

cell bodies of motor neurons that send axons via the ventral roots of the spinal nerves to terminate in striated (skeletal) muscles.

The white matter of the spinal cord represents a complex collection of axon tracts related to specific functions. Some of these tracts carry ascending (i.e., going toward the brain) sensory information from the body's mechanoreceptors, while others include axons that travel from the cerebral cortex and brainstem to contact spinal motor neurons and interneurons. Still others carry information locally between spinal cord levels to better coordinate motor actions.

Surface features of the brain

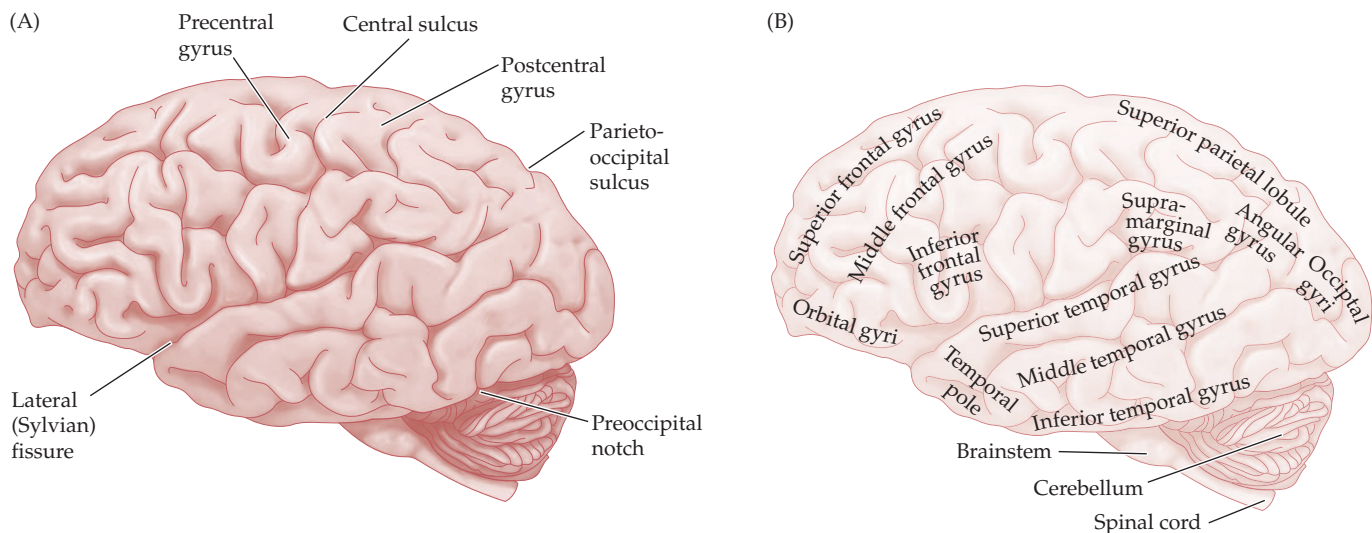
Many key features of the human brain are apparent simply from examining its surface. The major structures visible in this way are the cerebral hemispheres, the cerebellum, and the medullary (caudal) portion of the brainstem. The **cerebral hemispheres** are notable for their large size—they account for about 85 percent of the brain by weight—and their highly folded surface (**Figure A.10A**). Neuroanatomists and evolutionary biologists have argued for at least a century about the significance of cerebral convolutions, without reaching any clear resolution. All agree, however, that the infolding of the cerebral hemispheres allows a great deal more cortical surface area (about 0.6 square meters on average) to exist within the confines of the cranium than would otherwise be possible.

The convex convolutions of the brain are known as **gyri** (singular, *gyrus*), and the concavities between the gyri are called **sulci** (singular, *sulcus*) or, if they are especially deep, **fissures**. The brain's sulci and gyri figure heavily in the description of cognitive functions. The most important of the gyri are shown in **Figure A.10B**; although this figure may seem overly detailed, it is especially helpful in discussions of particular brain regions.

Despite its convolutions, the surface of the cerebral hemispheres is a continuous sheet of neurons and supporting cells about 2 millimeters thick called the **cerebral cortex** (recall that the term *cortex* is Latin for “bark”). The sheet is layered in a manner that varies from one region to another, and although they remain poorly understood, these differences are functionally important. Some of these differences and the generic organization of cortical circuitry (which is central to all cognitive functions) are described in **Box A2**.

The lateral surface view of the human brain in **Figure A.10** is also the best perspective from which to appreciate the **lobes** of the cerebral hemispheres, which are again essential descriptors in discussing cognitive functions. Each

Figure A.10 Surface views of the human brain (A) The left cerebral hemisphere in lateral view (the front of the brain is to the left). (B) Approximate location of some of the major gyri and other features of the brain surface that are important landmarks in several chapters of this book.



BOX A2 ORGANIZATION OF THE CEREBRAL CORTEX

Because cognitive functions are so closely tied to the cerebral cortex, a general understanding of cortical structure and the organization of its canonical circuitry is especially important. Most of the cortex that covers the cerebral hemispheres is *neocortex*, defined as cortex that has six cellular layers, or *laminae* (singular, *lamina*).

Each layer comprises populations of cells that are distinguished by their different densities, sizes, shapes, inputs, and outputs. The layers are designated by numerals 1 to 6 (or, alternatively, Roman numerals I to VI), with letters for laminar subdivisions (e.g., layers 4a, 4b, and 4c in the primary visual cortex).

