CHAPTER

2

How Is the Brain Organized?

A. Klehr / Stone Images
Micrograph: Carolina Biological Supply Co. / Phototake

When buying a new car, people first inspect the outside carefully, admiring the flawless finish and perhaps even kicking the tires. Then they open the hood and examine the engine, the part of the car responsible for most of its behavior—and misbehavior. This means gazing at a maze of tubes, wires, boxes, and fluid reservoirs. All most of us can do is gaze, because what we see simply makes no sense, except in the most general way. We know that the engine burns gasoline to make the car move and somehow generates electricity to run the radio and lights. But this tells us nothing about what all the engine's many parts do. What we need is information about how such a system works.

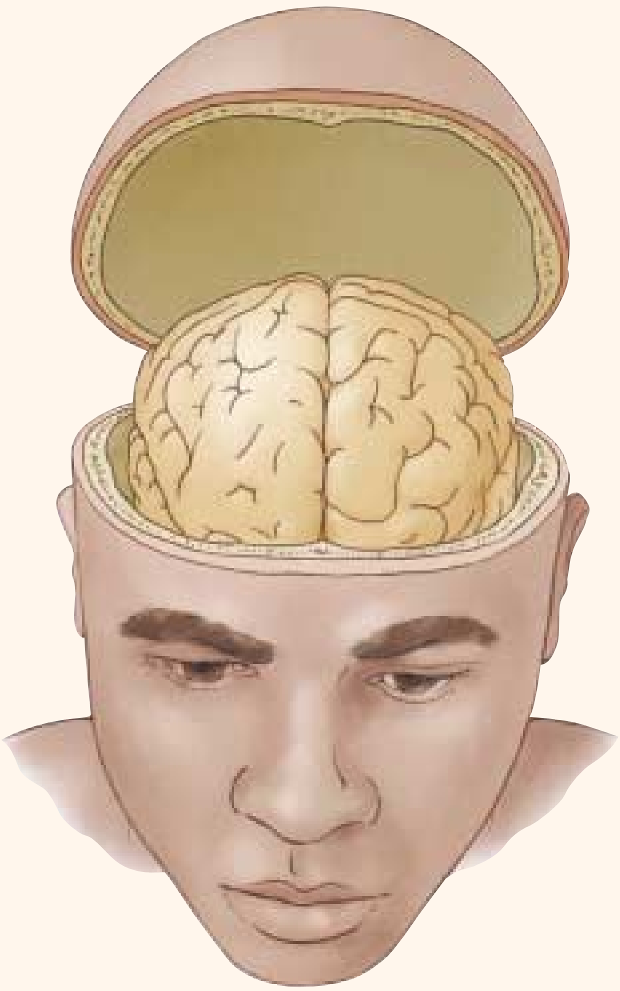


Figure 2-1
View of the human brain when the skull is opened. The gyri (bumps) and sulci (cracks) of the cerebral hemispheres are visible, but their appearence gives little information about their function.

In many ways, examining a brain for the first time is similar to looking under the hood of a car. We have a vague sense of what the brain does but no sense of how the parts that we see accomplish these tasks. We may not even be able to identify many of the parts. In fact, at first glance the outside of a brain may look more like a mass of folded tubes divided down the middle than like a structure with many interconnected pieces. See what you can make of the human brain in Figure 2-1. Can you say anything about how it works? At least a car engine has parts with regular shapes that are recognizably similar in different engines. This is not true of mammals' brains, as shown in Figure 2-2. When we compare the brain of a cat with that of a human, for example, we see that there is an enormous difference not just in overall size, but in the relative sizes of parts and in structure. In fact, some parts present in one are totally absent in the other. What is it that all these parts do that makes one animal stalk mice and another read textbooks?

To make matters worse, even for trained research scientists, the arrangement of the brain's parts does not just *seem* random, it really *is* haphazard. The challenge that we face in learning about the brain is to identify some regularities in its organization and to establish a set of principles that can help us understand how the nervous system works. After decades of investigation, we now have a good idea of how the nervous system functions, at least in a general way. That knowledge is the subject of this chapter. But before we turn our attention to the operation manual for the brain and the rest of the nervous system, let us examine what the brain is designed to do. Knowing the brain's functions will make it easier to grasp the rules of how it works.

