

young adults (21 to 24 years old) were scanned with fMRI during a simple task in which they were required to press a button in response to all letters except the letter X. This task shows clear developmental improvement, with adults making fewer erroneous button presses. When erroneous responses to Xs were successfully inhibited, activation was seen in several regions of the prefrontal cortex, including the anterior cingulate, orbitofrontal cortex, and inferior and middle frontal gyri in both children and adults. Compared to adults, children showed significantly greater activation in the dorsolateral prefrontal cortex and anterior cingulate cortex. By contrast, adults showed more activity in orbitofrontal cortex than did children. Across all ages, individuals with higher orbitofrontal activation and lower dorsolateral prefrontal activation performed better on the task. These findings suggest that changes in prefrontal cortex function throughout development shape changes in executive function.

### Brain size and the evolution of cognition

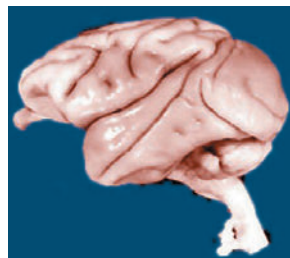
Given the relationship between brain maturation and cognition observed during development, it seems reasonable to suppose that differences in cognitive abilities between species are in some broad way dependent on differences in brain structure and function. Since most studies of cognitive evolution focus on complex, flexible, goal-directed behavior, a global metric such as brain size would seem a simple and reasonable starting point to test this idea.

Among vertebrates, mammals and birds generally have larger brains (and certainly larger volumes of cerebral cortex; see the next section) than do fishes, amphibians, or reptiles, and no one would dispute the fact that these differences in brain volume are somehow related to differences in the apparent cognitive abilities of these various taxonomic groups. Among mammals, moreover, rats have smaller brains than cats or monkeys, which in turn have smaller brains than dolphins and humans, seemingly confirming the general tendency of cognitive abilities and brain size to track together. Collectively, these observations suggest that brain size is indeed an important determinant of behavioral complexity and flexibility. This conclusion makes good sense because as the number of neurons in the brain increases, the number and complexity of functions that the brain can perform are likewise expected to increase.

A closer look at the relationship between absolute brain size and cognition, however, raises the troubling observation that some seemingly intelligent animals have smaller brains than other animals not known for their cognitive prowess (**Figure 15.6**). This observation implies that the relationship between absolute brain size and cognition is not so simple (see Box 15B).

The resolution of this puzzle is in part answered by the relation of brain size and body size: it makes little sense to consider the size of an animal's brain

