issue.

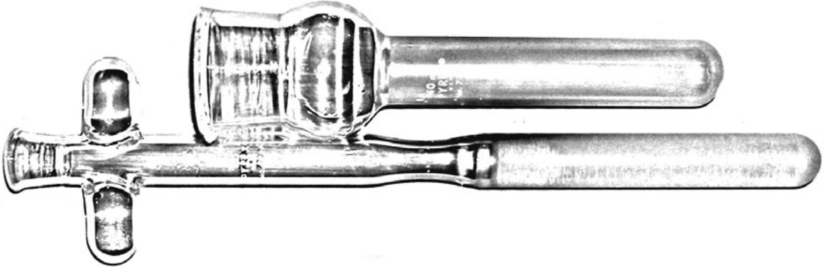


Figure 2.1

Glass tissue grinder, used like a cylindrical mortar and pestle to homogenize brain tissue.

Figure 3.1

Capybara (*Hydrochoerus hydrochoerus*), the largest rodent species (left), and agouti (*Dasyprocta primnolopha*), the fourth-largest rodent species (right).

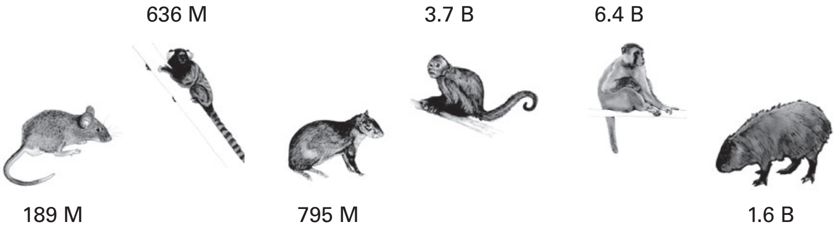


Figure 4.1

Rat, marmoset, agouti, owl monkey, rhesus monkey and capybara lined up by brain mass. The two monkey species have more neurons than the capybara, despite their smaller brains. Numbers of neurons are indicated (M, million; B, billion).

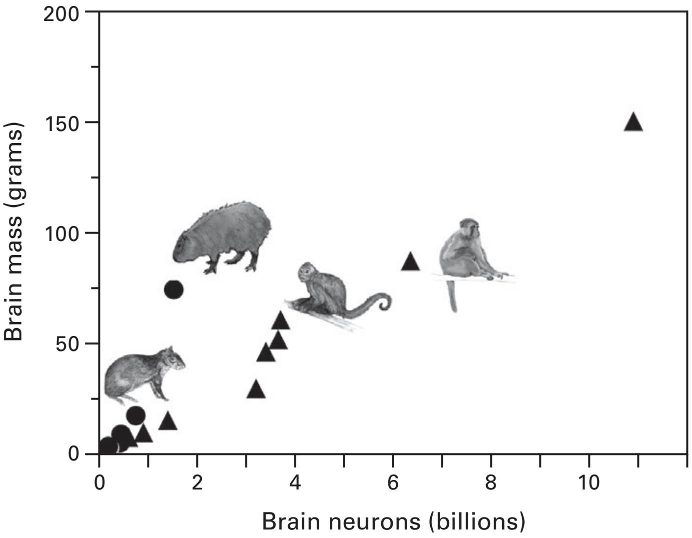


Figure 4.2

Linear plot shows what could still be a single relationship between brain mass and the number of neurons in the brain across rodents (circles) and primates (triangles), making the capybara appear to be an outlier.

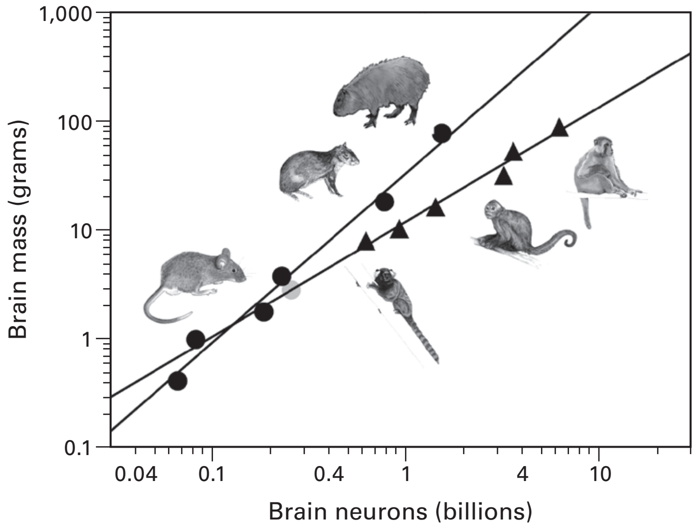


Figure 4.3
Double-log plot shows that different relationships exist between brain mass and the number of neurons in the brain for rodents (circles) and primates (triangles). The lines indicate the power laws that best describe the variation in brain mass as functions of numbers of neurons in the brain of rodents and primates, separately, with exponents of +1.6 in rodents and +1.0 in primates. Now the capybara no longer appears to be an outlier: it has the brain mass predicted for a rodent brain with its number of neurons.

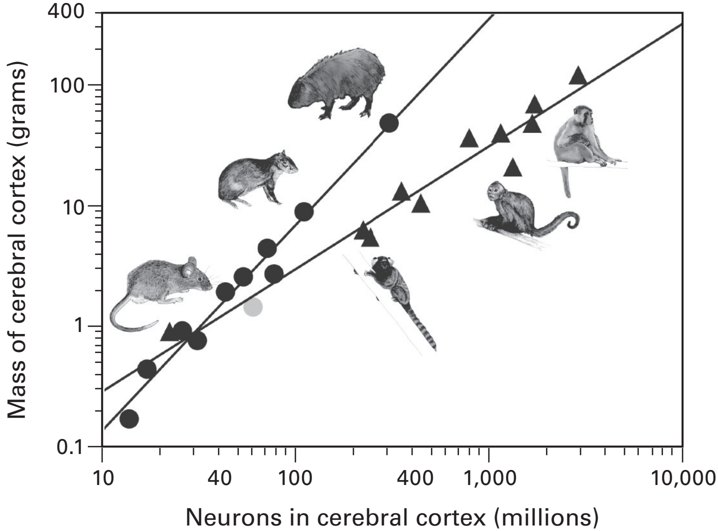


Figure 4.4

The cerebral cortex scales differently in mass between rodents (circles) and primates (triangles) as it gains neurons. The lines indicate the power laws that best describe the variation in cortical mass as functions of numbers of neurons in the cerebral cortex of rodents (exponent, +1.7) and primates (exponent, +1.0), separately. The larger the cerebral cortex, the larger the discrepancy in number of neurons found in primate and rodent species, with more and more neurons in primate than in rodent cortices.

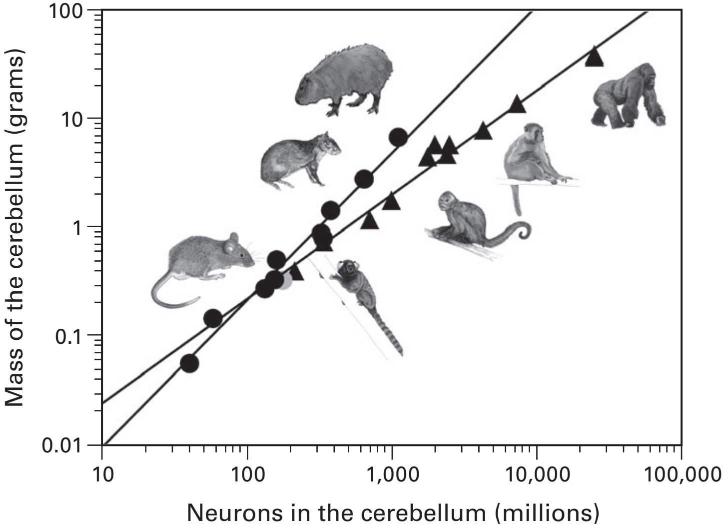


Figure 4.5

The cerebellum also scales differently in mass between rodents (circles) and primates (triangles) as it gains neurons. The lines indicate the power laws that best describe the variation in cerebellar mass as functions of numbers of neurons in the brain of rodents (exponent, +1.3) and primates (exponent, +1.0), separately. The larger the cerebellum, the larger the discrepancy in number of neurons found in primate and rodent species, with more and more neurons in primate than in rodent cerebellums.

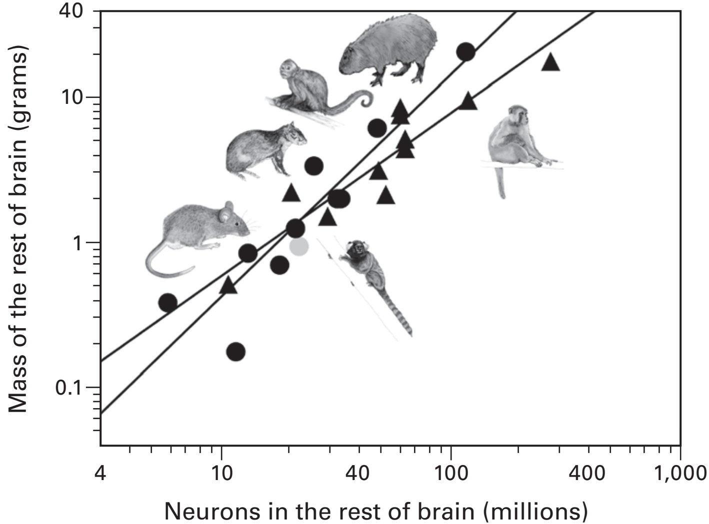


Figure 4.6

The rest of brain, in contrast to the cerebral cortex and cerebellum, initially appeared to scale fairly similarly in mass between rodents (circles) and primates (triangles) as it gains neurons. The lines indicate the power laws that best describe the variation in rest of brain mass as functions of numbers of neurons in the brain of rodents (exponent, +1.6) and primates (exponent, +1.1), separately. Although the exponents are nominally different, there is significant overlap between rodents and primates.

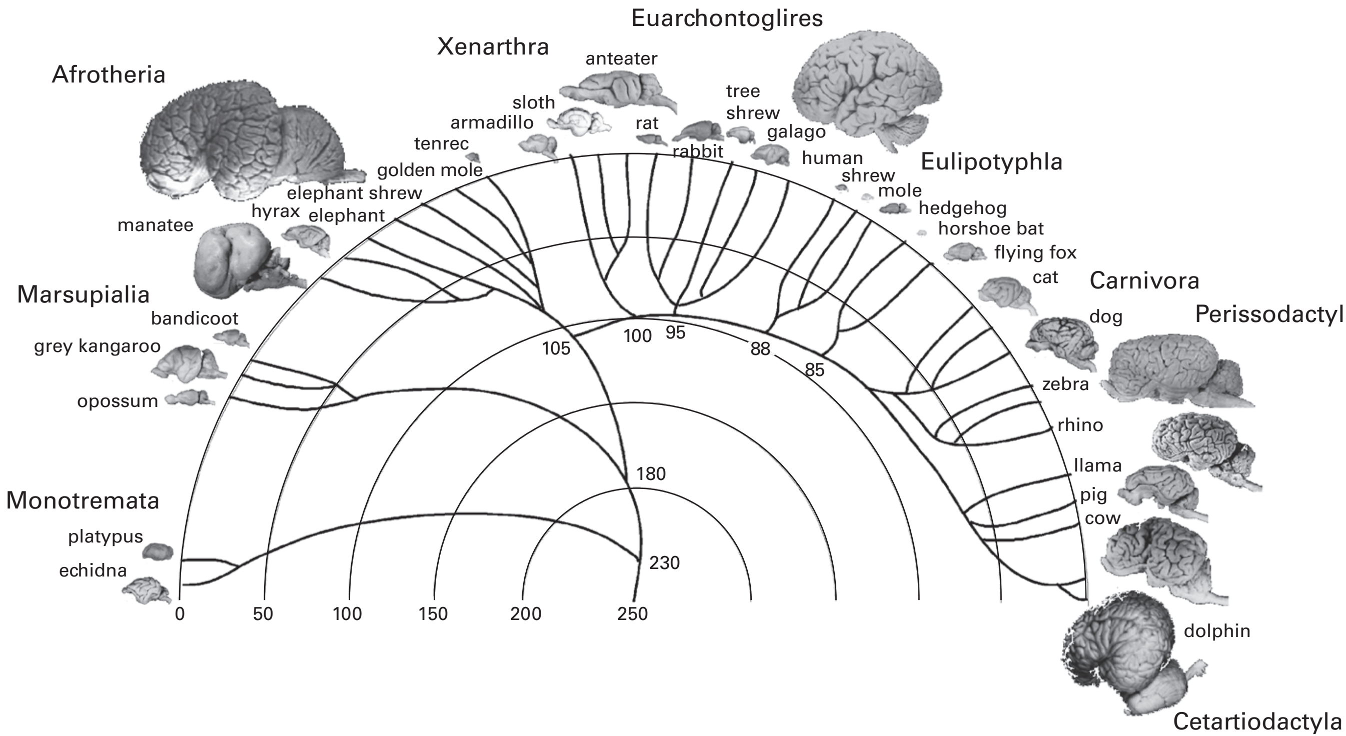


Figure 4.7

Consensus tree of the genealogical or evolutionary relationships among living mammalian species (dates are in millions of years ago). Rodents and primates are different branches of the same group, Euarchontoglires—and yet, different neuronal scaling rules apply to their cerebral cortex and cerebellum. Figure taken, with permission, from Herculano-Houzel, 2012.