Perhaps the simplest statement of the brain's functions is that it produces behavior, as seen in Chapter 1. There is more to this statement than is immediately apparent, however. In order for the brain to produce behavior, it must have information about the world, such as information about the objects around us—their size, shape, movement, and so forth. Without such information, the brain cannot know how to orient and direct the body to produce an appropriate response. This is especially true when the response needed is some complex behavior, such as

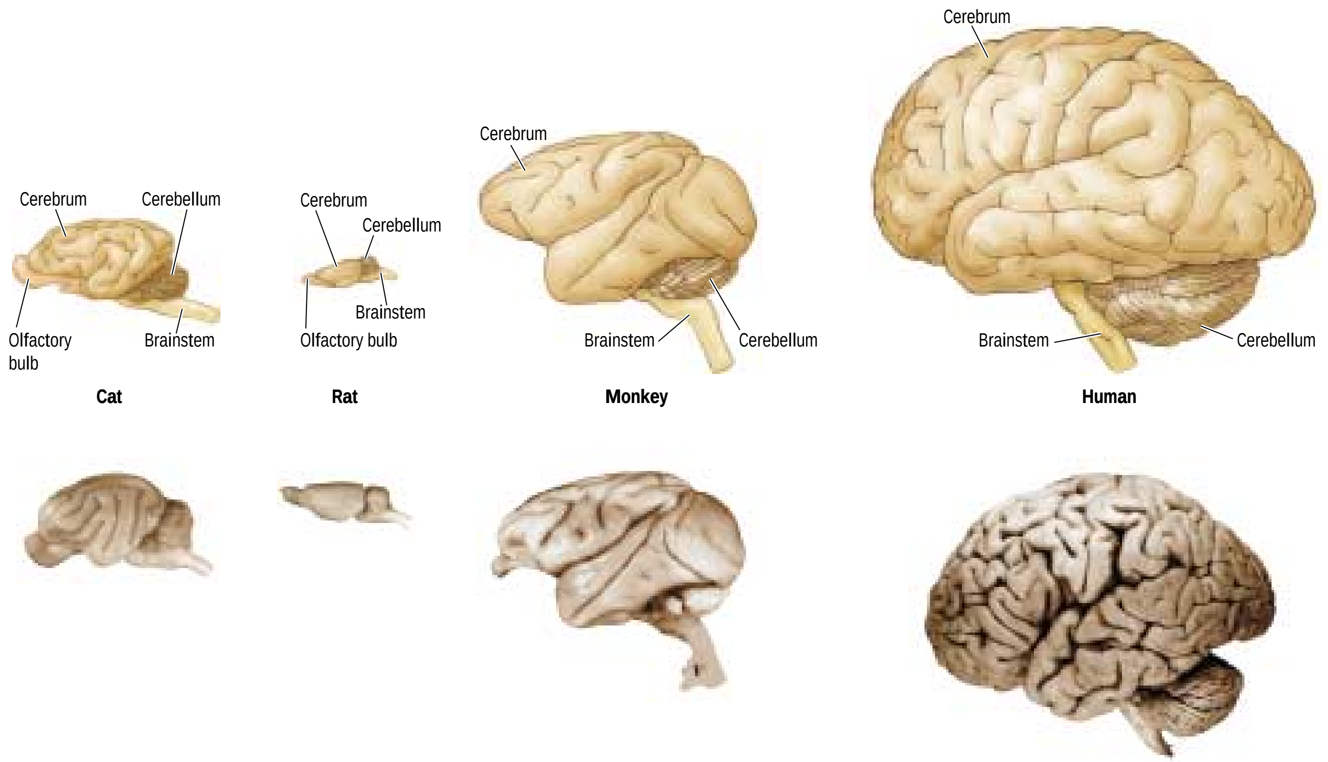


Figure 2-2

Inspection of the outside features of the brains of a cat, rat, monkey, and human shows them to differ dramatically in size and in general appearance. The rat brain is smooth, whereas the other brains have furrows in the cerebral cortex. The pattern of furrows differs considerably in the human, the monkey, and the cat. The cat brain and, to some extent, the monkey brain have long folds that appear to run much of the length of the brain, whereas the human brain has a more diffuse pattern. The cerebellum is wrinkled in all species and is located above the brainstem. The brainstem is the route by which information enters and exits the brain. The olfactory bulb, which controls the perception of smells, is relatively larger in cats and rats but is not visible in monkeys and humans, because it is small and lies under the brain.