Nerve cell bodies are rich in elements such as the cell nucleus and ribosomes, which tend to stain darkly with chemically basic nerve cell stains such as cresyl violet acetate. These so-called *Nissl stains* (named after Franz Nissl, who first described this technique when he was

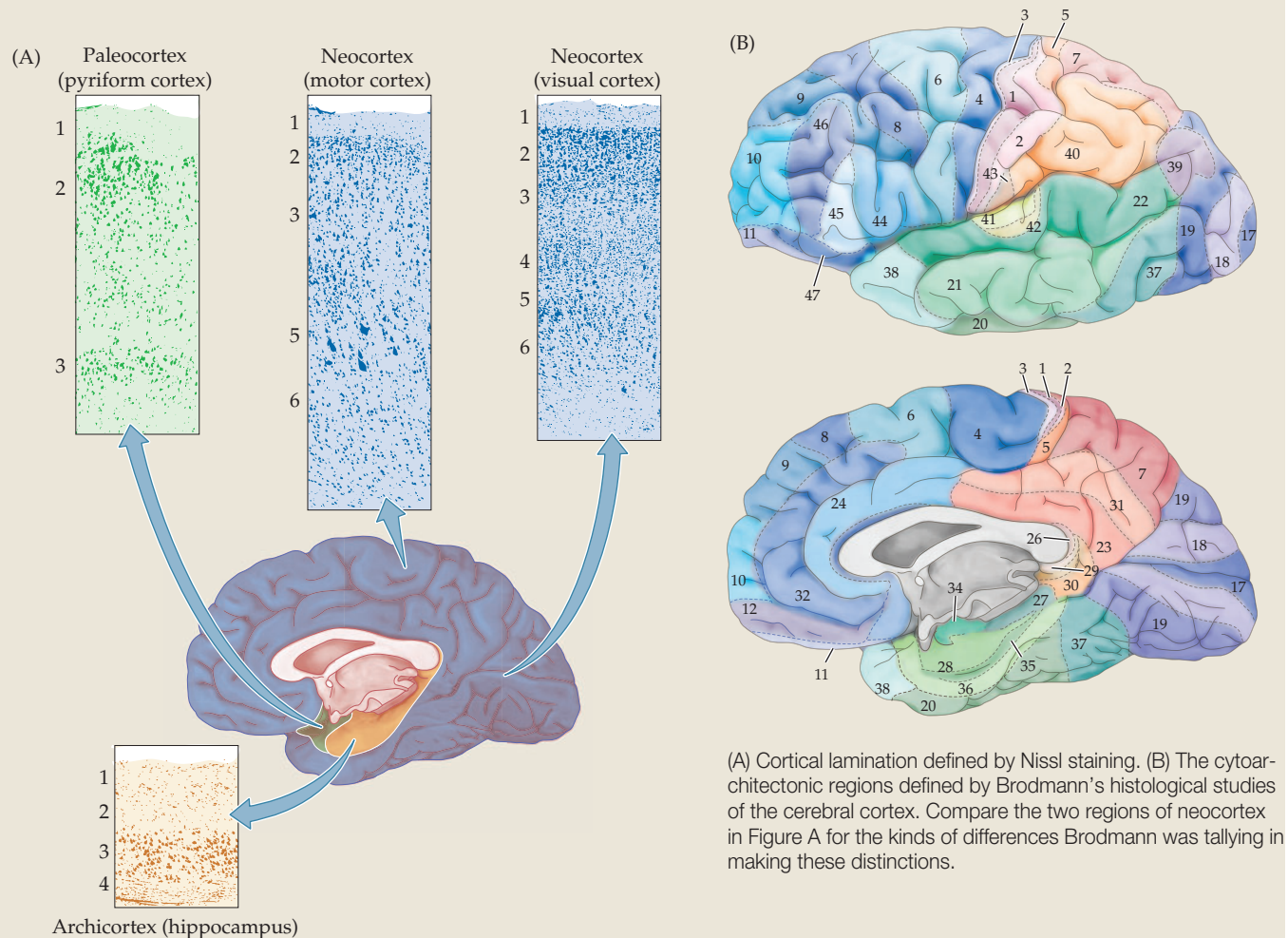
a medical student in nineteenth-century Germany) provide a dramatic picture of brain structure at the histological (microscopic) level. The most striking feature revealed in this way is the distinctive cortical lamination evident in humans and other mammals (Figure A).

Neocortex has six layers, but other brain regions have fewer. The infolded cortex of the hippocampus, for example, has only four laminae. The hippocampal cortex is regarded as evolutionarily more primitive and is therefore called *archicortex* to distinguish it from the six-layered neocortex. (All mammals have a well-developed hippocampus, but many have relatively rudimentary neocortex.) Another type of cortex, *paleocortex*, generally has three layers and is found on the ventral surface of the cerebral hemispheres and along the parahippocampal gyrus in the medial temporal lobe. The functional significance of different numbers of laminae in neocortex, archicortex,

and paleocortex is not known, although it seems likely that the greater number of layers in neocortex means that more complex processing takes place there than in archicortex or paleocortex.

To a considerable degree, cortical lamination corresponds to the predominance of different neuronal types, and generally different input/output characteristics. For example, neocortical layer 4 is typically rich in *stellate neurons*, which have locally ramifying axons; and in the primary sensory cortices, these neurons receive input from the thalamus, the major sensory relay from the peripheral nervous system. Layer 5, and to a lesser degree layer 6, contains large *pyramidal neurons* whose axons typically leave the cortex. The generally smaller pyramidal neurons in layers 2 and 3 (which are not as distinct as their differing numeral assignments

(Continued on next page)



■ BOX A2 (continued)

suggest) have primarily connections to and from other cortical regions (called *corticocortical connections*), and layer 1 contains mainly axons and dendrites, with few nerve cell bodies present.

Despite the overall uniformity of neocortical lamination, regional differences based on laminar features have long been apparent, allowing investigators to identify anatomically distinct subdivisions of the cerebral cortex (Figure B). Early in the twentieth century, the German neurologist Korbinian Brodmann described about 50 such distinct regions, which he called *cytoarchitectonic areas*; today they are more commonly referred to as *Brodmann areas* (the phrase *cytoarchitectonic area* is simply jargon for a cortical region defined by a specific distribution of neurons as revealed with Nissl

stains). Brodmann defined these regions with little or no knowledge of their functional significance. Eventually, however, studies of patients in whom one or more cortical areas had been damaged, along with much other evidence, showed that many of the regions neuroanatomists had identified on histological grounds are also functionally distinct. Although useful in a number of contexts, designating Brodmann areas is not particularly helpful in an introductory textbook like this.