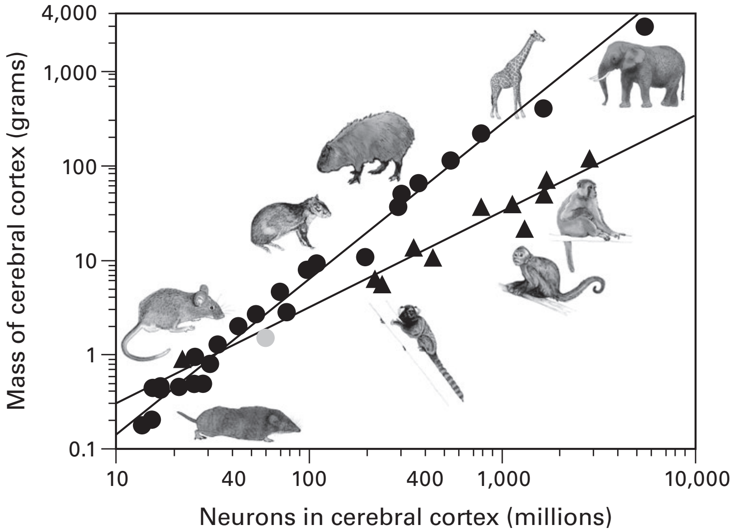


Figure 4.8
The cerebral cortex scales similarly in mass across rodents, afrotherians, eulipotyphlans, and artiodactyls (circles) as it gains neurons, but differently across primates (triangles). The lines indicate the power laws that best describe the variation in cortical mass as functions of numbers of neurons in the cortex of primates (exponent, +1.0) and of all other clades (exponent, +1.6). The larger the cerebral cortex, the larger the discrepancy in number of neurons found in primate and nonprimate cortices of similar mass, with more and more neurons in the cortices of primates than in those of nonprimates.

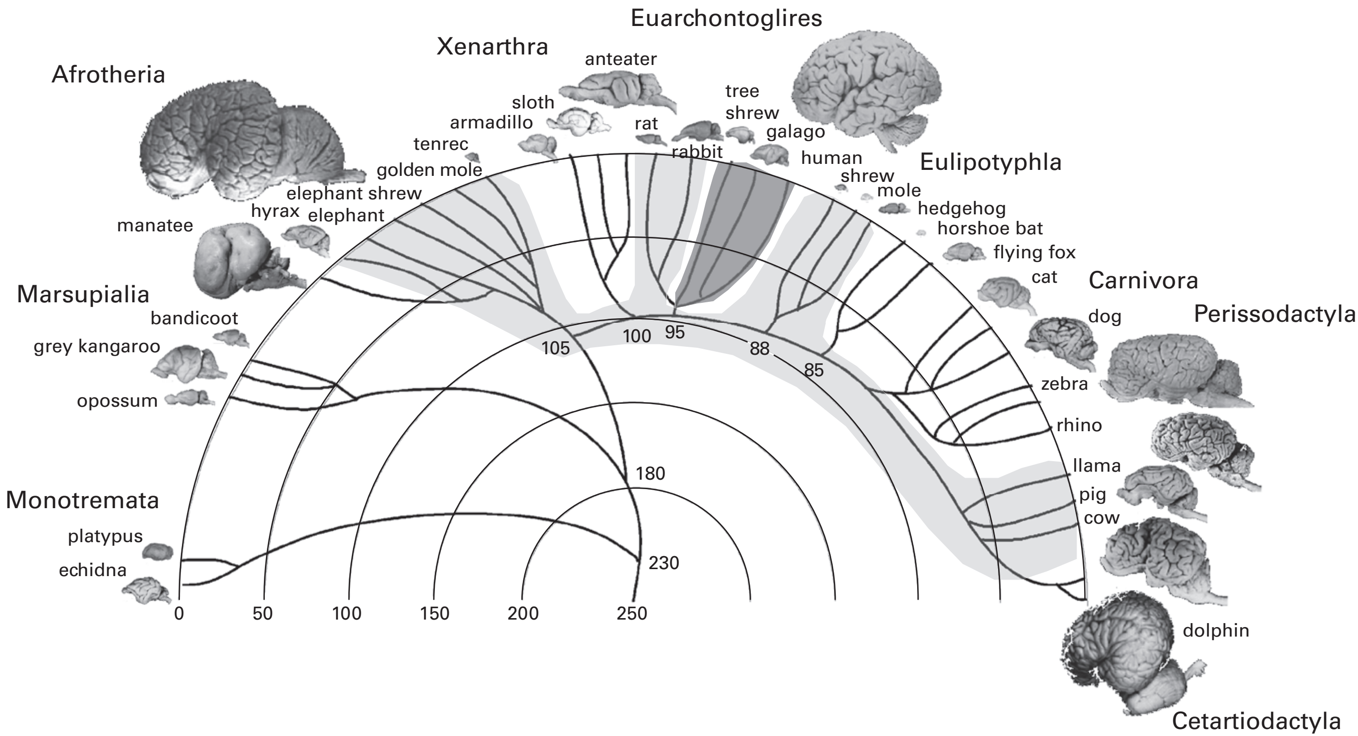


Figure 4.9

Proposed scheme for the evolution of the scaling of the cerebral cortical mass with increasing numbers of neurons: the neuronal scaling rules that apply to modern afrotherians, rodents, eulipotyphlans, and artiodactyls are presumed to already have applied to their common ancestor, to have been maintained in the evolution of these lineages, but to have changed in the divergence of the animals that later were found to have given rise to primates.

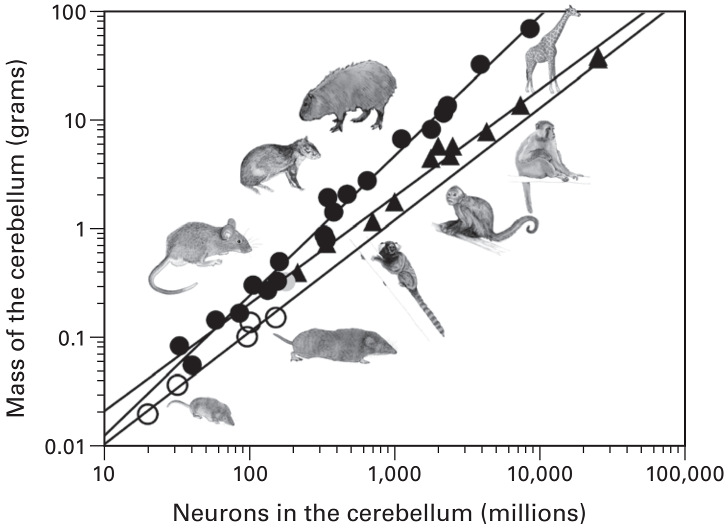


Figure 4.10
The cerebellum scales similarly in mass across rodents, afrotherians, and artiodactyls (filled circles) as it gains neurons, but differently across primates (triangles) and eulipotyphlans (open circles) as these gain neurons in the cerebellum. The lines indicate the power laws that best describe the variation in cortical mass as functions of numbers of neurons in the cortex of primates (exponent, +1.0), eulipotyphlans (exponent, also +1.0, but with a vertical offset in the graph), and all other clades (exponent, +1.3). The numbers of cerebellar neurons found in eulipotyphlans, though comparable to those found in small rodents and afrotherians, are packed into smaller volumes.

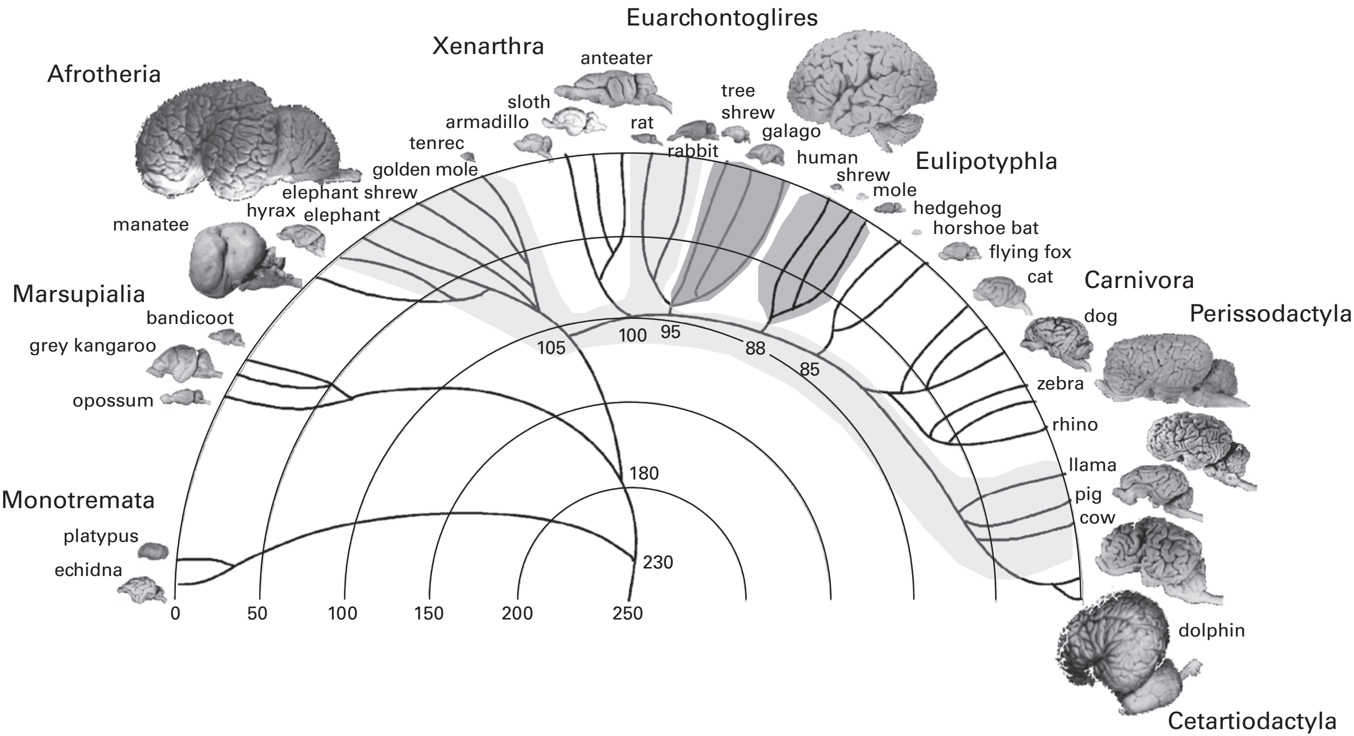


Figure 4.11

Proposed scheme for the evolution of the scaling of cerebellar mass with increasing numbers of neurons: the neuronal scaling rules that apply to modern afrotherians, rodents and artiodactyls are presumed to already have applied to their common ancestor, and to have been maintained in the evolution of these lineages, but changed twice, and separately, in the divergence of the animals that later were found to have given rise to primates and to eulipotyphlans.

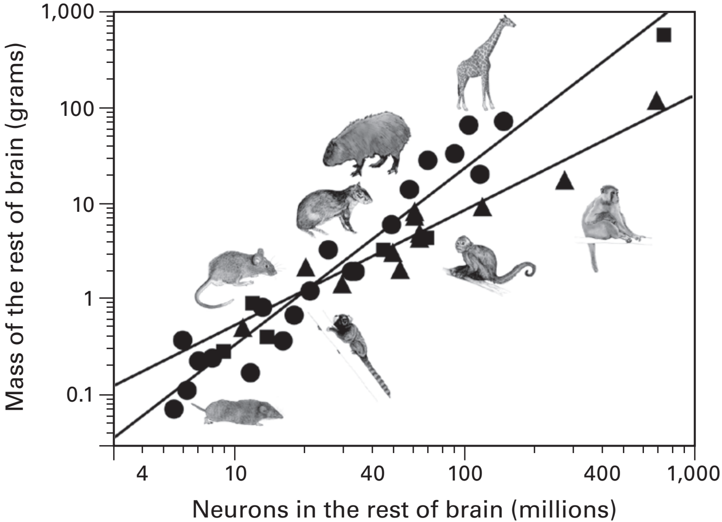


Figure 4.12

The rest of brain scales similarly in mass across afrotherians (squares), rodents, eulipotyphlans and artiodactyls (circles) as it gains neurons, but differently across primates (triangles). The lines indicate the power laws that best describe the variation in the mass of the rest of brain as functions of numbers of neurons in these structures in primates (exponent, +1.2) and all other clades (exponent, +1.9). For comparable numbers of neurons in the rest of brain, these structures are much smaller in primates than in other animals.

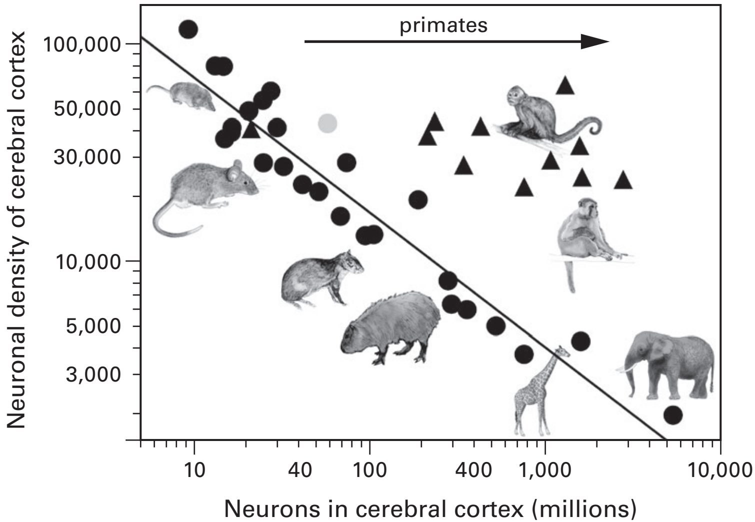


Figure 4.13

As the nonprimate cerebral cortex (circles) gains neurons, neuronal density (in neurons per milligram of cerebral cortex) drops with the number of neurons raised to the power of –0.6, which implies that the average mass of neurons increases with the number of neurons raised to the power of +0.6. In contrast, as the primate cortex (triangles) gains neurons, neuronal density does not decrease significantly. Considering that mammalian evolution started with small brains and cortices, it can be inferred that primates branched away from the common ancestor with changes that uncoupled the addition of neurons to increases in the average size of neurons in the cerebral cortex.