Photos courtesy of Wally Welker, University of Wisconsin Comparative Mammalian Brain Collection.

catching a ball. To perform complex behaviors, the nervous system has organs designed to receive information from the world and convert this information into biological activity that produces subjective experiences of reality. The brain thus produces what we believe is reality in order for us to move. These subjective experiences of reality are essential to carrying out any complex task.

This view of the brain's primary purpose may seem abstract to you, but it is central to understanding how the brain functions. Consider the task of answering a telephone. The brain directs the body to pick up the receiver when the nervous system responds to vibrating molecules of air by creating the subjective experience of a ring. We perceive this sound and react to it as if it actually existed, when in fact the sound is merely a fabrication of the brain. That fabrication is produced by a chain reaction that takes place when vibrating air molecules hit the eardrum. In the absence of the nervous system, especially the brain, there is no such thing as sound. Rather, there is only the movement of air molecules.

The subjective nature of the experiences that the brain creates can be better understood by comparing the realities of two different kinds of animals. You are probably aware that dogs perceive sounds that humans do not. This difference in perception does not mean that a dog's nervous system is better than ours or that our hearing is poorer. Rather, a dog brain simply creates a different world from that of our brain. Neither subjective experience is "right." The difference in experience is merely due to two different systems for processing physical stimuli. The same differences exist in visual perceptions. Dogs see very little color, whereas our world is rich with color because our brains create a different reality from that of a dog's brain. Such differences in subjective realities exist for good reason: they allow different animals to exploit different features of their environments. Dogs use their hearing to detect the movements of mice in the grass, whereas early humans probably used color for such tasks as identifying ripe fruit in trees. Evolution, then, equipped each species with a view of the world that would help it survive.

These examples show how a brain's sensory experiences help guide an organism's behavior. For this link between sensory processing and behavior to be made, the brain must also have a system for accumulating, integrating, and using knowledge. Whenever the brain collects sensory information, it is essentially creating knowledge about the world, knowledge that can be used to produce more effective behaviors. The knowledge currently being created in one sensory domain can be compared both with past knowledge and with knowledge gathered in other domains.

We can now identify the brain's three primary functions:

1. to produce behavior;
2. to create a sensory reality; and
3. to create knowledge that integrates information from different times and sensory domains and to use that knowledge to guide behavior.

Each of the brain's three functions requires specific machinery. The brain must have systems to create the sensory world, systems to produce behavior, and systems to integrate the two.

In this chapter, we consider the basic structures and functions of those systems. First, we identify the components of the nervous system. Then we look at what those components do. Finally, we look at how the parts work together and at some general principles of brain function. Many of the ideas introduced in this chapter are developed throughout the rest of the book, so you may want to return to this chapter often to reconsider the basic principles as new topics are introduced.

AN OVERVIEW OF BRAIN STRUCTURE

The place to start our overview of the brain's structure is to "open the hood" by opening the skull and looking at the brain snug in its home. Figure 2-1 shows a brain viewed from this perspective. The features that you see are part of what is called the brain's "gross anatomy," not because they are ugly, but because they constitute a broad overview. Zooming in on the brain's microscopic cells and fibers is largely reserved for Chapter 3, although this section ends with a brief introduction of some terms used for these tiny structures. Those terms are just a few of a great many new terms that you will encounter in this book, which is why we deal with brain terminology in general before moving on to a look at the brain itself. Because many of the words in this chapter will seem foreign to you, they will be accompanied by a pronunciation guide at their first appearance.