These variations notwithstanding, the circuitry of all cortical regions has common features. First, each cortical layer has a primary source of inputs and a primary output target. Second, each area has connections in the vertical axis (called *columnar* or *radial* connections), as well as connections in the horizontal

axis (*lateral* connections). Third, cells with similar functions tend to be arrayed in vertically aligned groups that span all of the cortical layers and receive inputs that are often segregated into radial or columnar bands. Finally, interneurons within specific cortical layers give rise to extensive local axons that extend horizontally in the cortex, often linking functionally similar groups of cells. The circuitry of any particular cortical region tends to be a variation on this canonical pattern of inputs, outputs, and vertical and horizontal patterns of connectivity. The similarity of neocortical structure and circuit organization across the entire cerebrum suggests that there must be a common denominator of cortical operation, although no one has yet deciphered what it is.

hemisphere is conventionally divided into four such lobes, named for the bones of the skull that overlie them: the frontal, parietal, temporal, and occipital lobes (Figure A.11A,B). The frontal lobe is the most anterior and is separated from the parietal lobe by the **central sulcus**. The central sulcus is an especially important landmark because it distinguishes the motor cortices anterior to it from the sensory cortices posterior to it. A particularly important feature of the frontal lobe is the **precentral gyrus**. (The prefix *pre-*, in anatomical contexts, refers to a structure that is anterior to, or in front of, another.) The cortex of the precentral gyrus is referred to as the **motor cortex** and contains neurons whose axons project to the motor neurons in the brainstem and spinal cord that innervate the skeletal muscles. The temporal lobe extends almost as far anterior as the frontal lobe but is inferior to (underneath) it, the two lobes being separated by the **lateral** (or **Sylvian**) **fissure**. The uppermost region of the temporal lobe contains cortex concerned with audition; the inferior portions deal with high-order visual information, object recognition, and categorization, among other functions. Hidden beneath the frontal and temporal lobes is the **insula**, which can be seen only if these two lobes are pulled apart or removed (Figure A.11C). The insular cortex is largely concerned with visceral and autonomic function, but it has also been implicated in a wide array of cognitive functions that involve motivational or emotional states.

The parietal lobe lies posterior to (behind) the central sulcus and superior to (above) the lateral fissure. The **postcentral gyrus**, the most anterior gyrus in the parietal lobe, harbors cortex that is concerned with somatic (bodily) sensation; this area is therefore referred to as the **somatic sensory** (or **somatosensory**) **cortex**. Other regions of the parietal lobe mediate aspects of attention, aspects of language, and a variety of other functions. The boundary between the parietal lobe and the occipital lobe (the most posterior of the hemispheric lobes) is a somewhat arbitrary line from the parieto-occipital sulcus to the preoccipital “notch.” The occipital lobe, only a small part of which is apparent from the lateral surface of the brain, is concerned primarily with the initial processing of visual information.

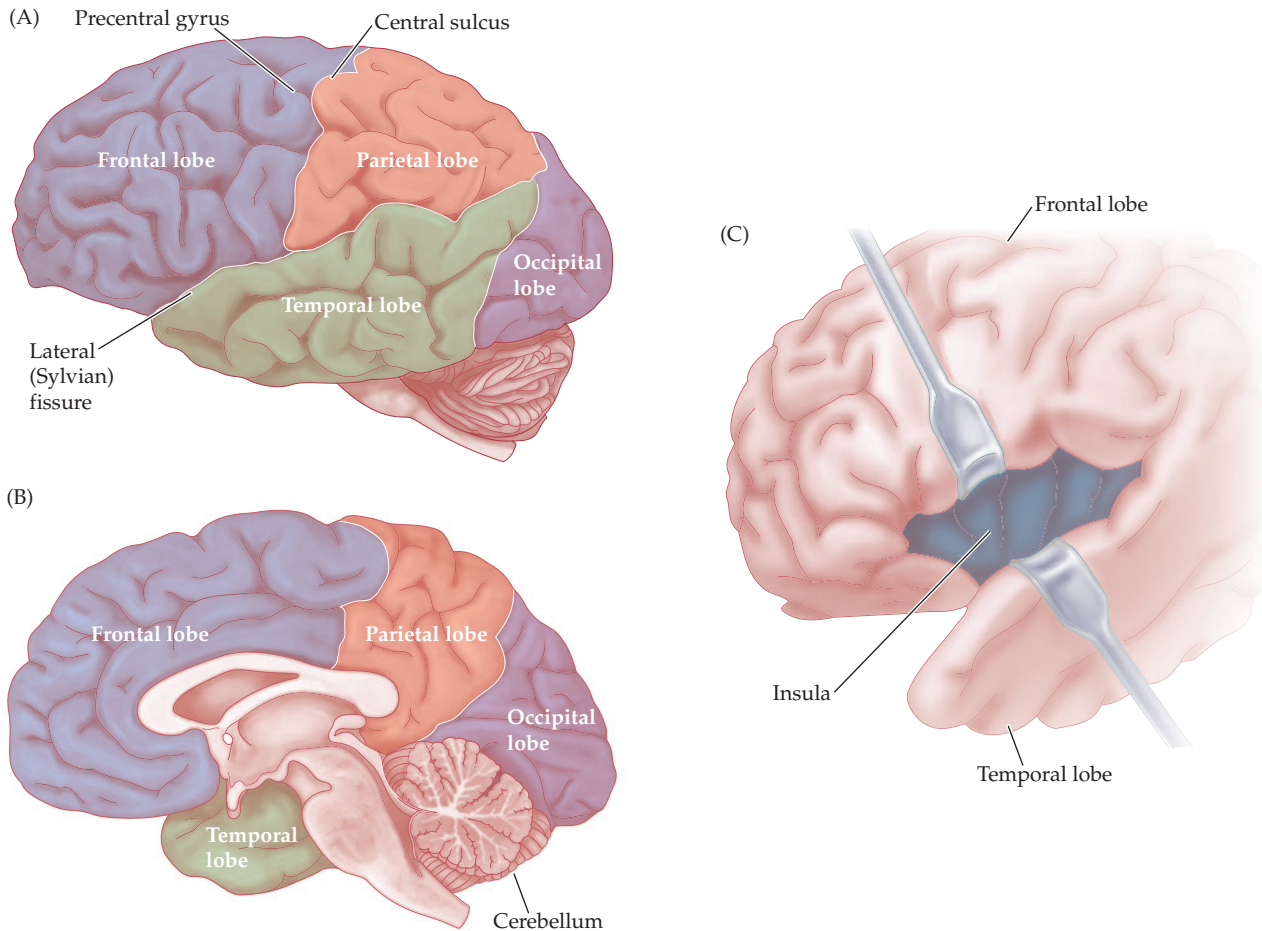
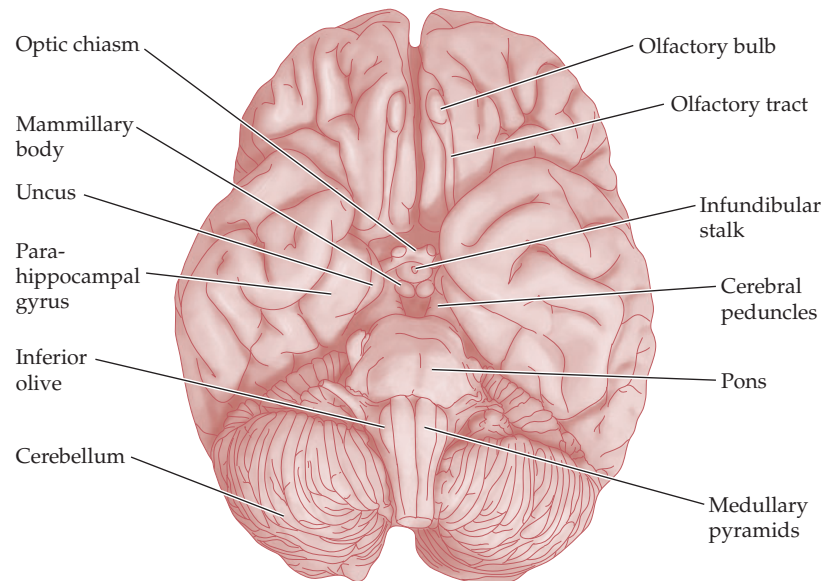