(A) Macaque



(B) Cow

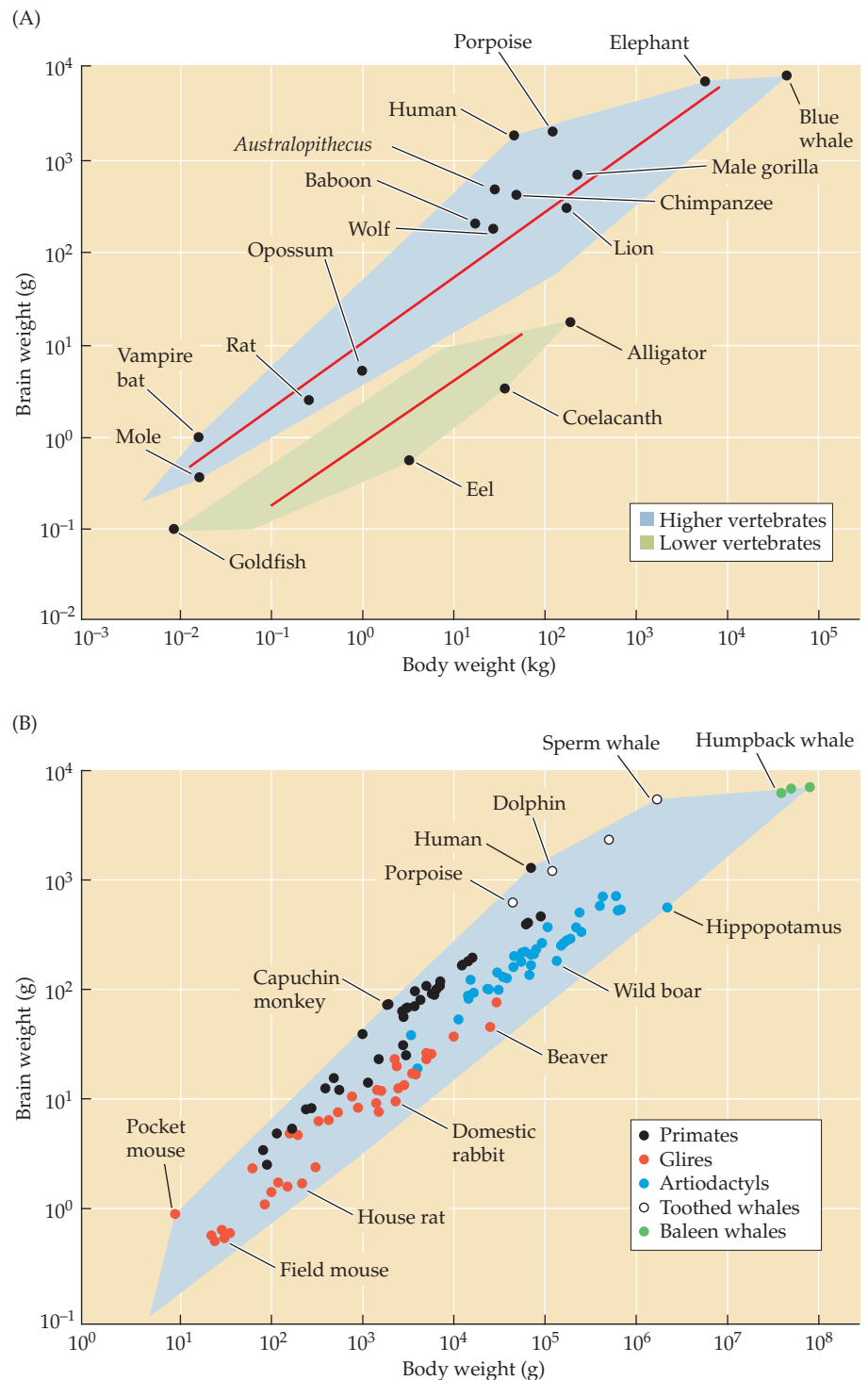


**Figure 15.6 Brain size does not correlate absolutely with cognitive ability** Lateral views of the brains of a macaque monkey (A) and a cow (B), shown to scale. Even though the macaque's cognitive abilities are superior to those of the cow, its brain is significantly smaller, as well as less folded. (Courtesy of the University of Wisconsin and Michigan State University Comparative Mammalian Brains Collection.)

without adjusting this metric for the size of the animal's body, since—cognitive abilities aside—the brain would presumably need to be somewhat larger simply to organize the behavior of larger bodies. The differential measurement of individual body parts in relation to the whole is known as allometry (the prefix *allo* means “other” in Greek), and the general proportionality of brain and body size reflects the fact that as the body grows larger, more neurons are needed to process sensory inputs, motor outputs, and their central interactions.

The allometric relationship of brain and body size is highly variable among species. Thus, the line that fits to the scatter of brain size plotted against body size in **Figure 15.7A** makes it obvious that some animals have brains that are larger than body size alone would suggest, whereas others do not. For instance, humans, dolphins, and crows have larger brains than expected for their average body size, whereas opossums, ostriches, and some other animals have smaller brains than one might expect. Moreover, birds and mammals have larger brains for their body size than do reptiles and fishes. These deviations from allometrically predicted brain size, often referred to as *residual brain size*, correspond more closely to relative cognitive ability than does brain size alone. Within any particular group of vertebrates, relative brain size is also correlated, at least roughly, with apparent cognitive capacity (**Figure 15.7B**). Whether or not relative brain sizes of individuals within a species scale with their specific cognitive abilities, however, remains hotly debated (**Box 15B**).