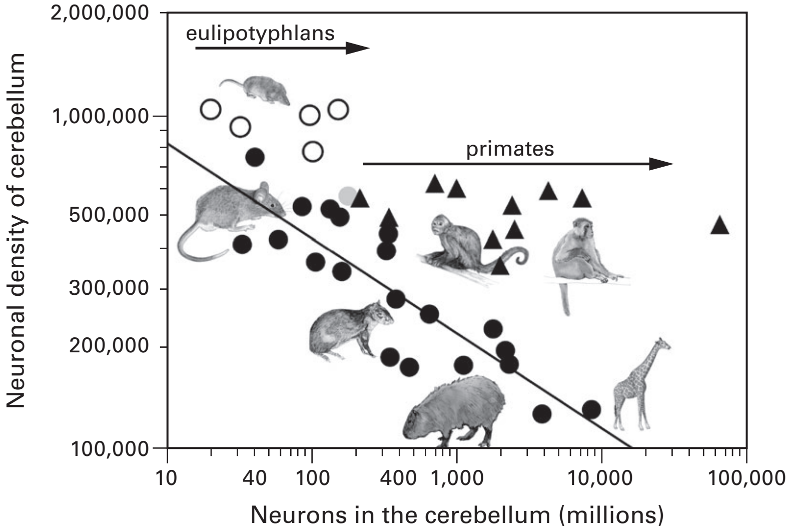


Figure 4.14

As the nonprimate, noneulipotyphlan cerebellum gains neurons (filled circles), neuronal density drops with the number of neurons raised to the power of –0.3, which implies that the average mass of neurons increases with the number of neurons raised to the power of +0.3. In contrast, as the cerebellum gains neurons across primate (triangles) and eulipotyphlan species (open circles), there is no significant decrease in neuronal density. Considering that mammalian evolution started with small brains and cortices, it can be inferred that primates and eulipotyphlans branched away from their respective ancestors with changes that uncoupled increases in the number of cerebellar neurons from increases in their average size.

Nonprimates			Primates		
398.8 g	Giraffe	1.7 B	~ 6 B	Chimpanzee	400.0 g
111.3 g	Blesbok	571 M	2.9 B	Baboon	120.2 g
68.8 g	Springbok	397 M	1.7 B	Rhesus monkey	69.8 g
42.2 g	Pig	303 M	1.6 B	Bonnet monkey	48.3 g
8.9 g	Agouti	111 M	442 M	Owl monkey	10.6 g
4.4 g	Rabbit	71 M	245 M	Marmoset	5.6 g
0.9 g	Spiny rat	26 M	22 M	Mouse lemur	0.9 g

Figure 4.15

Cortical mass (in grams) and number of neurons (in millions, M, or billions, B) in different nonprimate and primate species, according to our estimates.

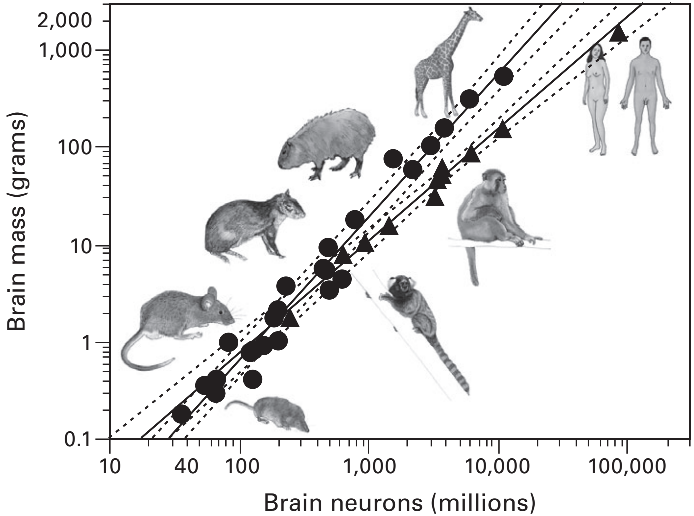


Figure 5.1

The human brain has the relationship between brain size (mass) and number of neurons that would be expected for a generic primate. The power function plotted for nonprimates (circles) has an exponent of 1.5, whereas the power function plotted for primates (triangles), excluding the human species, has an exponent of 1.1. The dashed lines indicate the 95 percent confidence intervals for each function—and the fact that the human species is well contained within that interval for primates indicates that it obeys the same neuronal scaling rule that applies to other primate species.

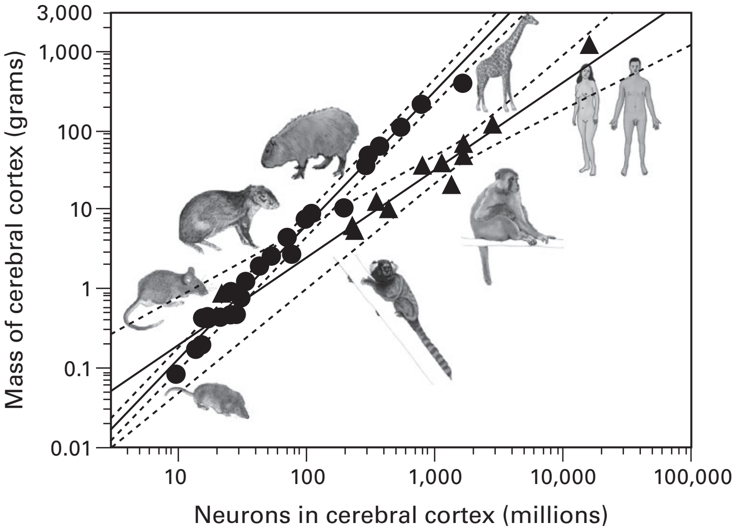


Figure 5.2
The human cerebral cortex has the mass expected for a generic primate with its number of neurons (or the number of neurons expected for its mass). The power function plotted for nonprimates (circles) has an exponent of 1.6, whereas the power function plotted for primates (triangles), excluding the human species, has an exponent of 1.1. The dashed lines indicate the 95 percent confidence intervals for each function—and the fact that the human species is well contained within that interval for primates indicates that its cerebral cortex is made according to the same neuronal scaling rule that applies to the cortex of other primate species.

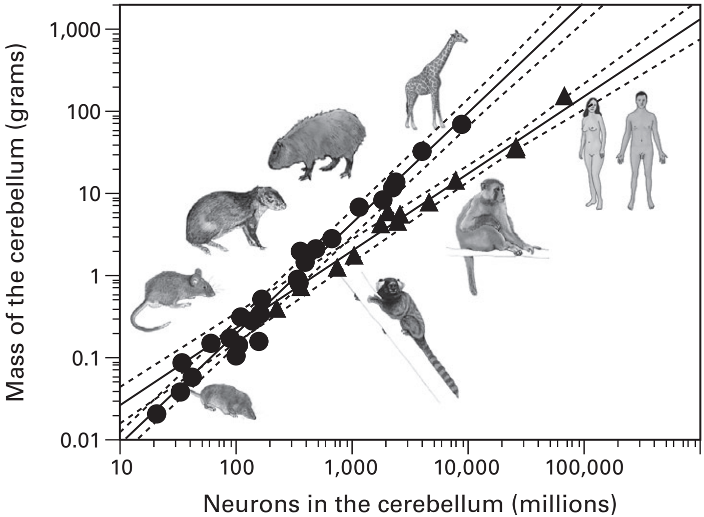


Figure 5.3

The human cerebellum has the mass expected for a generic primate with its number of neurons (or the number of neurons expected for its mass). The power function plotted for nonprimates (circles) has an exponent of 1.3, whereas the power function plotted for primates (triangles), excluding the human species, has an exponent of 1.0. The dashed lines indicate the 95 percent confidence intervals for each function—and the fact that the human species is well contained within that interval for primates indicates that its cerebellum is made according to the same neuronal scaling rule that applies to the cerebellum of other primate species.

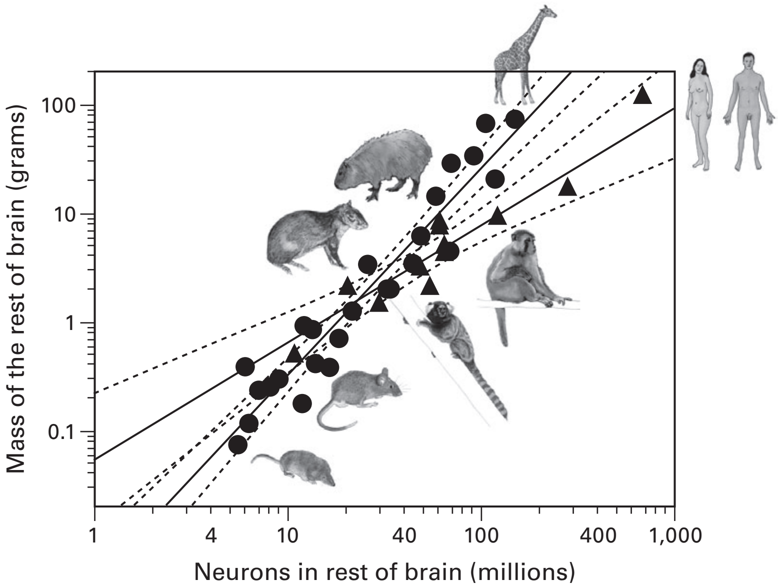


Figure 5.4

Human rest of brain has the mass expected for a generic primate with its number of neurons (or the number of neurons expected for its mass). The power function plotted for nonprimate species (filled circles) has an exponent of 1.9, which excludes primates (triangles), whereas the power function plotted for primates, excluding the human species, has an exponent of 1.2. The dashed lines indicate the 95 percent confidence intervals for each function—and the fact that the human species is well contained within that interval for primates indicates that its rest of brain is made according to the same neuronal scaling rule that applies to the rest of brain of other primate species.

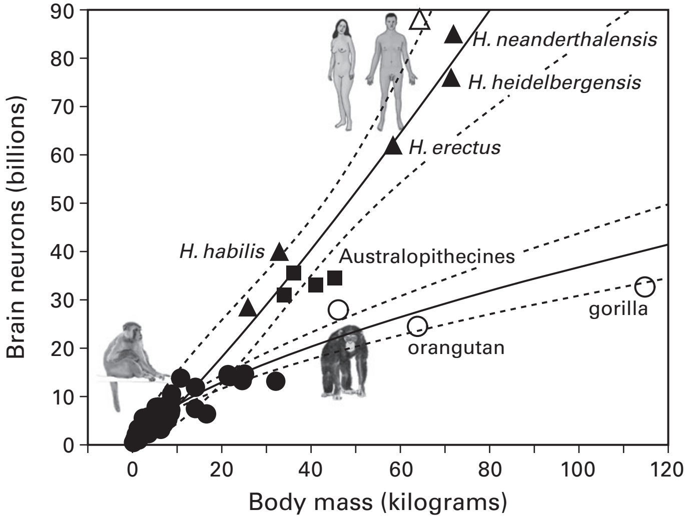


Figure 5.5

Numbers of brain neurons predicted in living and extinct primate species from the neuronal scaling rules that apply to nonhuman, non–great ape primates. *Sahelanthropus tchadensis* (not shown, for its body mass is unknown) is predicted to have had slightly fewer neurons than living great apes. The upper function is plotted exclusively for *Homo* (triangles) and its australopithecine ancestors (squares), but it predicts the number of brain neurons and body mass for most non-great ape primates; the lower function is plotted exclusively for living nonhuman primate species, including great apes (open circles), and it excludes humans. Thus, whether or not modern humans fit the scaling rules for other modern primates depends on whether or not great apes are included in the comparison—a clear sign that great apes might be the outliers themselves.

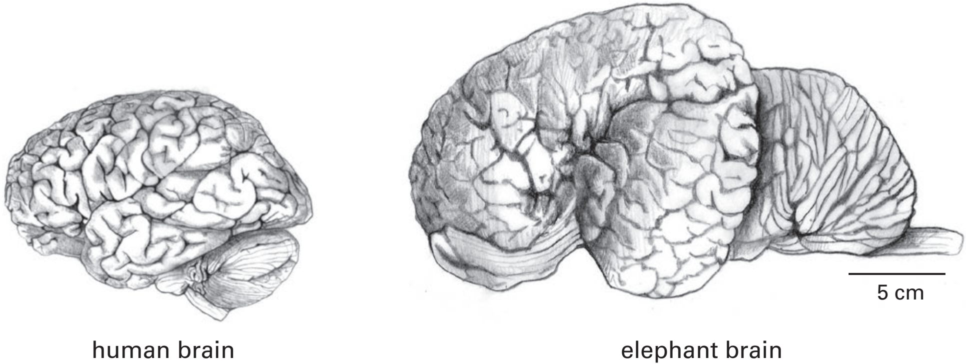


Figure 6.1
Side-by-side view of human and African elephant brains.

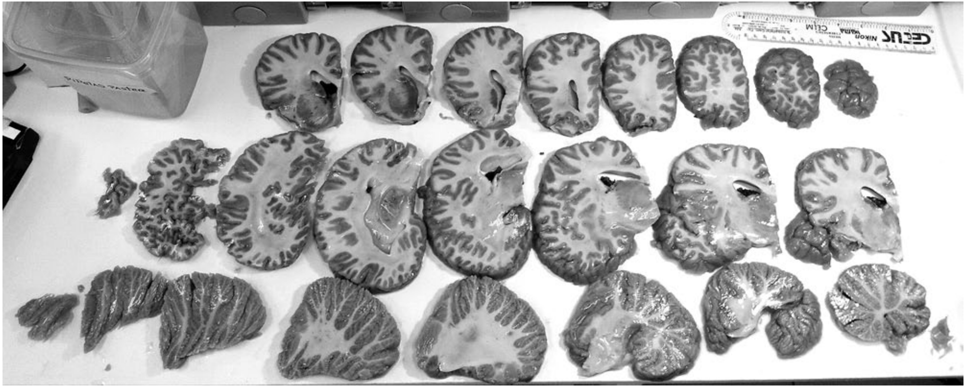


Figure 6.2

Right hemisphere of the brain of an African elephant cut into sixteen sections (top two rows; the front of the brain is at the top right), and its right cerebellum cut into eight sections (bottom row; the medial part of the cerebellum is to the right). This is a truly large brain: the ruler at the top of the image measures 15 centimeters (6 inches). The gray and white matter of the cerebral cortex and of the cerebellum are clearly distinguishable in the sections.