Figure A.11 Four lobes of the human brain (A) The lobes as seen from the lateral surface of the left hemisphere. (B) The lobes as seen from the medial surface. (C) Location of the insula.

Other surface features of the brain are best seen from a ventral perspective (**Figure A.12**). Extending along the inferior (lower) surface of the frontal lobe near the midline are the **olfactory tracts**, which arise from enlargements at their anterior ends called the **olfactory bulbs**. The olfactory bulbs receive input from neurons in the epithelial lining of the nasal cavity; the axons from these neurons make up the **olfactory nerve**. On the ventromedial surface of the temporal lobe, the **parahippocampal gyrus** conceals the **hippocampus**, a highly convoluted cortical structure that figures importantly in certain kinds of memory. Medial to the parahippocampal gyrus is the **uncus**, a protrusion that includes the **pyriform cortex**. The pyriform cortex is the target of the olfactory tract and processes olfactory information.

In the central region of the ventral surface of the forebrain is the **optic chiasm**; immediately posterior to it lies the ventral surface of the **hypothalamus**, including the base of the **pituitary gland** (the infundibular stalk in figure A.12) and the **mammillary bodies**. Posterior to the hypothalamus are two large tracts, oriented roughly rostral–caudally, the **cerebral peduncles**. These tracts contain axons from the cerebral hemispheres that project to the motor neurons in the brainstem and into the lateral and ventral columns of the spinal cord, as well as axons traveling to forebrain structures. Finally, the ventral surfaces of the

Figure A.12 Ventral view of the human brain Some brain structures, including the olfactory tract and the optic chiasm, are best seen from this ventral (“bottom-up”) perspective.



pons, medulla, and cerebellar hemispheres are all readily apparent on the ventral surface of the brain.

When the two cerebral hemispheres of the brain are pulled apart and the underlying brainstem is divided by cutting in the midline, all of the brain's major subdivisions plus a number of additional structures are visible on the medial surface of the hemispheres (**Figure A.13A,B**; see also **Figure A.11B**). In this view, the frontal lobe extends forward from the central sulcus, the medial end of which can just be seen. The **parieto-occipital sulcus**, running from the superior to the inferior aspect of the hemisphere, separates the parietal and occipital lobes. The **calcarine sulcus** marks the location of the primary visual cortex on the medial surface of the occipital lobe, running at very nearly a right angle from the parieto-occipital sulcus. A long, roughly horizontal sulcus, the **cingulate sulcus**, stretches across the medial surface of the frontal lobe, extending into the anterior parietal lobe. The prominent gyrus below it, the **cingulate gyrus**, figures prominently in discussions of emotion and social cognition. These structures are also important in the regulation of visceral motor activity, which is closely tied to emotional expression. Finally, ventral to the cingulate gyrus is the midsagittal surface of the **corpus callosum**, a massive white matter tract that is the major route for the transfer of information between the two cerebral hemispheres.

Although parts of the diencephalon, brainstem, and cerebellum are visible on the ventral surface of the brain, their overall structure is especially clear in views of the medial surface. From this perspective, the **diencephalon** can be seen to consist of two parts (**Figure A.13C**). The **thalamus**, the largest component of the diencephalon, comprises a number of nuclear subdivisions, all of which relay information to the cerebral cortex from other parts of the brain; the most posterior part of the thalamus is called the **pulvinar** (see **Figure A.9A**), which is important in visual attention. The **hypothalamus**, a small but crucial part of the diencephalon, is devoted to the control of homeostatic (stability-maintaining) and reproductive functions, often over natural cycles such as days or months. The hypothalamus is intimately related, both structurally and functionally, to the pituitary gland, an endocrine organ whose posterior part is attached to the hypothalamus by the pituitary stalk.