**Figure 15.7 Importance of brain size relative to body size** Note that the scale is logarithmic in all cases. (A) Brain weight as a function of body weight. Red lines indicate the allometric scaling relationship between brain size and body size, determined by linear regression. The blue and green areas indicate minimal polygons enclosing the data points for mammals (blue) and for fishes and reptiles (green). (B) Allometric relationship of brain size and body size for placental (modern) mammals. Note that primates (black dots) have much larger brains given their body sizes than do rodents and rabbits (Glires; red dots) or deer, antelope, and the like (artiodactyls; blue dots)—animals not known for their cognitive skills. (A after Jerison 1977; B after Striedter 2005.)



## ■ BOX 15B BRAIN DIFFERENCES IN MODERN HUMANS: IMPLICATIONS FOR COGNITION

A wealth of neuroanatomical, physiological, and behavioral data support the hypothesis that brain size and complexity predict cognitive abilities across a wide diversity of species. However, whether differences in brain size *within* a species are associated with differences in cognition remains a subject of debate. The debate is especially heated when differences in brain size and cognitive behavior in humans are being considered. Historically, scientists have often tried to link overall brain size to differences in performance by using global measures of cognitive performance such as IQ tests.

Several prominent nineteenth-century scientists—including the statistician Francis Galton (who, incidentally, was Darwin's cousin), the American physician Samuel Morton, and the French neuroanatomist Paul Broca (who determined that the left frontal lobe is responsible for articulate speech; see Chapter 12)—argued that individual differences in brain size (often estimated by a method no more scientific than simply measuring the head) accurately predicted a person's intelligence. Unfortunately, this approach was used to support, either implicitly or explicitly, notions of racial and gender superiority that buttressed Western conventional wisdom of the time, which asserted that white European males had larger brains—and consequently greater intelligence—than everyone else in the world.

Careful reanalysis revealed much of this original research to be badly flawed. For example, evolutionary biologist Stephen Jay Gould demonstrated that Morton's measurements of cranial capacity (an index of brain size based on measuring the interior volume of the skull) in specimens of different races were inaccurate and highly biased toward finding larger brain sizes for European males. Moreover, it is now clear that it is difficult to measure general intelligence in individuals with different cultural, educational, and socioeconomic backgrounds. De-

spite recognition of these methodological problems, the legacy of this nineteenth-century mind-set has continued to bedevil psychology, neuroscience, and society right into the twenty-first century.

Individual human beings clearly vary in cognitive ability, as well as in brain size. But such differences among human groups are small and often difficult to interpret, not least because the brain is a mosaic of interrelated modules and systems serving distinct behavioral functions. It thus makes more sense to consider more specifically whether variation in the size, physiology, cell structure, and molecular biology of such components corresponds to the efficiency or complexity of the behavioral functions they enable.

For example, the size of each of the various components of the visual system, including the optic tracts, lateral geniculate nucleus, and primary visual cortex, is intimately related within an individual; across subjects, however, these elements vary substantially in size. As described in Chapter 3, visual acuity corresponds closely to the cortical space allocated to each part of the visual field, suggesting (along with much other evidence) that the quality of cortical processing is a function of the amount of cortical space given over to that function. Structural differences of this sort may also underlie gender differences in cognitive abilities such as language and spatial navigation. It has long been known, for example, that women are much less likely than men to suffer a debilitating loss of language (aphasia) following strokes involving cortical language areas in the left hemisphere. This gender difference suggests that women process language more bilaterally than men do—a hypothesis supported by recent neuroimaging studies demonstrating stronger lateralization of language processing in males than in females.