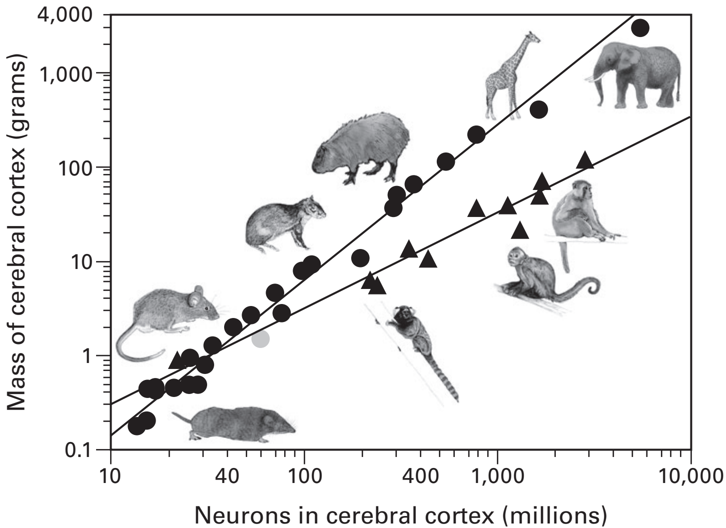


Figure 6.3

The cerebral cortex of the African elephant fits the neuronal scaling rules that apply to nonprimates: its 5.6 billion neurons are very close to the number of neurons predicted for a cortex of its mass.

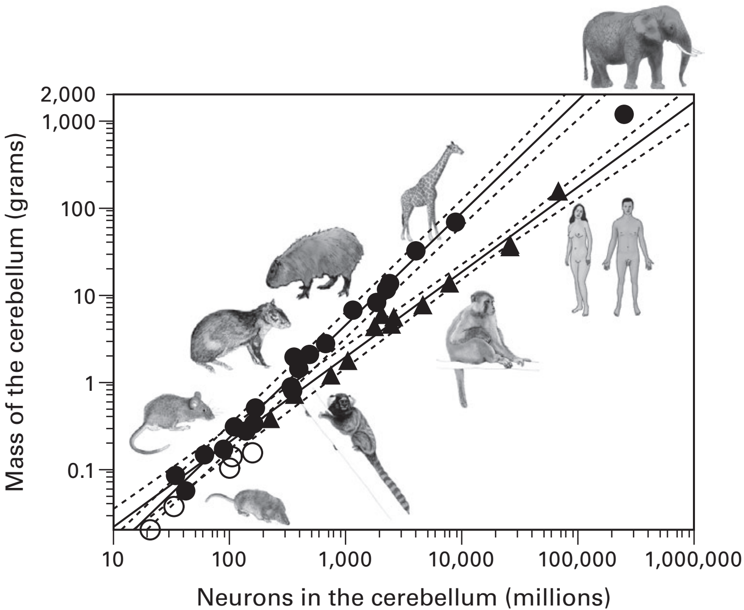
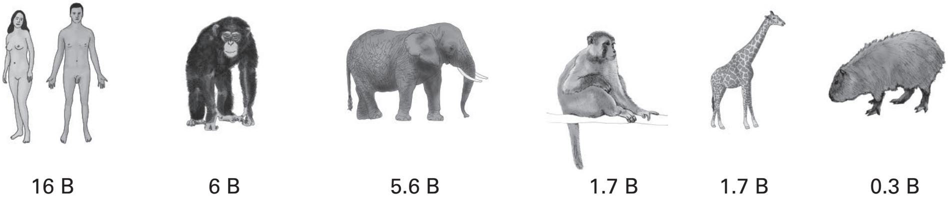


Figure 6.4

The cerebellum of the African elephant has many more neurons than expected for its mass according to the scaling rules that apply to other afrotherians as well as to rodents and artiodactyls (filled circles), nearing (but not quite reaching) the scaling rules that apply to the primate cerebellum.


16 B
6 B
5.6 B
1.7 B
1.7 B
0.3 B

4.6 kg 1.5 kg 700 g 400 g 87 g 75 g

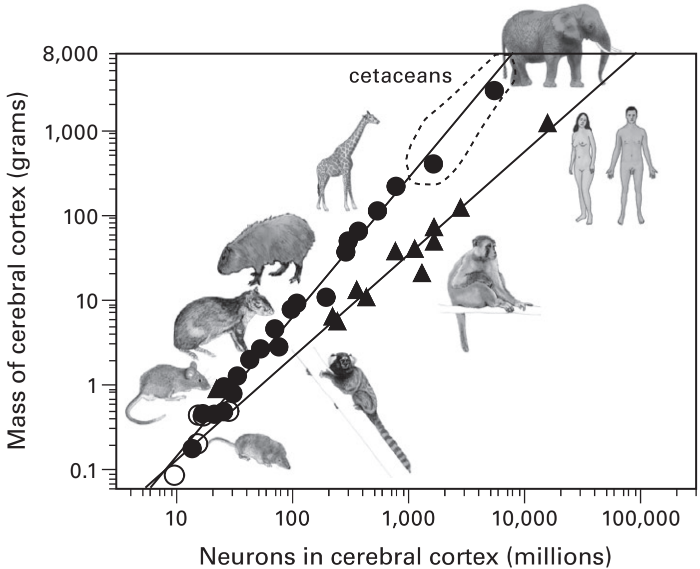


Figure 6.5

The cetacean cerebral cortex (values within dashed oval) is expected to share the neuronal scaling rules that apply to the closely related artiodactyls and to the more distant rodents, afrotherians, and eulipotyphlans (circles), and thus to hold a smaller number of neurons than a smaller primate cortex such as the human.

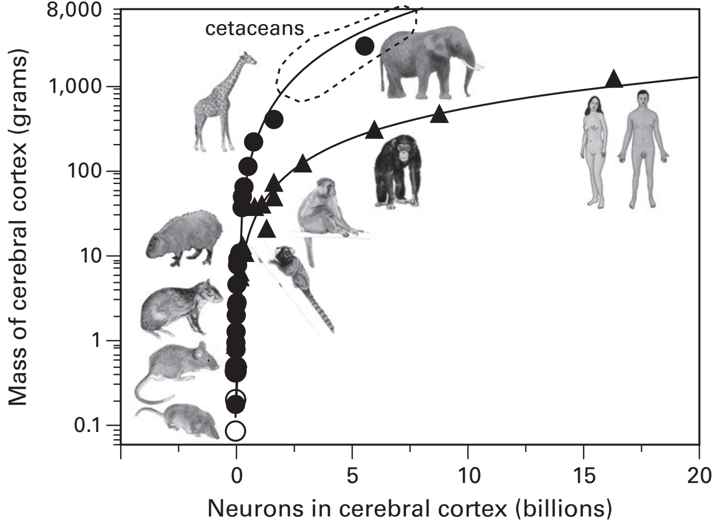


Figure 6.6

Same data as in figure 6.5 plotted on a semilog scale to make it easier to appreciate the distance between the number of neurons in the cerebral cortex of humans and in that of other mammals. Cetaceans (values within dashed oval), the African elephant, and great apes are estimated to share the same range of numbers of neurons in the cerebral cortex—between 3 and 9 billion neurons—which is well beyond the number contained in the cortex of other, smaller mammalian species, but still far fewer than found in the cerebral cortex of humans.

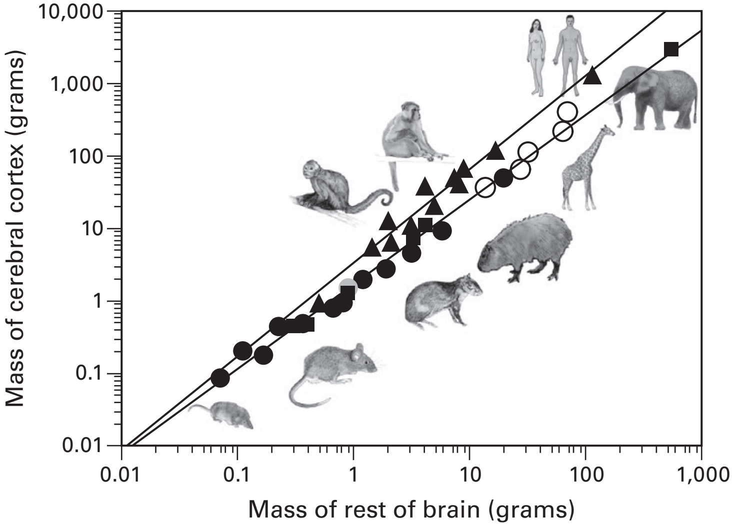


Figure 7.1

The mass of the cerebral cortex increases faster than the rest of brain in all mammals, but particularly faster in primates (exponent, 1.3; triangles) than in other species (exponent, 1.2). Additionally, for a similar mass in the rest of brain, primates (triangles) have a larger cerebral cortex than nonprimates (rodents and eulipotyphlans, filled circles; artiodactyls, open circles; afrotherians, squares). The human cerebral cortex has the mass predicted to accompany the mass of its rest of brain for a primate.

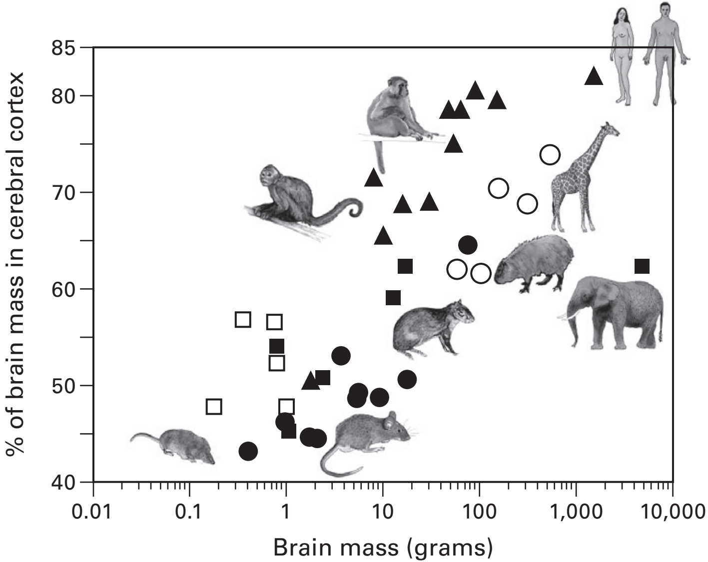


Figure 7.2

Larger brains have relatively larger cortices, but the relative mass of the cerebral cortex is different across mammalian groups. The cortex is relatively larger in eulipotyphlans (open squares) than in afrotherians (filled squares) and rodents (filled circles) of similar brain mass, and larger in primates (triangles) than in artiodactyls (open circles) and rodents of similar brain mass. The relative mass of the cerebral cortex is largest in humans than in all other species in our dataset.

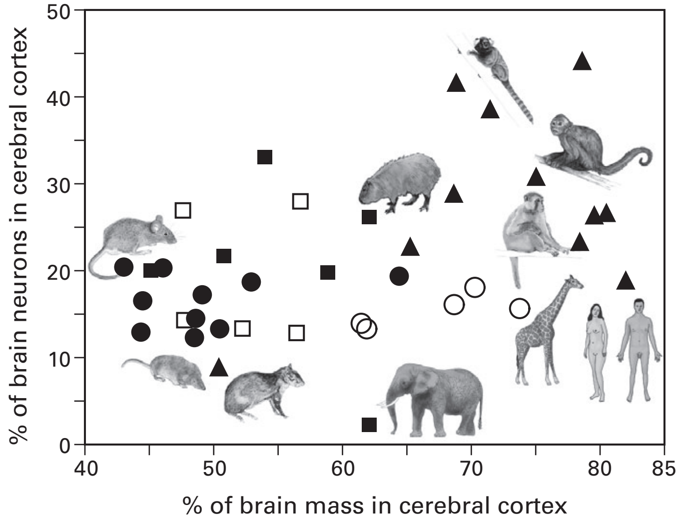


Figure 7.3

Relatively larger cortices do not concentrate relatively more of all brain neurons. There is a fair amount of variation, but in most species, the cerebral cortex holds 15–25 percent of all brain neurons, regardless of its relative mass, in eulipotyphlans (open squares), afrotherians (filled squares), rodents (filled circles), artiodactyls (open circles) and primates (triangles) alike. The main exception is the African elephant, whose cerebral cortex holds only 2 percent of all brain neurons.

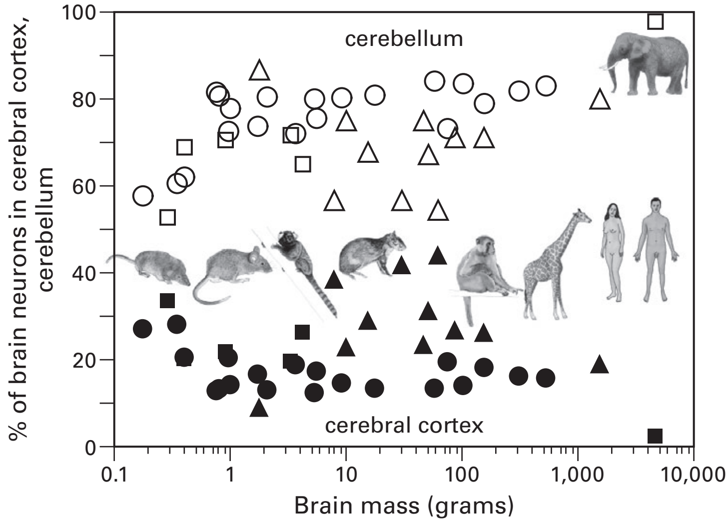


Figure 7.4

The cerebellum (open symbols) holds around 80 percent of all brain neurons in most mammalian species, while the cerebral cortex (filled symbols) holds 15–20 percent of all brain neurons in eulipotyphlans, rodents, and artiodactyls (circles); afrotherians (squares; except for the elephant); and primates (triangles). The main outlier is the elephant, whose cerebral cortex holds only 2.2 percent of all brain neurons, with 97.5 percent of all brain neurons in the cerebellum and only 0.3 percent in the rest of brain.