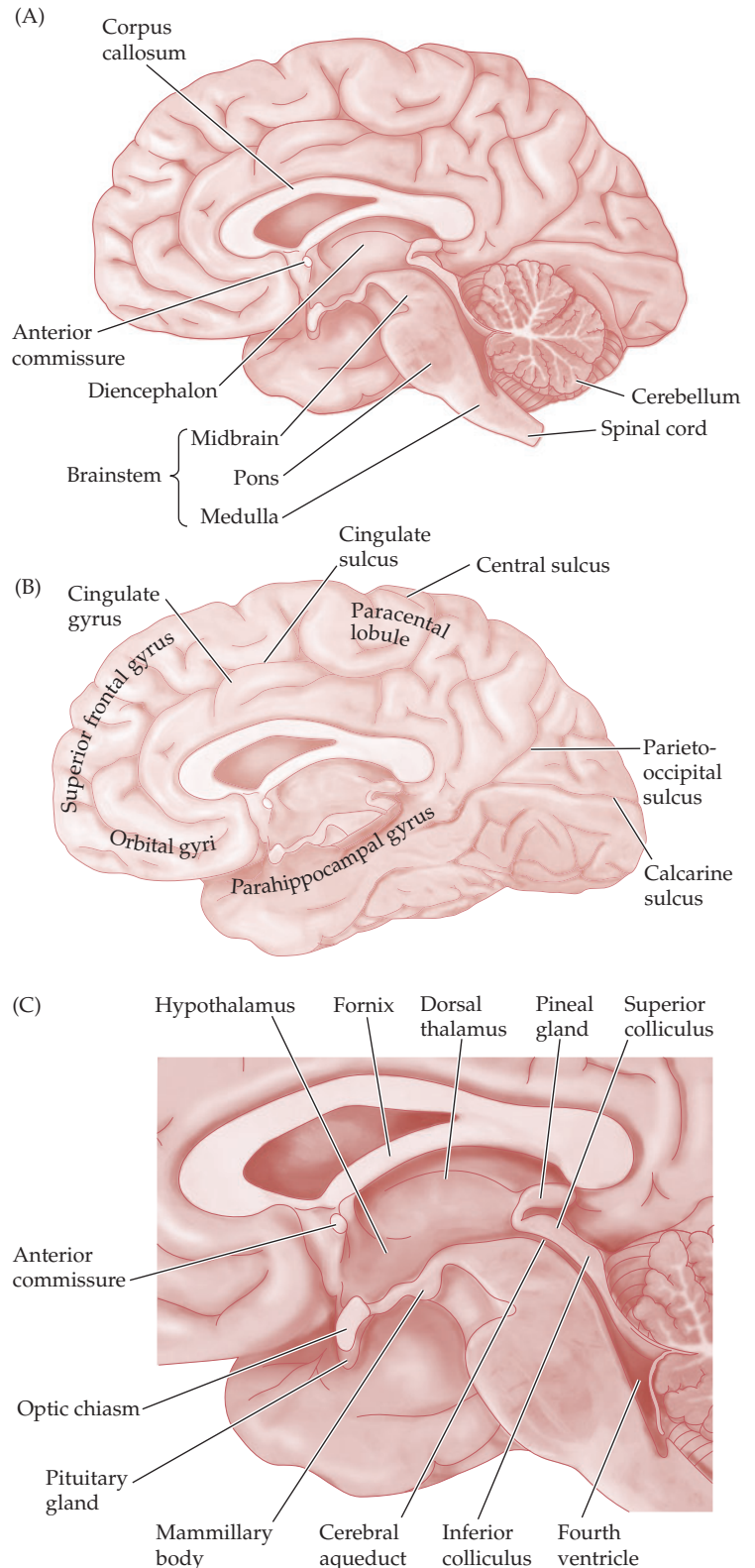
Figure A.13 View of the brain surface after separating the hemispheres at the midline (A) An overview of the major features visible after bisecting the brain in the midsagittal plane (see Box A3). (B) The major gyri, sulci, and other features visible in this view after removal of the brainstem. (C) Blowup of a region of the diencephalon, indicating the thalamus and some of the major landmarks that are important in the text.

The midbrain, which can be seen only in this medial view, lies caudal to the thalamus; as noted, the superior and inferior colliculi define the midbrain's dorsal (back-facing) surface, or *tectum* (meaning "roof"). Several midbrain nuclei, including the substantia nigra, lie in the ventral portion, or **tegmentum** ("covering") of the midbrain. The pons ("bridge") lies caudal to the midbrain along the midsagittal surface, and the **cerebellum** lies over the pons, just beneath the occipital lobe of the cerebral hemispheres; in fact the pons is largely a collection of nerve cell axons and nuclei related to the cerebellum. The cerebellum's major function is coordination of motor activity, posture, and equilibrium, although it is implicated in some cognitive functions as well. From the midsagittal surface, the most visible feature of the cerebellum is the **cerebellar cortex**, a continuous, layered sheet of cells folded into ridges and valleys called **folia** (singular, *folium*).

Finally, the most caudal structure seen from the midsagittal surface of the brain is the medulla, which merges into the spinal cord.

Internal features of the brain

Many structures are not visible from any brain surface but are apparent when the organ is cut in sections and examined grossly (i.e., with the unaided eye) or, as is commonly done, stained with one of a variety of chemical agents that highlight different structures, such as the stains for myelin that accentuate the brain's white matter tracts. Understanding this sectional anatomy is especially pertinent to cognitive neuroscience because internal structures can be seen quite easily in the sections routinely generated by the noninvasive brain imaging techniques that are described in detail in Chapter 2. Modern brain imaging methods are used far more widely today than is the examination of postmortem brain sections in the pathology laboratory (see Figure A.7B). Thus, a major challenge—and a basic requirement in cognitive neuroscience—is learning to move easily from surface neuroanatomy to recognizing the brain's internal structures. **Box A3** provides a brief overview of some anatomical terminology needed for understanding the brain as a whole and in histological or MRI sections.