Stronger lateralization in males also extends to visuospatial information processing, as revealed by both lesion and functional neuroimaging studies. These observed sex differences in brain organi-

zation could be related to differences in cognitive performance, specifically to the superior verbal abilities of females, on average, and to the superior visuospatial navigation abilities in males revealed by standardized tests. Note, however, that such tests are subject to the same criticisms as the IQ tests described earlier.

These and other differences in brain structure and cognitive performance in men and women seem likely to derive from the interplay of sex hormones and experience during development. Gender differences in the spatial navigation ability of experimental animals, for example, have been linked to differences in the size of the hippocampus in male and female voles and rats, which is known to be determined by the action of sex hormones during development.

These observations notwithstanding, the links among gender, hormones, experience, brain structure, and cognition in humans remain hotly debated. Given the enormous cultural, political, and educational implications of these kinds of findings, much more work will be required to understand the biological mechanisms that contribute to the wide range of differences in cognitive performance seen across groups and across individuals within groups.

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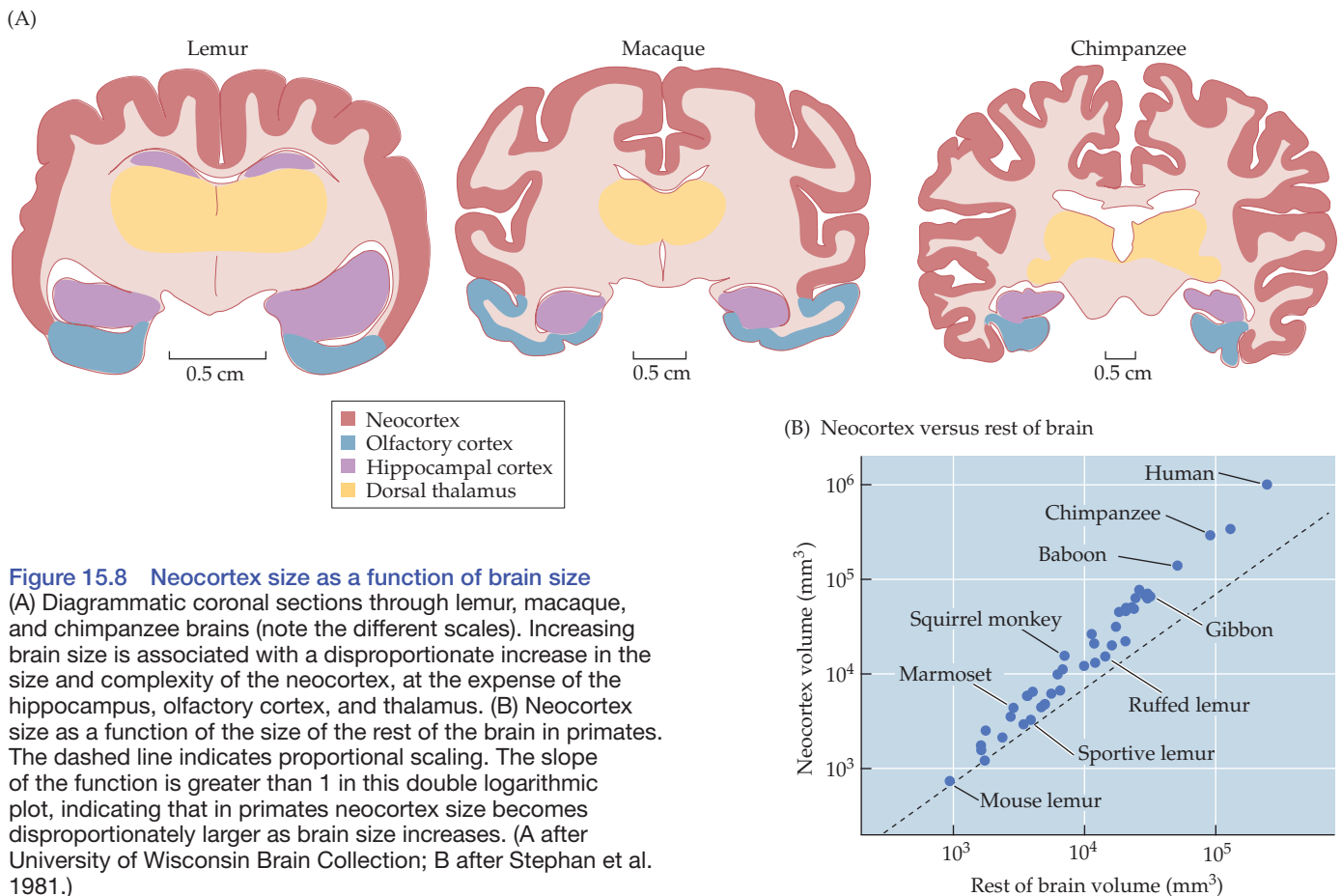
### Relative brain size and cerebral complexity