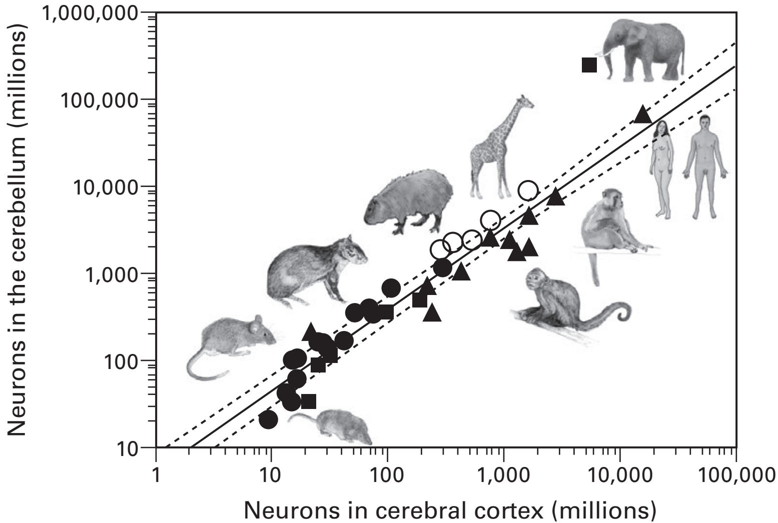


Figure 7.5

Cerebellum and cerebral cortex gain neurons proportionately, with, on average, four neurons added to the cerebellum for every neuron added to the cerebral cortex across mammalian species. The obvious exception is the African elephant, which has more than ten times the number of neurons in its cerebellum than predicted for the number of neurons in its cerebral cortex.

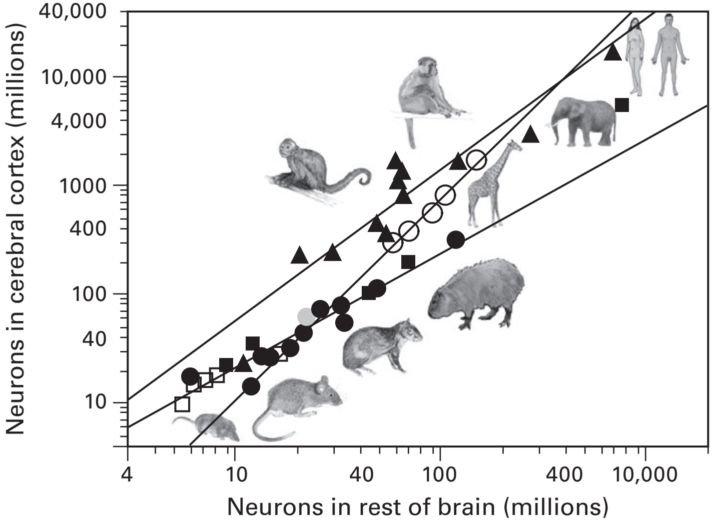


Figure 7.6

Number of neurons in the cerebral cortex scales linearly with the number of neurons in the rest of brain across eulipotyphlans (open squares), afrotherians (filled squares, excluding the African elephant), and rodents (filled circles), but it scales with the number of neurons in the rest of brain raised to the power of 1.9 in artiodactyls (open circles) and to the power of 1.4 in primates (triangles). Thus, both primates and artiodactyls gain cortical power of information processing faster than they gain neurons in the rest of brain to convey information to be processed.

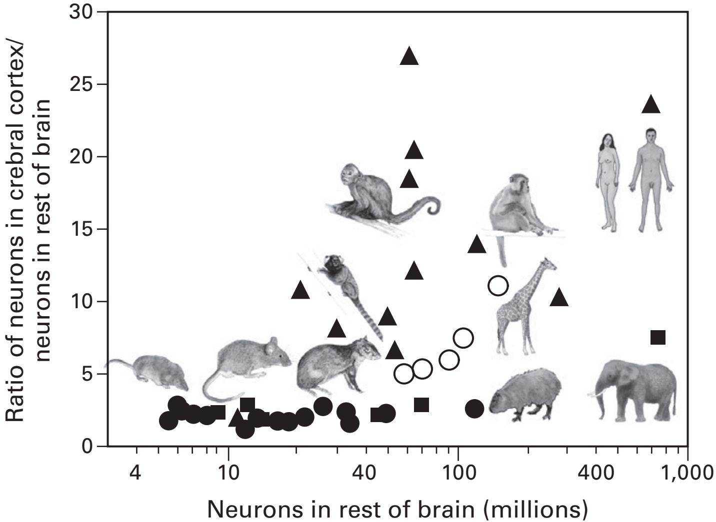


Figure 7.7

There are on average two neurons in the cerebral cortex for every neuron in the rest of brain in eulipotyphlans (filled circles), afrotherians (squares, excluding the African elephant), and rodents (filled circles), but between 5 and 11 cortical neurons for every neuron in the rest of brain of artiodactyls (open circles) and between 2 and 27 in primates (triangles). The human brain has 24 neurons in its cerebral cortex for every neuron in its rest of brain, although the maximal ratio is found in the bonnet monkey brain.

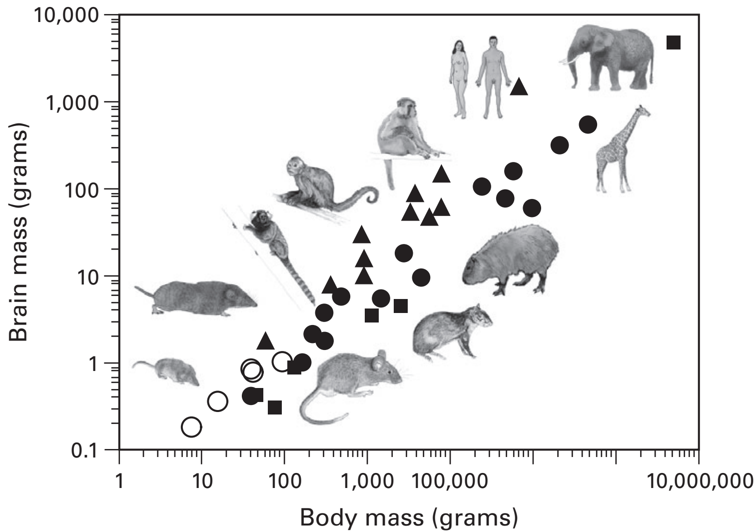


Figure 8.1

Larger body mass is loosely correlated with larger brain mass across mammalian species, but different scaling rules apply to different mammalian orders. For a similar body mass, eulipotyphlans (open circles) have larger brains than afrotherians (squares), and primates (triangles) have larger brains than both rodents and artiodactyls of similar body mass (filled circles). The respective power functions can be found in the appendix.

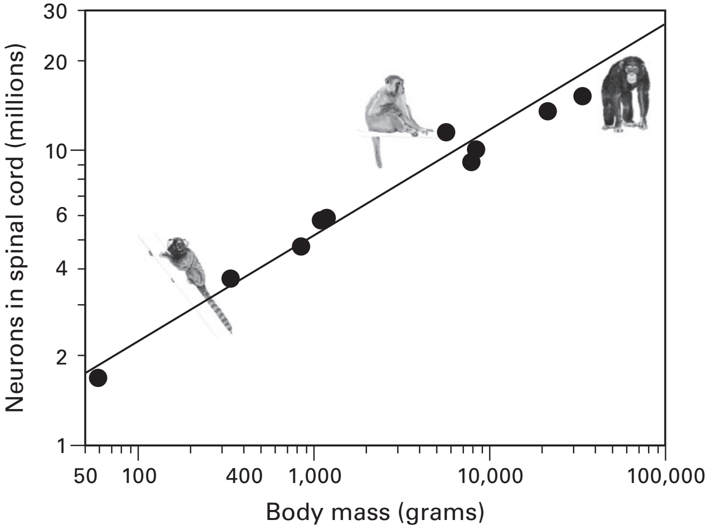


Figure 8.2

Number of neurons in the spinal cord scales with body mass raised to the power of +0.36 across primate species. The number of neurons expected for the chimpanzee spinal cord is indicated on the same graph. Whereas body mass of the species examined varies by a factor of nearly 1,000, the number of neurons in the spinal cord varies by a factor of only 10.

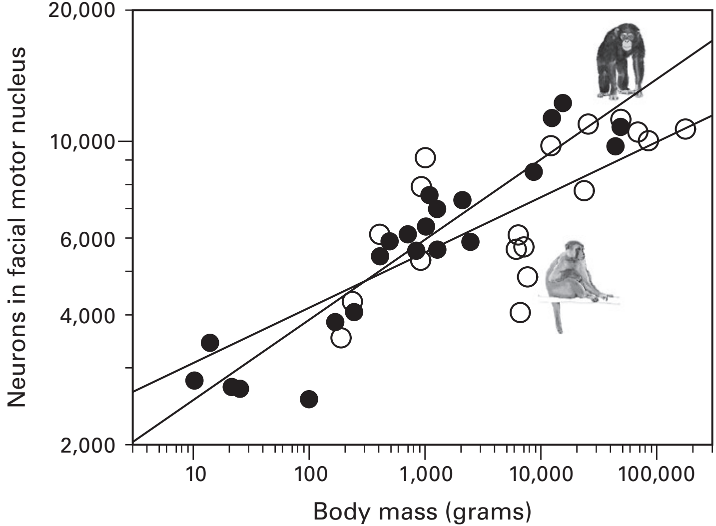


Figure 8.3

Number of motor neurons in the brain's facial motor nucleus, which controls the movements of the face, scales with body mass raised to the power of +0.18 across marsupials (filled circles) and the power of +0.13 across primate species (open circles). For a similar body mass, the facial movements of marsupials and primates are controlled by similar numbers of motor neurons—and quite few of them.

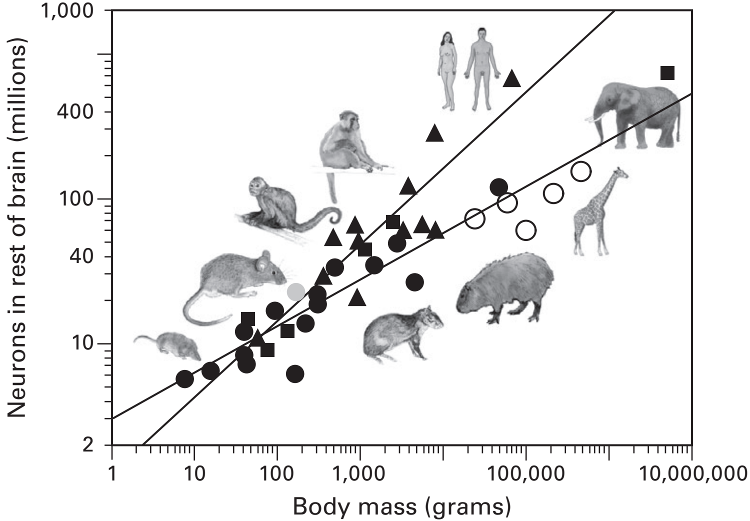


Figure 8.4

Number of neurons in the rest of brain scales with body mass raised to the power of +0.5 across primate species (triangles), but to the smaller power of +0.3 across all other species (afrotherians, squares; eulipotyphlans and rodents, filled circles; artiodactyls, open circles). For a similar body mass, primates have more neurons in the rest of brain structures than nonprimates. The number of neurons in the human rest of brain matches the number expected for a generic primate of its body mass.

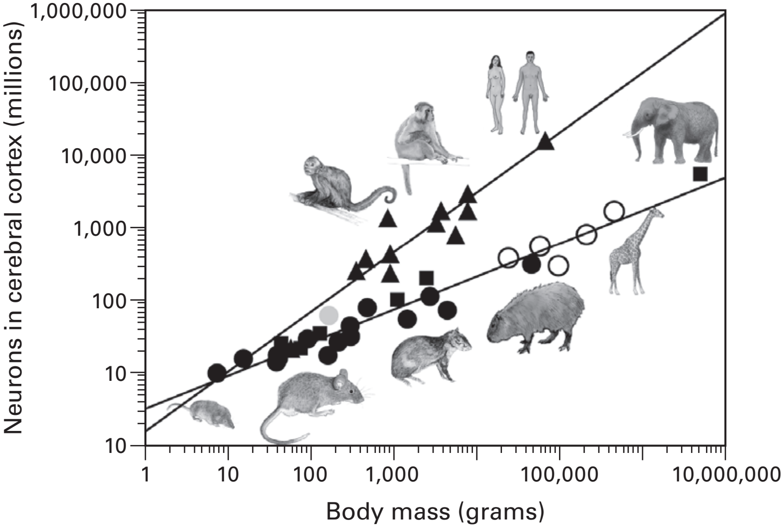


Figure 8.5

Number of neurons in the cerebral cortex scales with body mass raised to the power of +0.8 across primate species (triangles), but to the smaller power of +0.5 across all other species (afrotherians, squares; eulipotyphlans and rodents, filled circles; artiodactyls, open circles). For a similar body mass, primates have more neurons in the cerebral cortex than nonprimates.