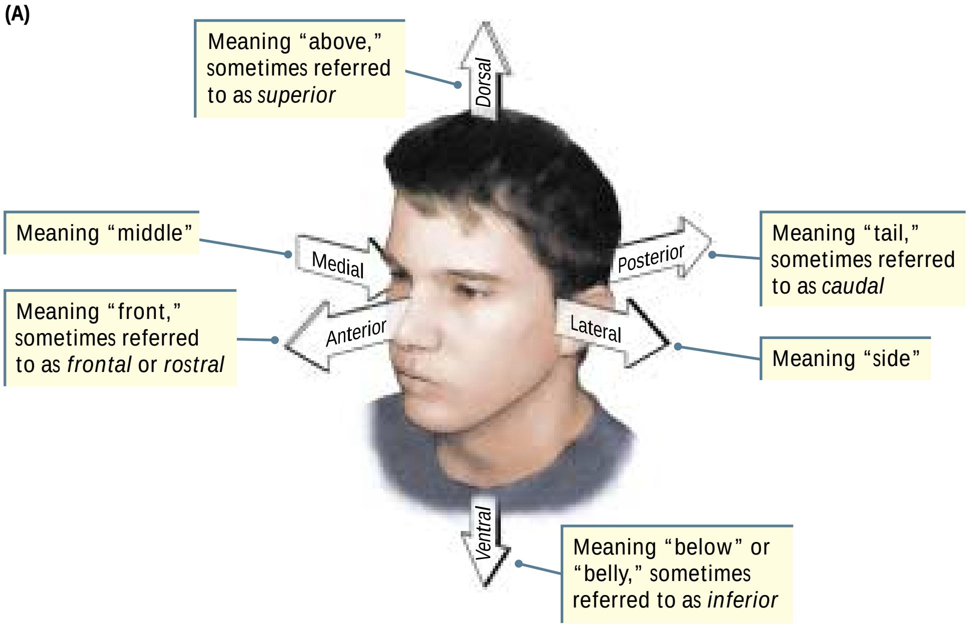
Brain Terminology

There are hundreds, even thousands of brain regions, making the task of mastering brain terminology seem daunting. To make matters worse, many structures have several names, and many terms are often used interchangeably. This peculiar nomenclature arose because research on brain and behavior has spanned several centuries. When the first anatomists began to examine the brain with the primitive tools of their time, they made many erroneous assumptions about how the brain works, and the names that they chose for brain regions are often manifestations of those errors. For

Link to an index listing the roots of neuroanatomical terms at **www.worthpublishers.com/kolb/chapter2.**

Figure 2-3

Anatomical terms are used to describe anatomical locations. **(A)** Anatomical directions relative to the head and brain. Because a human is upright, the terms *posterior* and *caudal* (both meaning "tail") refer to a slightly different orientation for the human head compared with the head of a four-legged animal. **(B)** Anatomical directions relative to the body.