Although the ratio of brain size to body size predicts cognitive abilities fairly well across a wide range of animals, this observation does not explain why or how this correlation exists. One argument is that the scaling relationship between brain size and body size in Figure 15.7 reflects the average amount of

neural processing “machinery” necessary for maintaining a body of a particular size. According to this view, positive deviations in brain size from expectations based on body size would afford the animal extra neural processing capacity for additional abilities that transcend the usual housekeeping functions (**Box 15C**). The extra capacity could then be devoted to cognitive functions that are particularly advantageous for behavioral success in some ecological niches.

A second, not mutually exclusive, possibility is that changes in the relationship of brain and body size are associated with concomitant changes in the *structure* of the brain, as well as in its size. For example, the six-layered neocortex is the most recently evolved part of the forebrain, is found only in mammals, and is widely agreed to be the seat of many advanced cognitive functions. Allometric analyses indicate that the size of the neocortex scales positively with the size of the rest of the brain: as the brain gets larger, the neocortex gets larger.

This proportionality, however, varies among different animal groups. That is, the allometric relationship relating neocortex size to brain size has the same slope, but different intercepts in different species. For example, simian primates (monkeys and apes) have proportionately larger neocortices given the size of the rest of their brains than do prosimian primates (lemurs and lorises; **Figure 15.8**), which in turn have proportionately larger neocortices than would be expected compared to insectivores (e.g., hedgehogs and shrews). Thus, as the size of the brain relative to body size increases, the relative size of the neocortex also increases. In at least this respect, the differential scaling of brain structures is important in the evolution of cognitive capacities.