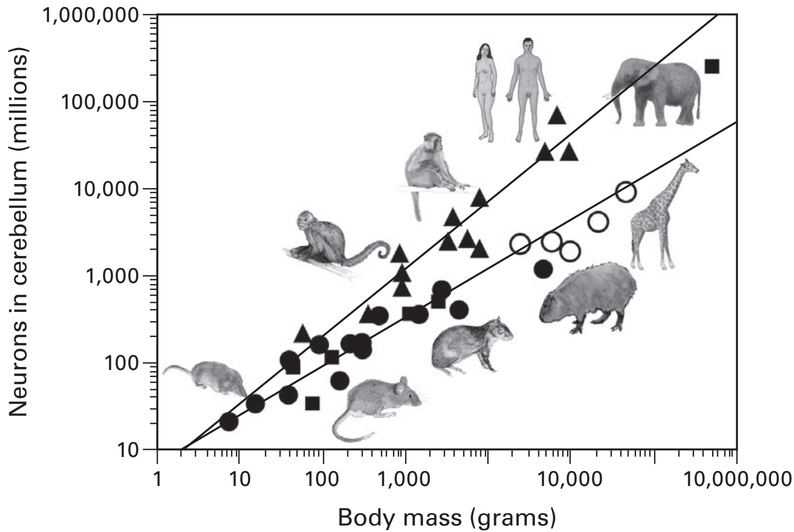


Figure 8.6

Number of neurons in the cerebellum scales with body mass raised to the power of +0.8 across primate species (triangles), but to the smaller power of +0.5 across all other species, not including the elephant, which has an extraordinarily large number of neurons in the cerebellum for its body mass (afrotherians, squares; eulipotyphlans and rodents, filled circles; artiodactyls, open circles). For a similar body mass, primates have more neurons in the cerebellum than nonprimates.

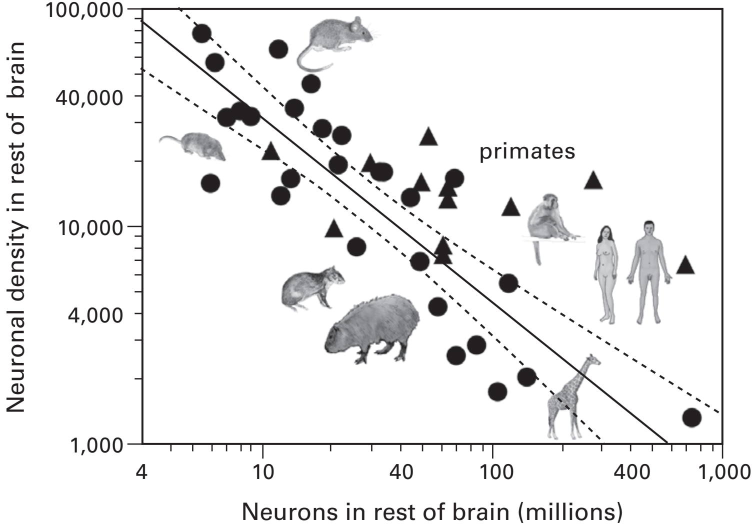


Figure 8.7

There is a strong, negative correlation between neuronal density (in neurons per milligram of rest of brain) and number of neurons in the rest of brain across nonprimate species (circles); density scales with number of neurons to the power of –0.9, which implies that the average mass of neurons in the rest of brain increases with the number of neurons raised to the power of +0.9. In contrast, neuronal density does not decrease significantly across primates (triangles), as the rest of brain gains neurons. The strikingly different neuronal densities across primates and nonprimates with similar numbers of neurons in the rest of brain mean that its neurons are much smaller in primate than in nonprimate species.

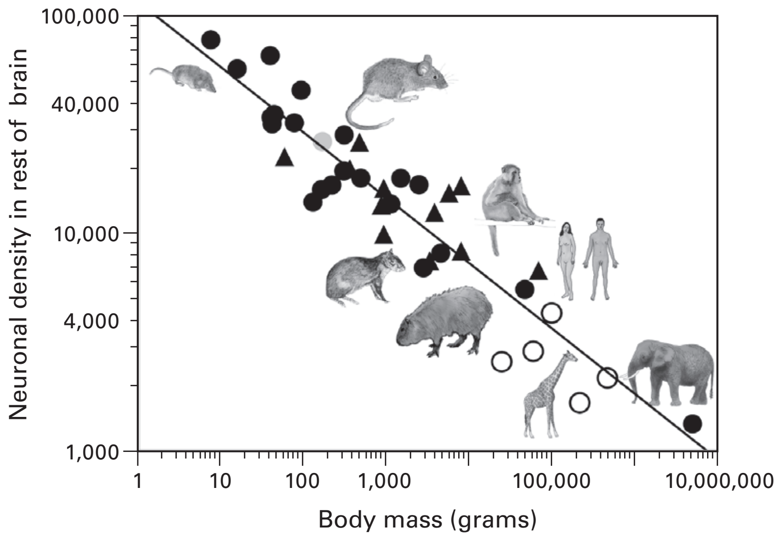


Figure 8.8

Very diverse mammalian species (artiodactyls, open circles; eulipotyphlans, afrotherians, and rodents, filled circles; primates, triangles) share a single, inverse relationship between body mass and neuronal density in the rest of brain (in neurons per milligram), which indicates that neurons in the rest of brain on average become larger with increasing body mass across all species alike. This power function has the exponent –0.30.

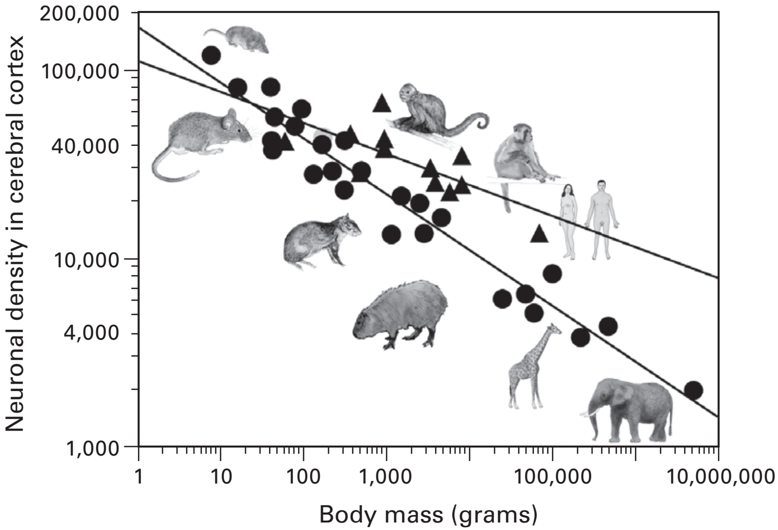


Figure 8.9

Neuronal density in the cerebral cortex (in neurons per milligram) scales with body mass across nonprimates (circles) but not across primates (triangles). Neurons in the cerebral cortex on average become larger as a power function of increasing body mass with the exponent –0.29 across nonprimates.

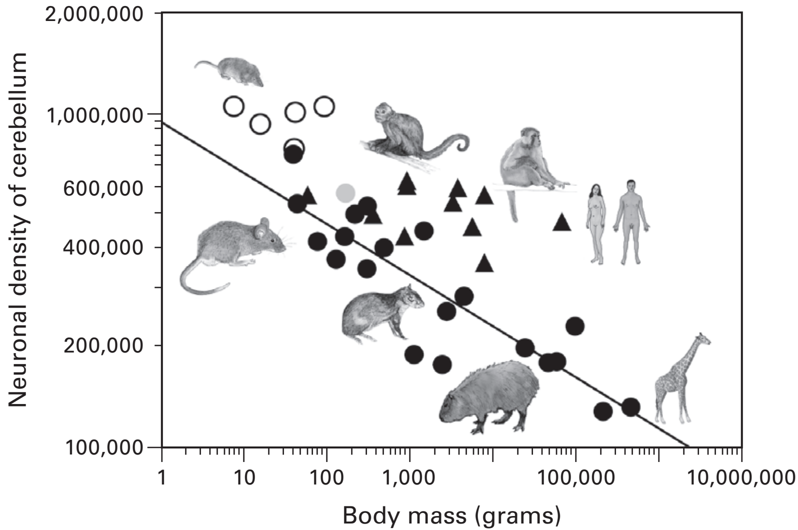


Figure 8.10

Neuronal density in the cerebellum (in neurons per milligram) also scales differently with body mass across primates (triangles), eulipotyphlans (open circles), and other species (filled circles). Neuronal density in the cerebellum of noneulipotyphlan, nonprimate species scales as a power function of increasing body mass with the exponent –0.16, but does not scale significantly in size across eulipotyphlans or primates of increasing body mass (as indicated by the lack of significant correlation between neuronal density across these species and body mass).

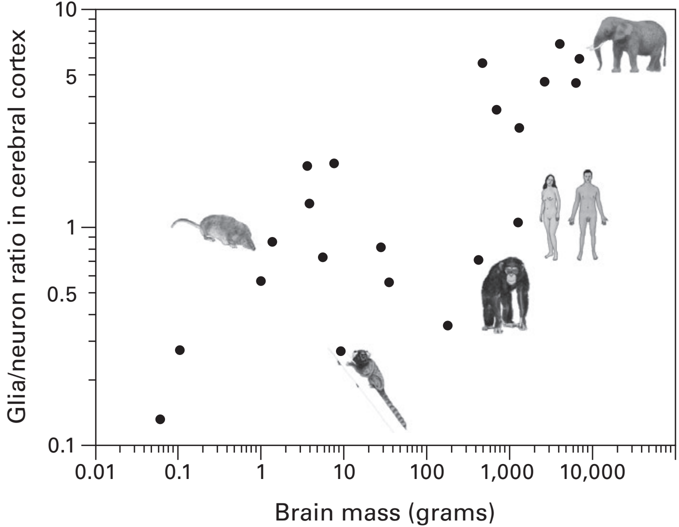


Figure 9.1

Ratio of numbers of glial to neuronal cells in the cerebral cortex seems to increase together with brain size across species as diverse as the marmoset, mole, cat, human, African elephant, and various species of whales. Data from Haug, 1987, Stolzenburg, Reichenbach, and Neumann, 1989, and Hawkins and Olszewski, 1957.

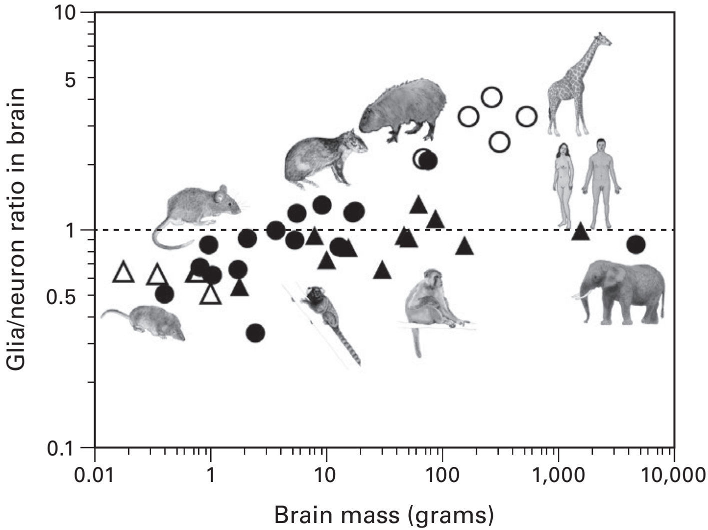


Figure 9.2
Ratio of numbers of glial to neuronal cells in the whole brain has no obvious overall correlation with brain size across species: it increases together with brain mass in rodents (filled circles), but not across eulipotyphlans (open triangles) or primates (filled triangles). The dashed line indicates a ratio of 1, below which neurons are more numerous than glial cells. Only artiodactyls (open circles) have brains consistently composed of more neurons than glial cells. Remarkably, the African elephant brain, the largest in our data set, has a glia/neuron ratio of only 0.84—that is, it has more neurons than glial cells—as do the brains of most of the species in our data set.

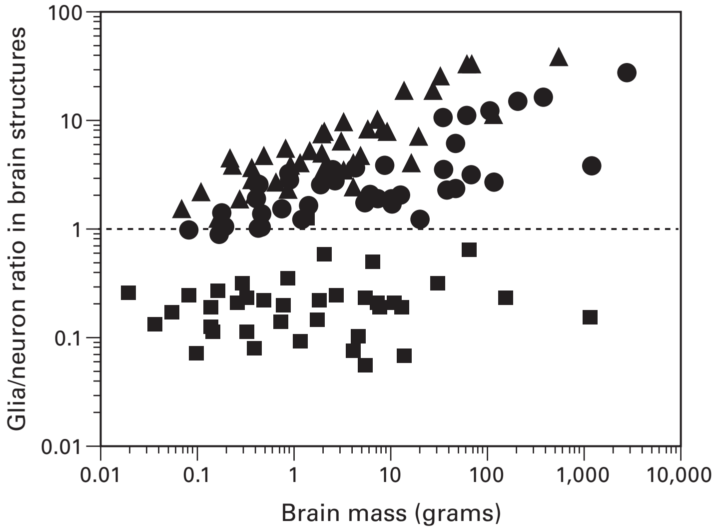


Figure 9.3

There is no universal correlation between the glia/neuron ratio in a brain structure and the mass of the structure across species: it increases in the cerebral cortex (circles) and rest of brain (triangles) in some mammalian orders, but not all, together with structure mass, but not in the cerebellum (squares). The dashed line indicates a ratio of 1, below which neurons are more numerous than glial cells. In the cerebellum, there are always more neurons than glial cells, and usually at least five times as many neurons as glial cells. In the cerebral cortex and rest of brain, in contrast, glia/neuron ratios are almost always above 1, indicating a predominance of glial cells.