BOX A3 ANATOMICAL TERMINOLOGY

An obstacle to understanding the internal structure of the brain is the sometimes confusing nomenclature used to specify anatomical locations. Although many of the terms used to describe spatial orientation in the brain are the same as those used for anatomical descriptions of the rest of the body, the meanings of some of the terms differ. For the body, the anatomical terms in common use refer to the long axis, which is more or less straight. The long axis of the central nervous system, however, has a bend in it. Thus, in describing the brain the simplest terms are *anterior* and *posterior*, which indicate the direction of the front (face) and back of the head, respectively. However, the somewhat more difficult terms *rostral* and *caudal* are also used for some descriptions; *rostral* indicates the direction toward the nose (Latin *rostrum* means “beak”) and *caudal* toward the “tail” (*caudum*), which refers to the base of the skull. When applied to the long axis of the body, the distinctions anterior–posterior and rostral–caudal

are synonymous, both indicating “top to tail”; but because of the bend in the axis of the nervous system, they have somewhat different meanings in brain anatomy, as indicated in Figure A. This discrepancy is not a major problem but is important to be aware of.

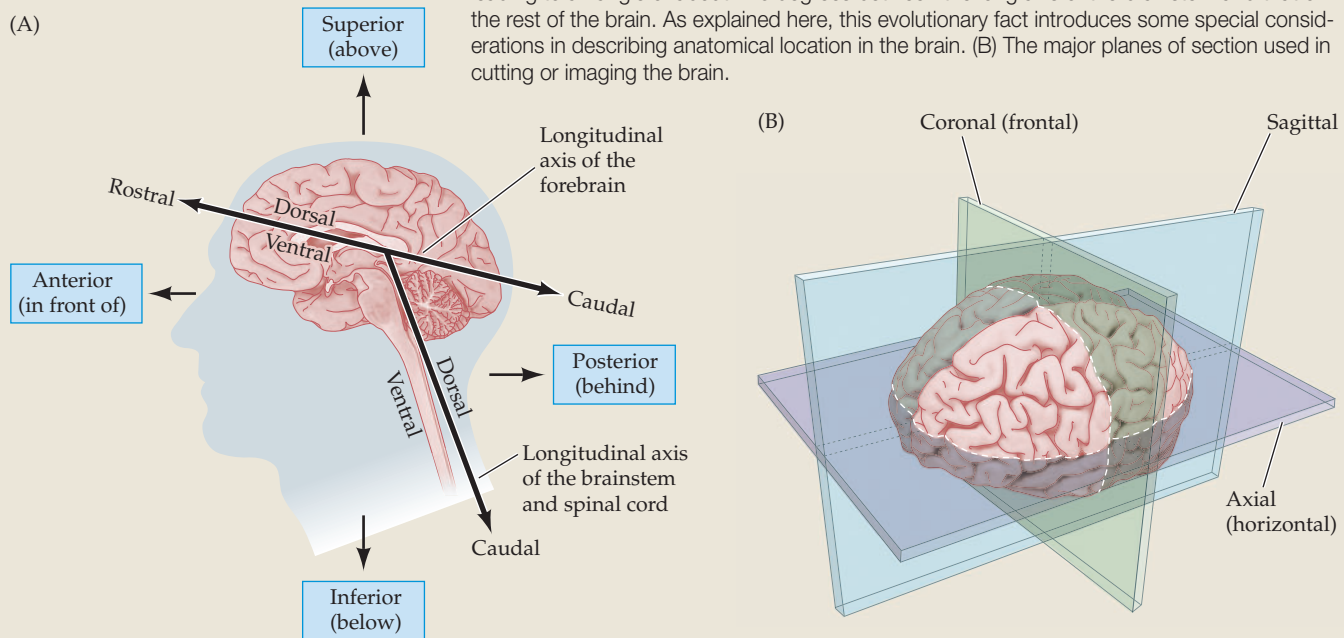
The terms *dorsal* and *ventral* present a similar case. When speaking of the body or spinal cord axes, *dorsal* refers to the back (Latin *dorsum*) and *ventral* to the front, or belly (Latin *ventrum*). When referring to the brain, however, *dorsal* refers to the upper and *ventral* to the lower surface (see Figure A). Other spatial descriptions apply in the same way to the brain and the body. These include *medial* and *lateral*, toward the midline (center) or to the side (left or right), respectively; and *inferior* and *superior*, above and below.

More significant for cognitive neuroscience is the terminology applied to *sections* (i.e., slices) of the brain—either those made by a knife in the neuropa-

thology lab, or the sections that are now routinely visualized by noninvasive brain imaging techniques (see Chapter 2). By convention, sections of the brain that are parallel to the rostral–caudal axis are referred to as *horizontal* or *axial*, sections taken in the plane that divides the brain’s two hemispheres are called *sagittal*, and sections in the plane of the face are called *frontal* or *coronal* (Figure B).

The sectional terminology for the spinal cord, though it does not figure significantly in this book, is based on the terms used in considering sections of the body as a whole. Thus, the plane of section perpendicular to the long axis of the body or spinal cord is called a *transverse* (or “cross”) section, and sections parallel to the long axis of the body or spinal cord are called *longitudinal*. In a transverse section through the spinal cord, the terms *dorsal–ventral axis* and *anterior–posterior axis* indicate the same direction.

(A) A bend in the long axis of the nervous system arose as humans evolved upright posture, leading to an angle of about 120 degrees between the long axis of the brainstem and that of the rest of the brain. As explained here, this evolutionary fact introduces some special considerations in describing anatomical location in the brain. (B) The major planes of section used in cutting or imaging the brain.



In any plane of section, the cerebral cortex is evident as a thin layer of neural tissue that covers the entire cerebrum. The largest structures embedded within the cerebral hemispheres are two nuclei called the **caudate** and **putamen** (together these nuclei are referred to as the **striatum**), which are closely associated with another nucleus, called the **globus pallidus** (Figure A.14A,B). Because of the related location and function of these three nuclei, they are referred to

collectively as the **basal ganglia** (the use of the term *ganglia* in this case is an exception to the usual usage of this word described earlier in its application to collections of peripheral nerve cells; this idiosyncratic use is historical and refers to a collection of related nuclear structures). As **Figure A.14C** suggests, the basal ganglia are visible in horizontal sections through the mid-dorsal to mid-ventral portion of the forebrain, in frontal sections from just rostral to the uncus to the level of the diencephalon, and in all paramedian sagittal sections.