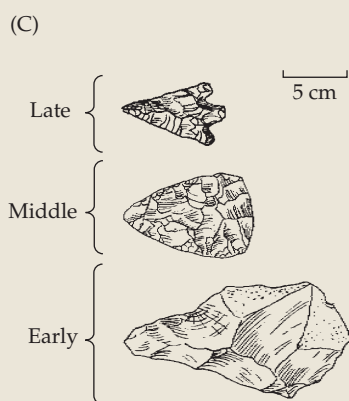
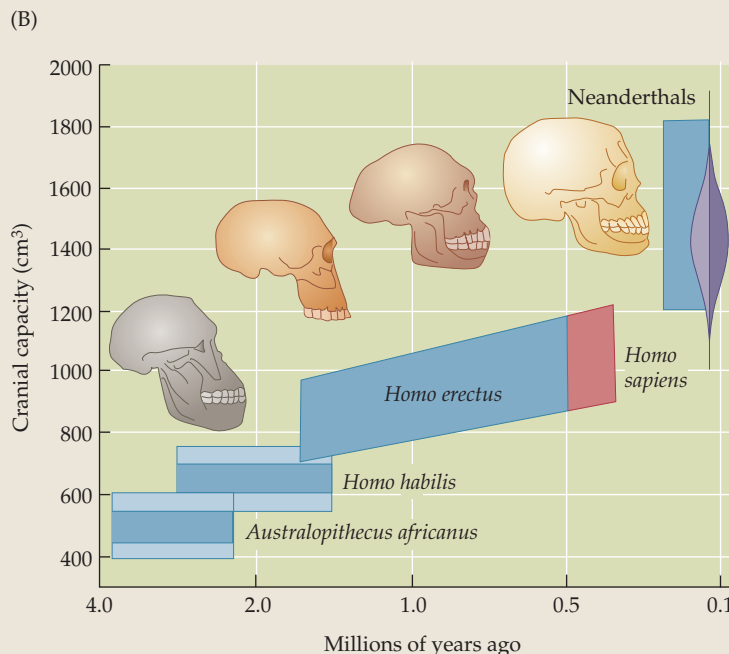
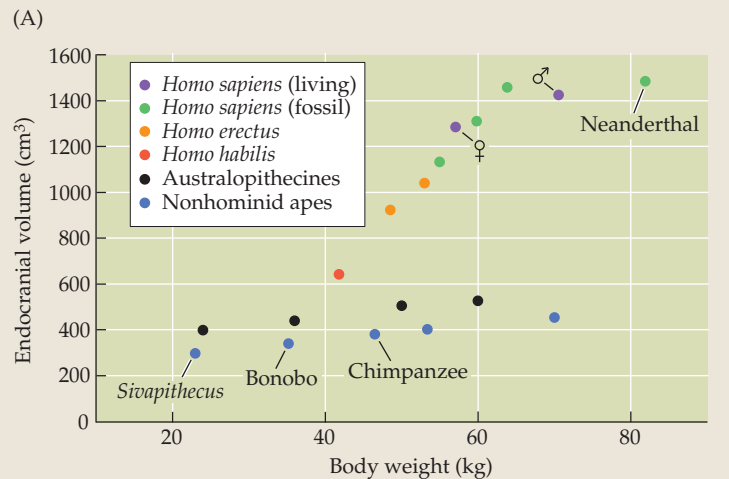


## BOX 15C EVOLUTION OF HUMAN BRAIN AND COGNITION EVIDENT IN THE FOSSIL RECORD

In many respects, human neural and cognitive evolution has simply elaborated on trends that are well established in non-human primates; in other respects, however, human brain evolution has been marked by distinctive deviations from other primates. For example, like other primates, the human brain represents a larger fraction of body size than in other mammals. Nonetheless, the trajectory of brain evolution relative to body size has been steeper within the lineage leading to modern humans compared to the lineage of non-human primates (Figure A).

The fossil (i.e., skeletal and other organismal remains) and archaeological (i.e., artifacts of human activity) records provide clues about the coevolution of brain structure and cognition in humans. The primate lineage leading to humans first diverged from the great apes between 5 and 8 million years ago. Somewhat surprisingly, this divergence was not characterized by major neurological changes. The first adaptive change distinguishing ancestral humans, or **hominids**, from apes was not neurological, but morphological, entailing upright bipedal walking. The first human ancestors, known as **australopithecines** and found in eastern and southern African fossil beds dated to 3 to 4 million years ago, had brains about the same size as modern-day chimpanzees (see Figure A). However, the human evolutionary career thereafter (Figure B) is characterized by both gradual, progressive changes and relatively rapid advancements in brain size and cognition.

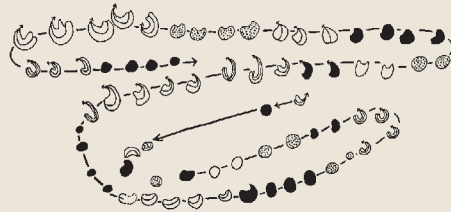
The first member of the genus **Homo**, the group to which modern humans belong, diverged from an australopithecine ancestor around 2.5 million years ago (see Figure B). This species, dubbed *Homo habilis* ("handy man"), had a brain that was about 50 percent larger than those of its ancestors, and it was the first human ancestor to produce crude stone tools (Figure C). About 800,000 years later, *Homo erectus* ("erect man") diverged from an earlier *Homo* species. Again, this evolutionary event was characterized by major advancements in brain size and cognition. Early *Homo erectus* fossils reveal brains that were about a third larger than the brains of early *Homo habilis*. Moreover, *Homo erectus* made stone tools of greater complexity and symmetry than those made by earlier humans (see Figure C) and also began