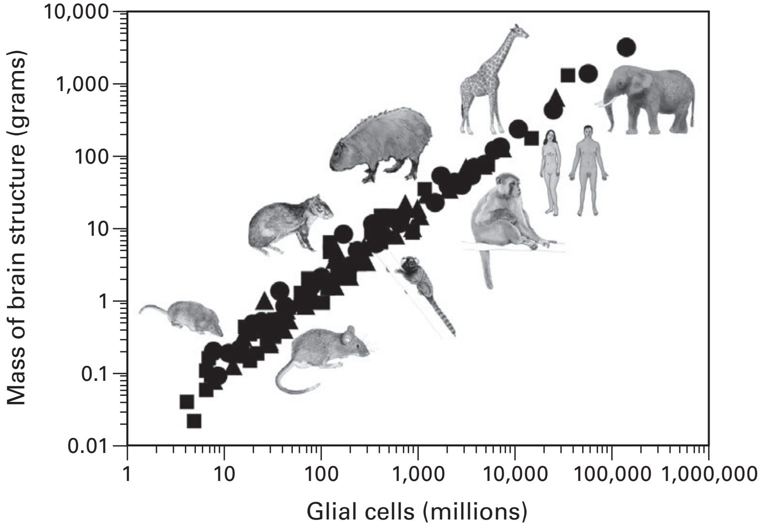


Figure 9.4

There is a universal correlation between the mass of a brain structure and its number of glial cells that applies equally across brain structures, species, and mammalian orders: it is a power function with the exponent +1.05, only slightly above linearity (not plotted).

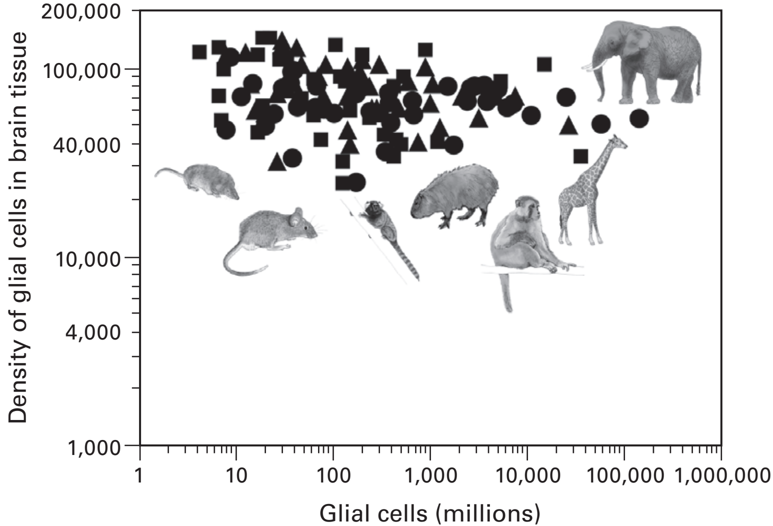


Figure 9.5
Glial cell density varies by a factor of 3 across most brain structures and species, and there is no systematic variation in glial cell density across brain structures as they gain glial cells. This is in stark contrast to the large variation in neuronal density and its systematic decrease in most mammalian orders as brain structures gain neurons. For the sake of comparison, the data plotted here (cerebral cortex, circles; cerebellum, squares; rest of brain, triangles) are shown in the same scale as the plots of neuronal density in chapter 4.

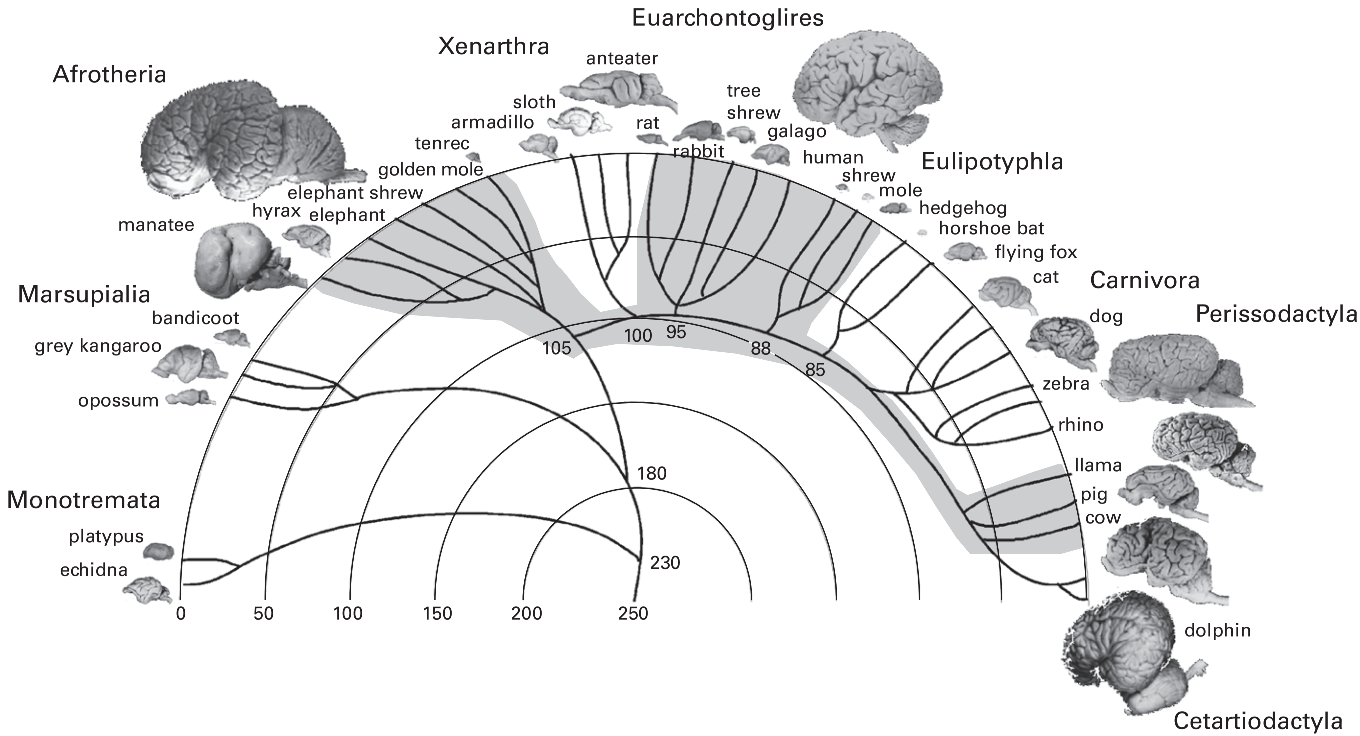


Figure 9.6

Same glial scaling rules apply to groups as evolutionary diverse and distant as afrotherians, rodents, primates, eulipotyphlans, and artiodactyls. Given that their last shared common ancestor lived some 105 million years ago, it is likely that the same glial scaling rules seen today applied at that time—and have been conserved since then.

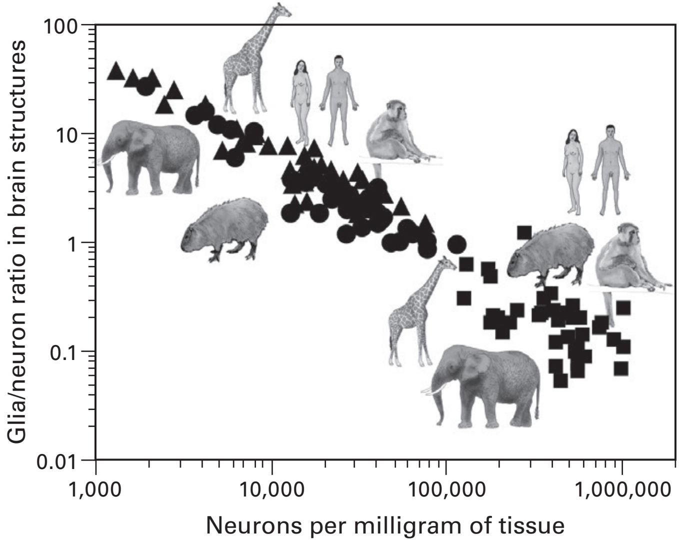


Figure 9.7

Glial/neuron ratio varies as a single, universal function of neuronal density (in neurons per milligram of tissue) in all brain structures, species, and mammalian orders in our data set. For each species, there are three data points in the graph (cerebral cortex, circles; cerebellum, squares; rest of brain, triangles).

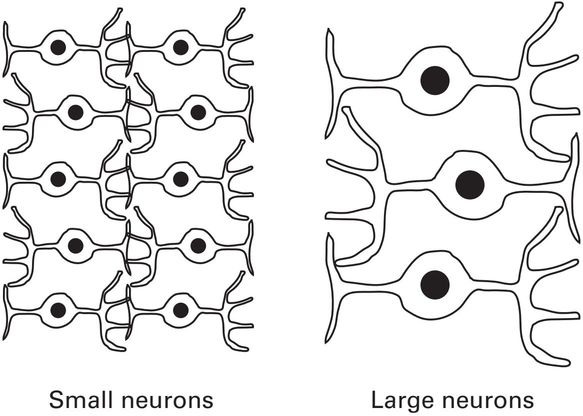


Figure 9.8

Same volume of brain tissue can be composed of a large number of small neurons (*left*) or a small number of large neurons (*right*).

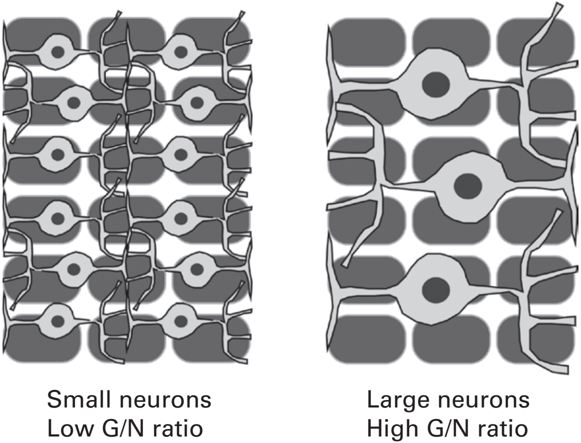


Figure 9.9

When the average size of glial cells (the rounded rectangles in the schemes) is nearly invariant, the number of glial cells per given volume of brain tissue is constant. However, because the same volume of tissue can be made of a large number of small neurons (*left*), a small number of large neurons (*right*), or any combination in between, the glia/neuron ratio in each tissue depends simply on the average size of the neurons in the tissue: the larger the average size of neurons, the higher the glia/neuron ratio in the tissue.

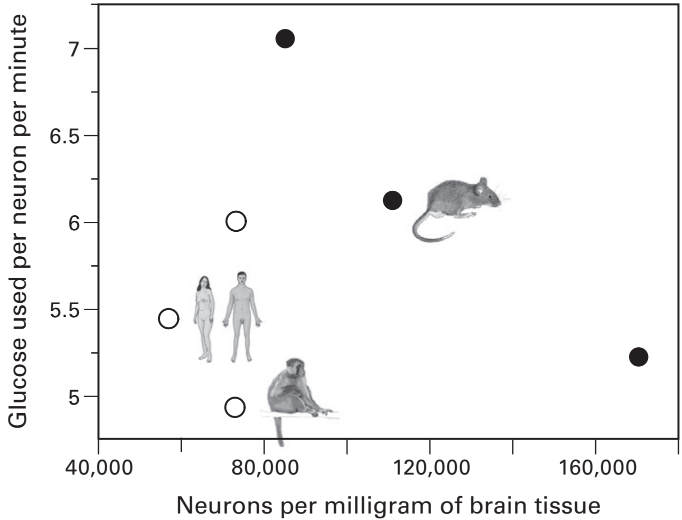


Figure 9.10

Average energy cost per neuron in the brain (in micromoles of glucose per neuron per minute) varies little across mouse, rat, squirrel (filled circles), macaque, baboon, and human (open circles) and, most important, with no obvious correlation with average neuronal density in the brain: larger neurons (at lower neuronal densities) do not use more glucose per minute than smaller ones (at higher neuronal densities).

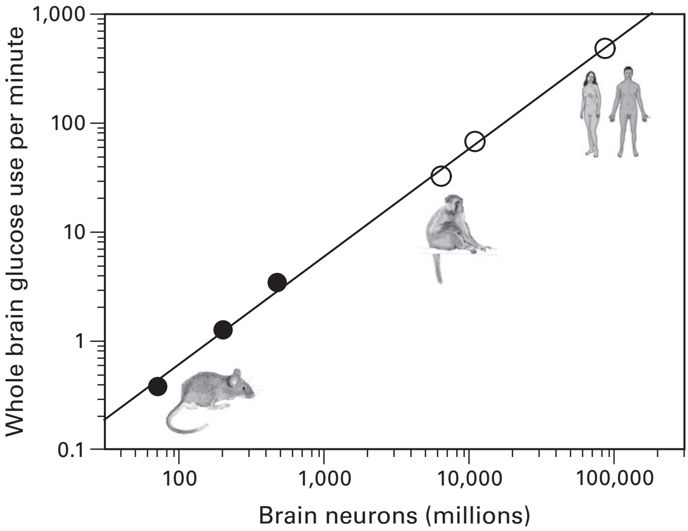


Figure 9.11
Total energy cost of the brain (in micromoles of glucose per minute) scales as a single linear function across mouse, rat, squirrel (filled circles), macaque, baboon, and human (open circles). That is, the more neurons in a brain, the more energy it costs, in a simple proportion.