The neurons in the large nuclear complexes of the basal ganglia receive input from the cerebral cortex and participate in the organization and guidance of complex motor functions, as well as many other cortical feedback loops, many of which are relevant to a range of cognitive functions. In the base of the forebrain, ventral to the basal ganglia, are several smaller clusters of nerve cells known as the **septal**, or **basal, forebrain nuclei**. The function of these latter nuclei is not well understood, but they are of particular interest because of their involvement in the early signs and symptoms of Alzheimer's disease.

The other clearly discernible structure visible in coronal sections through the cerebral hemispheres at the level shown in **Figure A.14A** is the **amygdala**, a collection of nuclei that lies in front of the hippocampus in the anterior pole of the temporal lobe. Some nuclei of the amygdala are especially important in emotional processing.

In addition to these cortical and nuclear structures, the internal anatomy of the brain shows the major axon tracts mentioned earlier. As already mentioned, the two cerebral hemispheres are interconnected by the corpus callosum, which is apparent in the majority of coronal sections; in some anterior sections, the much smaller **anterior commissure**, another interhemispheric tract, can also be seen (as in **Figure A.14A**). Another tract that is pertinent in the text is the **fornix**, which connects the hippocampus and the hypothalamus (see **Figure A.14B**). Finally, axons descending from and ascending to the cerebral cortex assemble into another very large and extensive tract called the **internal capsule**. The internal capsule lies just lateral to the thalamus (which is how it gets its name, since it forms a sort of

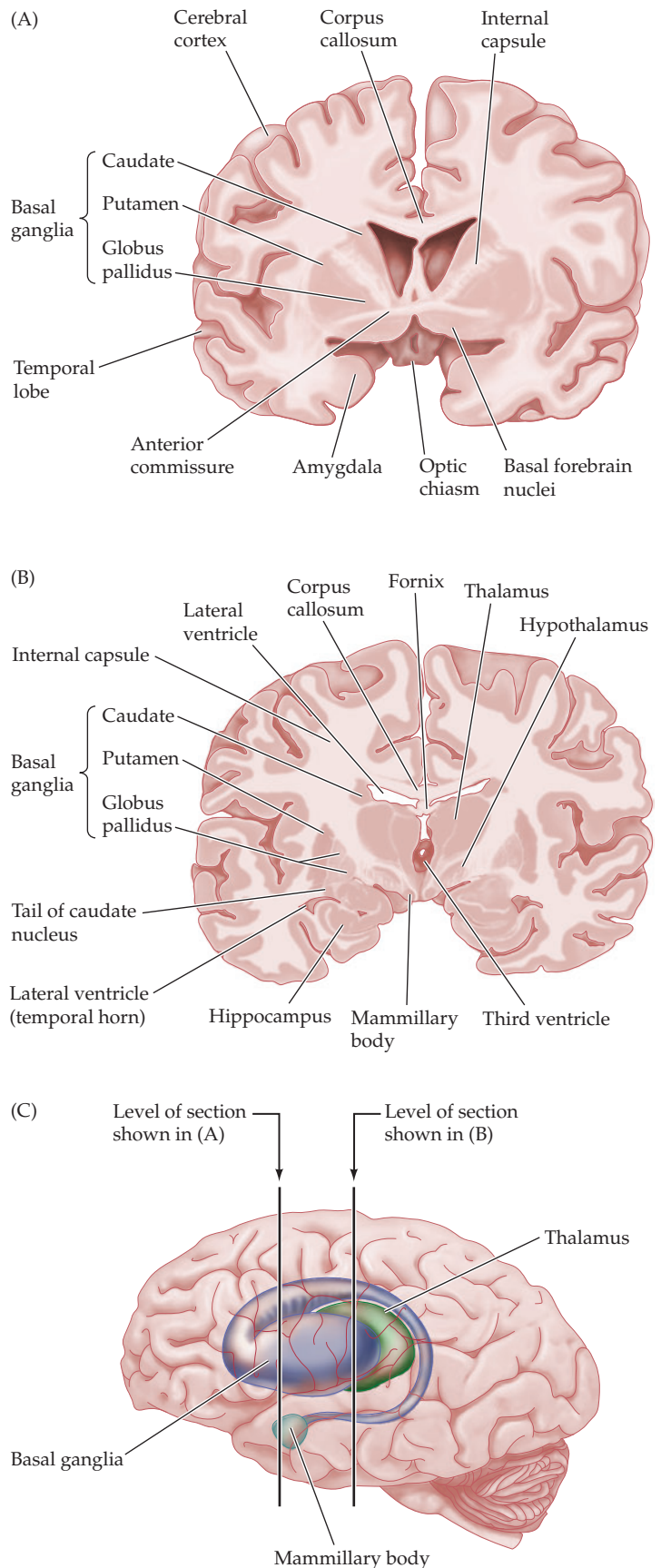
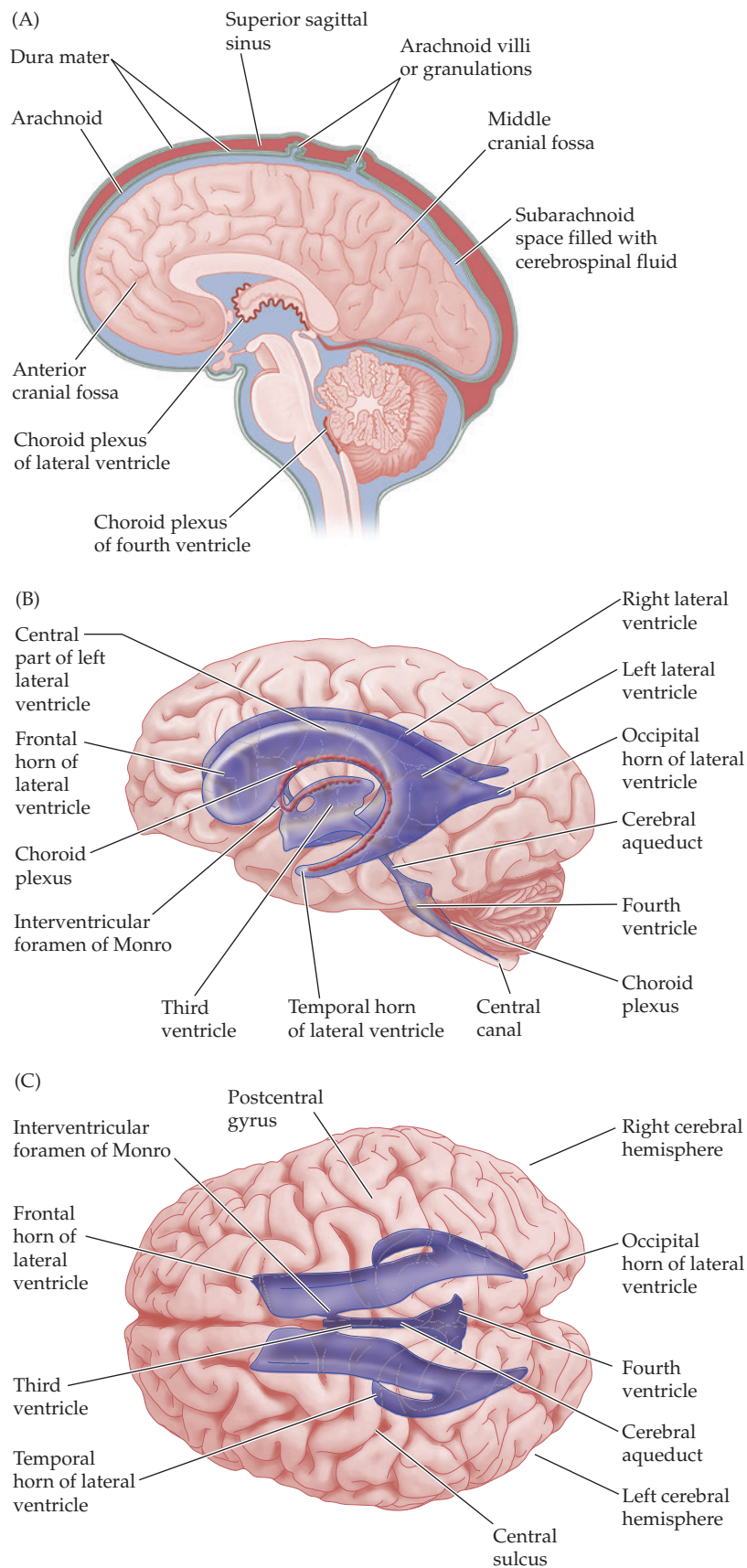