(A) Brain size is disproportionately large in relation to body size in humans and their immediate ancestors (hominids) compared to apes. (B) Brain size has increased in sudden jumps, as well as gradual changes, during hominid evolution. Shaded regions indicate the range of variation in brain size. (C) The sophistication of the stone tools produced by hominids increased in parallel with increasing brain size over the course of evolutionary time. Bottom: Early Paleolithic tools associated with *Homo habilis* and early *Homo erectus*. Middle: Middle Paleolithic tools associated with late *Homo erectus* and early *Homo sapiens*. Top: Upper Paleolithic tools found with the skeletal remains of anatomically modern humans. (A after Hofman 1983; C after Tattersall et al. 1988.)

## ■ BOX 15C (continued)

(D)



(D) Anatomically modern humans in Ice Age Europe began to produce symbolic art indicative of greatly enhanced cognitive abilities. Shown here are a carved woman's head from Brassempouy, in southern France, about 23,000 years old; lunar phases incised on a piece of bone, 30,000 to 40,000 years old; and a cave painting of a horse from Lascaux, France, approximately 15,000 years old.

to use fire, presumably reflecting greater cognitive capacity.

*Homo erectus* was an extremely successful species, persisting for about 2 million years and colonizing what are now Africa, Europe, and Asia. During that time, hominid brain size increased gradually, and the stone tools produced by *Homo erectus* progressed in sophistication. These advances in brain and cognitive ability apparently permitted *Homo erectus* to survive in a wide variety of climates, utilize a variety of resources, and even navigate open oceans to reach Australia. Throughout the Old World, *Homo erectus* continued to evolve and adapt to local conditions until the late Pleistocene era, from 200,000 to about 50,000 years ago. In what is today western Europe and the Middle East, *Homo*

*erectus* evolved into **Neanderthals**, who, rather surprisingly, had brains that were even larger than those of modern humans (although it should be noted that their bodies were slightly heavier as well); in this instance, overall brain size does not align very well with the relatively primitive material culture of Neanderthals.

Modern humans, *Homo sapiens* (meaning, for better or worse, "wise man") evidently arose on the African continent about 200,000 years ago and rapidly spread throughout the world, in some cases driving other hominid populations, including Neanderthals, to extinction, and in other cases interbreeding with them. The competitive advantage of anatomically modern humans was almost certainly due, at least in part, to their superior cognitive abilities. Early *Homo sapiens*

possessed an extremely sophisticated arsenal of stone tools, including long blades and hafted spear points (i.e., points with handles, which make much more effective weapons than a simple pointed implement with no handle). These were also the first humans to produce symbolic representations and art (Figure D). In addition, they buried their dead with jewelry and other items, indicating that they apparently had religious beliefs of some type.

Together, the size and morphology of the brain, and archaeological traces of ancient behavior, suggest that adult human cognitive capacities have changed little in the past 200,000 years. Although some evidence suggests that certain aspects of human biology continued to evolve (e.g., the sickle-cell trait and malarial resistance in sub-Saharan Africans; adult lactose-tolerance in northern European dairying cultures), the technological and intellectual achievements of today's humans largely reflect the accumulation and storage of knowledge by purely cultural means—and often outside the brain, in books and computers. These feats highlight the remarkable capacity of the human brain to rapidly adapt to new physical and social contexts, and to use information in new ways unanticipated by evolution.