Table 9.1

Energy cost of mammal brains compared across species

Number of neurons	Total glucose use per day (g/day)	Total caloric cost per day (kCal/day)
1 million	**0.0015**	**0.006**
10 million	**0.015**	**0.060**
Smoky shrew, 36 million	0.05	0.2
Mouse, 71 million	0.11	0.4
100 million	**0.15**	**0.6**
Rat, 200 million	0.30	1.2
Marmoset, 636 million	1.0	3.8
Agouti, 795 million	1.2	4.8
1 billion	**1.5**	**6.0**
Owl monkey, 1.5 billion	2.2	9.0
Capybara, 1.5 billion	2.2	9.0
Macaque, 6.4 billion	9.6	38
10 billion	**15**	**60**
Baboon, 11 billion	16	66
Orangutan, 30 billion	45.02	180
Human, 86 billion	129	516
100 billion	**150**	**600**

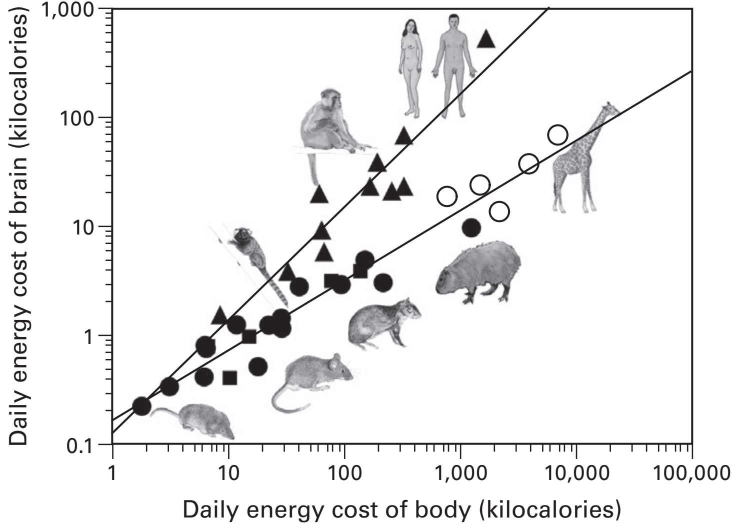


Figure 9.12

Total daily energy cost of the brain (in kilocalories), predicted to vary across species as a simple, linear function of the total number of neurons in the brain (at an average cost of 6 kilocalories per billion neurons per day), scales as different functions of the daily energy cost of the body (also in kilocalories) across primates (triangles; with the exponent +1.0, that is, linearly) and nonprimates (squares, open and filled circles; with the exponent +0.6).

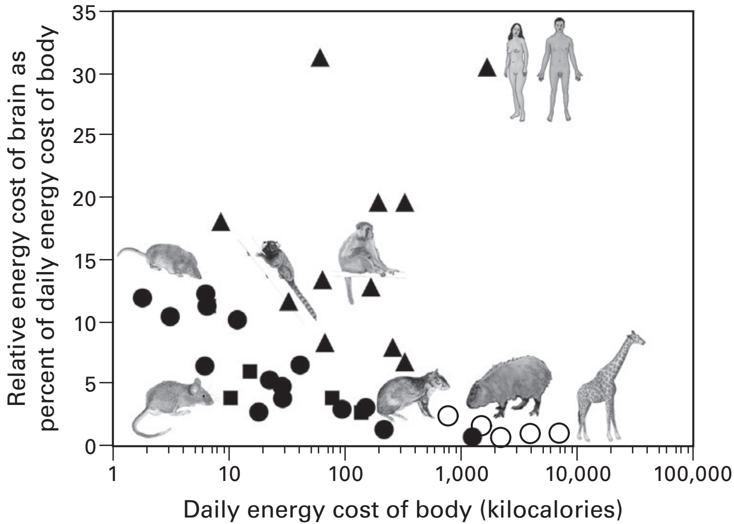


Figure 9.13

Relative daily energy cost of the brain, expressed as a percentage of the daily energy cost of the body (in kilocalories), becomes lower with increasing body mass across nonprimates (squares, open and filled circles), but varies nonsystematically across primates (triangles)—and is predicted to be even higher in the squirrel monkey than in the human.

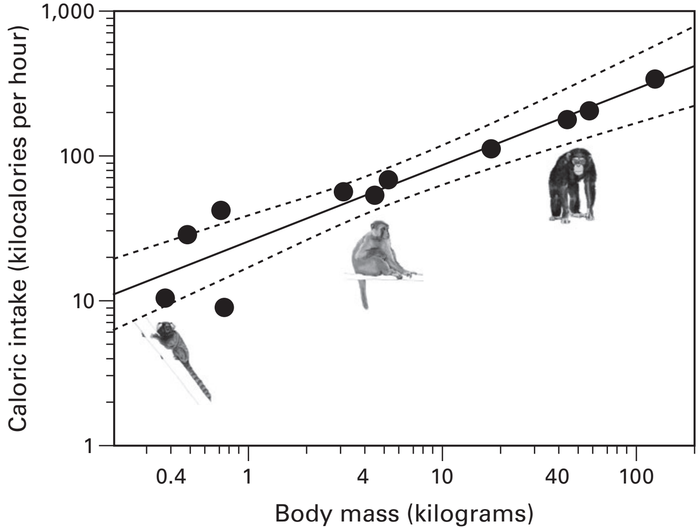


Figure 10.1

Larger primates have an increasing capacity for caloric intake (in kilocalories per hour spent foraging and feeding). However, the hourly caloric intake scales with body mass raised to the power of 0.53 (with dashed lines indicating the 95 percent confidence interval for the scaling function), more slowly than the energy cost of the body, which scales with body mass raised to the power of 0.75.

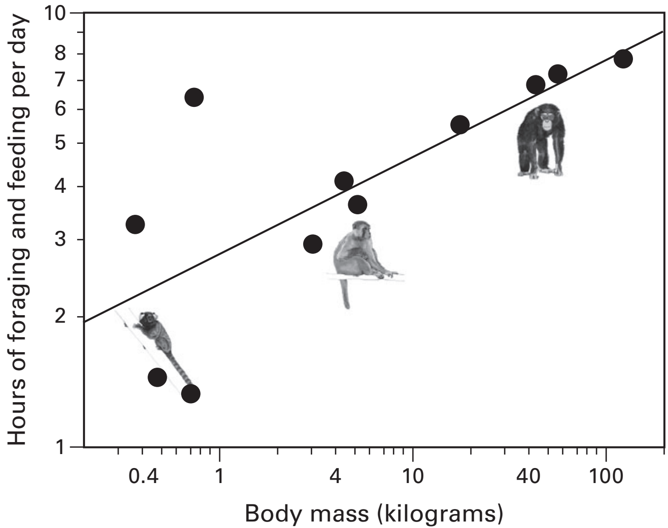


Figure 10.2

Larger primates spend more hours per day foraging and feeding. Although the number of hours per day they spend in these activities scales slowly, with body mass raised to the power of 0.22, the large range of primate body sizes is enough to increase the required number of hours spent amassing kilocalories from less than 2 to almost 8 hours per day.

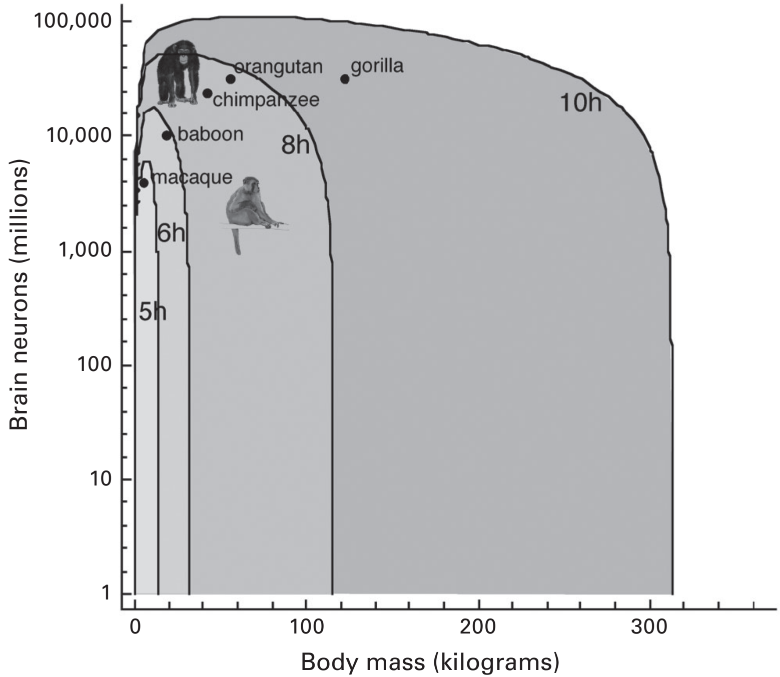


Figure 10.3
Shaded zones for each curve indicate the viable combinations of number of brain neurons and body mass that can be sustained for a given number of hours per day spent foraging and feeding (h). The downward slopes to the right of each curve indicate a trade-off: past a maximum number of brain neurons, body mass can increase only at the expense of the number of neurons; by the same token, the number of neurons at the limit of the curves can increase only at the expense of body mass.

53 B neurons	25 kg
45 B neurons	50 kg
30 B neurons	75 kg
12 B neurons	100 kg
not viable	150 kg

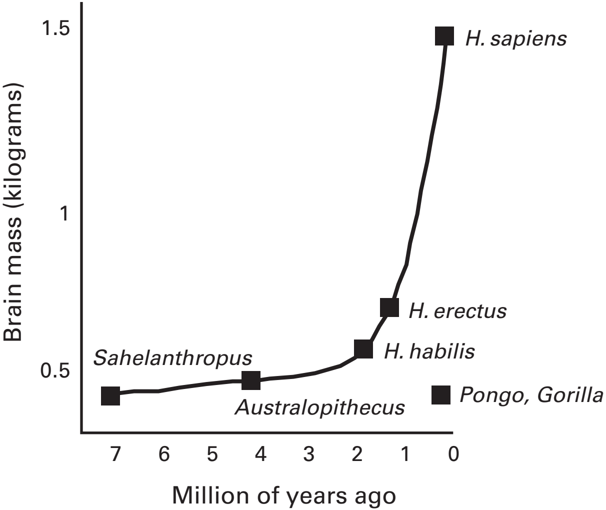


Figure 11.1
Rapid increase of brain mass in the *Homo* lineage in the last 1.5 million years, but not in the lineages that led to modern great apes.

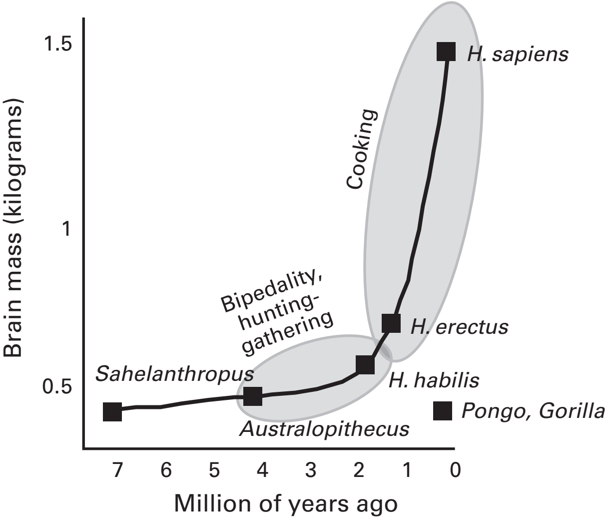


Figure 11.2

Rapid increase of brain mass in the *Homo* lineage in the last 1.5 million years coincides with the invention of cooking, probably by *Homo erectus*.

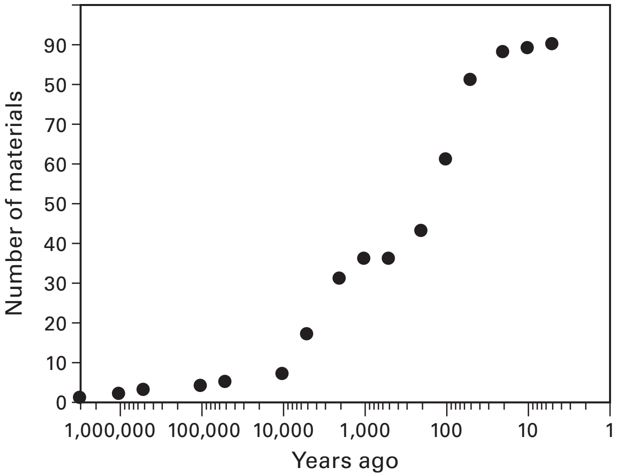


Figure 12.1

Total number of materials (of the first ninety that come to mind) available to humans or developed by humans over time.* Notice that with the advent of agriculture, 10,000 years ago, the number of materials available started to increase rapidly—just as brain mass did around 1.5 million years ago.

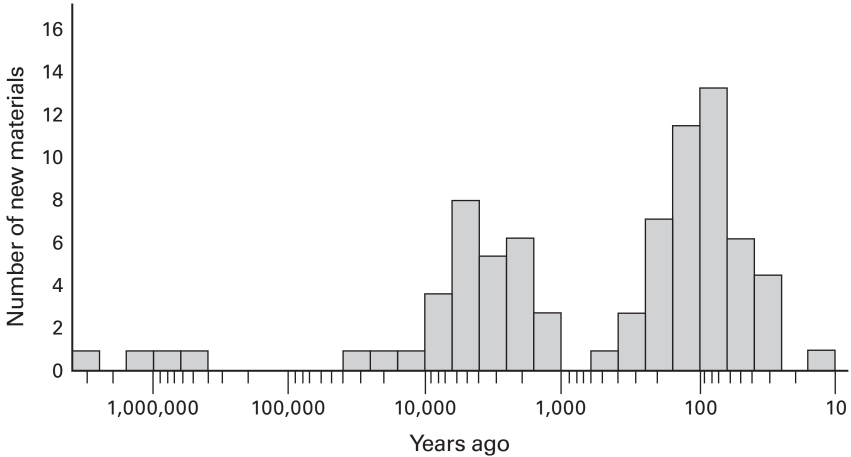


Figure 12.2

There is a gap in the number of materials (of the first ninety that come to mind) newly available to humans or developed by humans around 1,000 years ago—but starting some 400 years ago, new materials once again became available rapidly. Although this involves only the first ninety materials I could think of, it shows an important difference in their dates of creation: The history of development of new materials has not been a linear, progressive one.‡