Figure A.14 Internal brain structures seen in coronal sections These coronal views reveal important structures in the deep gray matter of the brain. (A) This section passes through the basal ganglia (caudate, putamen, and globus pallidus) and the amygdala. (B) This more posterior coronal section includes the thalamus. All of these structures are of major significance in cognitive studies. (C) This “transparent” lateral view shows the approximate locations of the sections in (A) and (B).

Figure A.15 The ventricular system

The ventricles are a series of interconnected spaces deep in the fore-brain and brainstem. These spaces are filled with cerebrospinal fluid. (A) Lateral view showing the main features of the system. (B) This “transparent” lateral view shows the ventricular system as a whole. (C) Another “transparent” view of the ventricles, this one from the brain’s dorsal surface, looking downward.



“capsule” around the thalamus), and many internal capsule axons arise from or terminate in the dorsal thalamus. As might be expected from its location, the internal capsule is most obvious in frontal sections through the middle third of the rostral–caudal extent of forebrain, or in horizontal sections through the level of the thalamus. The axons of the internal capsule enter the cerebral peduncles that connect the cerebral hemispheres to the brainstem. Thus, the internal capsule is the major pathway linking the cerebral cortex to the rest of the brain and spinal cord.

The ventricular system

It is important to be familiar with another feature of the internal anatomy of the brain: the ventricular system (**Figure A.15**), the location of which is particularly helpful in interpreting noninvasive brain images. The ventricles of the brain are a series of interconnected, fluid-filled spaces that lie deep in the forebrain and brainstem. Ventricles are the adult reflection of the open space (the *lumen*) of the embryonic neural tube, around which the central nervous system initially develops (see Chapter 15). The largest of these spaces are the **lateral ventricles** (one within each of the cerebral hemispheres). The lateral ventricles are best seen in frontal sections, where their ventral surface is defined by the basal ganglia, their dorsal surface by the corpus callosum, and their medial surface by the septum pellucidum, a membranous tissue sheet that forms part of the midline sagittal surface of the cerebral hemispheres.

The **third ventricle** forms a narrow midline space between the right and left thalamus, and it communicates with the lateral ventricles through a small opening (the *interventricular foramen*) at the anterior end of the third ventricle. The third ventricle is continuous caudally with the **cerebral aqueduct**, which runs through the midbrain. At its caudal end, the aqueduct opens into the **fourth ventricle**, a larger space in the dorsal pons and medulla. The fourth ventricle narrows caudally to form the central canal of the spinal cord.

The ventricles are filled with **cerebrospinal fluid**, and the lateral, third, and fourth ventricles are the sites of the **choroid plexus**, which produces this fluid. Cerebrospinal fluid percolates through the ventricular system and flows into the subarachnoid space through perforations in the thin covering of the fourth ventricle; the fluid is eventually absorbed by specialized structures called arachnoid villi, and is thus returned to the venous circulation. Although the ventricles have no obvious function other than serving as conduits for the circulation of cerebrospinal fluid, their locations provide excellent landmarks for deciphering brain sections.

The Brain's Blood Supply

As is apparent in various chapters of this text, much insight into cognitive functions has come from the clinical consequences of **stroke**, a generic term that refers to the clinical and neuropathological results of interrupting the blood supply to one or another region of the brain. Such interruptions can be caused by the obstruction of an artery or by hemorrhage (bleeding) from a blood vessel that ruptures. The resulting damage is referred to as a **brain lesion**, a term that also refers to damage from other causes, including trauma and tumors.

The blood supply of the brain is particularly significant because neurons are more sensitive to oxygen deprivation than are other kinds of cells, which generally have lower rates of metabolism. Brain tissue deprived of oxygen and glucose as a result of compromised blood supply is especially likely to sustain transient or permanent damage. Even a brief loss of blood supply (a few minutes), referred to as **ischemia**, can cause cellular changes that, if not quickly reversed, lead to cell death.