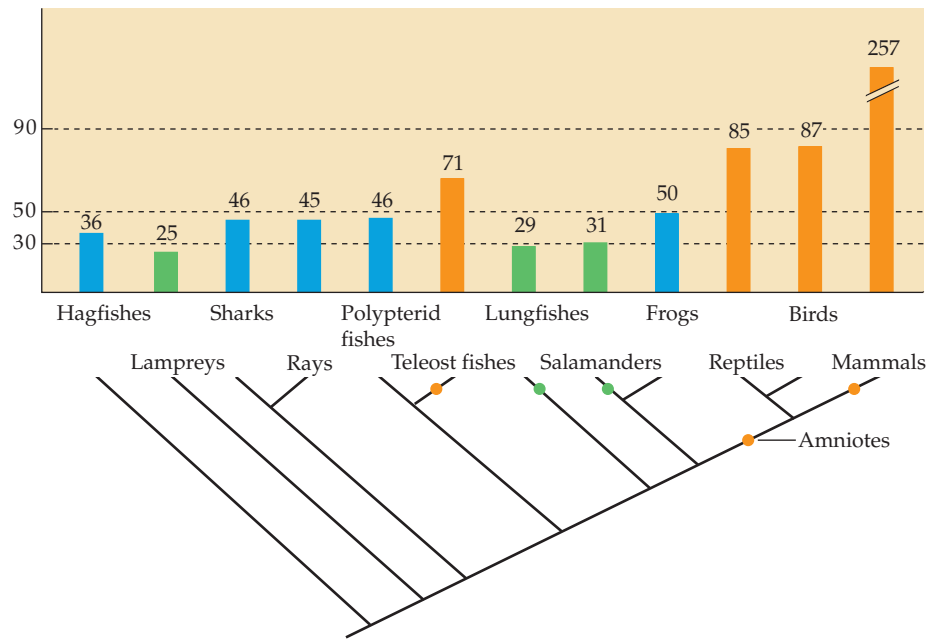
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In addition to changes in the size of the brain itself and the relative size and complexity of structures like the neocortex, there is evidence that the complexity of neuronal circuitry has increased during evolution. A family tree (properly called a *cladogram*) plotting the number of distinct neuronal cell types found in several vertebrate taxonomic group indicates that, as brain-to-body-weight ratios increased over evolutionary time, so did forebrain complexity (Figure 15.9). If the number of neuronal cell types found within a brain underlies the

**Figure 15.9 Forebrain complexity**

In this cladogram, each bar indicates the number of different cell groups found in representative species of each major vertebrate group. Colored dots indicate when forebrain complexity is likely to have increased (orange) or decreased (green). (After Striedter 2005.)



number and complexity of the computations that the brain can perform, then the impact of brain size on cognitive capacity may be due in part to increases in the complexity of neuronal circuitry.

## Evolution of Brain Development

The overall size, regional complexity, and histological diversity of the brain would seem to reflect both prior adaptations of ancestral species and contemporary responses to adaptive pressures favoring the evolution of particular behavioral capacities. An important question raised by these observations is how these changes in brain size and structure are generated during development. The question becomes particularly intriguing when one considers the relatively small number of coding sequences available in animal genomes for specifying the size and structure of the brain (keeping in mind that the entire human genome contains fewer than 30,000 genes).

In fact, recent genetic discoveries revealed a family of genes that seem to play a role in controlling brain size development. Evolutionary changes in cognitive ability appear to be strongly related to the way brain size scales with body size across species, suggesting that relatively small changes in the genetic programs controlling brain size could result in profound changes in cognition. This argument is endorsed by the recent finding that genes involved in determining brain size in humans have evolved rapidly within the primate lineages leading to humans (**Figure 15.10**). Genes such as *microcephalin-1* (*MCPH1*) appear, in part, to underlie the growth and differentiation of neurons. Mutations in the *microcephalin* gene family lead to severe reductions in head and brain size, resulting in adults with brains about the size of chimpanzee brains; not surprisingly, such individuals have severe mental retardation. Relatively small changes in such genes could, in principle, provide a mechanism for scaling brain size across primates, at the same time providing the wherewithal for enhanced cognitive function.

Just how such a small number of genes might actually generate the diversity of brain size and complexity in different animals is not known. One model, developed by neurobiologist Barbara Finlay and her collaborators, suggests that