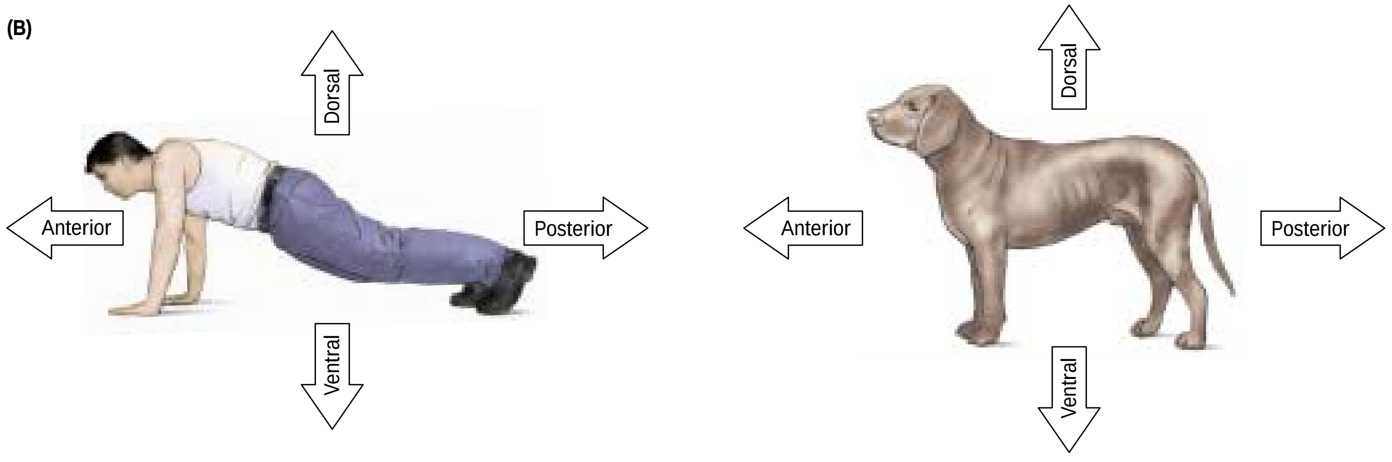
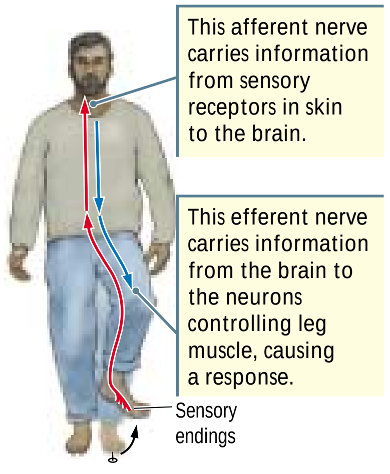


Figure 2-4

An afferent nerve carries information into the brain, and an efferent nerve takes information out of the brain and controls movement of a muscle.



instance, they named one region of the brain the *gyrus fornicatus* because they thought it had a role in sexual function. In fact, most of this region has nothing to do with sexual function. Another area was named the *red nucleus* because it appears reddish in fresh tissue. This name denotes nothing of the area's potential functions, which turn out to be the control of limb movements.

As time went on, the assumptions and tools of brain research changed, but the naming continued to be haphazard and inconsistent. Early investigators named structures after themselves or objects or ideas. They used different languages, especially Latin, Greek, and English. More recently, investigators have often used numbers or letters, but even this system lacks coherence because the numbers may be Arabic or Roman numerals and are often used in combination with letters, which may be either Greek or Latin. When we look at current brain terminology, then, we see a mixture of all these naming systems.

Despite this sometimes confusing variety, many names do include information about a structure's location in the brain. Table 2-1 summarizes these location-related terms, and Figure 2-3 shows how they relate to body locations. Structures found on the top of the brain or on the top of some structure within the brain are *dorsal*. Structures located toward the bottom of the brain or one of its parts are *ventral*. Structures found toward the middle of the brain are *medial*, whereas those located toward the side are *lateral*. Structures located toward the front of the brain are *anterior*, whereas those located toward the back of the brain are *posterior*. Sometimes the terms *rostral* and *caudal* are used instead of *anterior* and *posterior*, respectively. And, occasionally, the terms *superior* and *inferior* are used to refer to structures that are located dorsally or ventrally (these terms do *not* label structures according to their importance). It is also common to combine terms. For example, a structure may be described as *dorsolateral*, which means that it is located "up and to the side."

You should also learn two terms that describe the direction of information flowing to and from cells in the brain. **Afferent** refers to information coming into the brain or a part of the brain, whereas **efferent** refers to information leaving the brain or one of its parts, meaning that efferent refers to brain signals that trigger some response (Figure 2-4). These words are very similar, but there is an easy way to keep them straight. The letter "a" in *afferent* comes alphabetically before the "e" in *efferent*, and sensory information must come into the brain *before* an outward-flowing signal can trigger a response. Therefore, *afferent* means "incoming" and *efferent* means "outgoing."

Table 2-1 Orientation Terms for the Brain

Term	Meaning with respect to the nervous system
Anterior	Located near or toward the front or the head
Caudal	Located near or toward the tail
Dorsal	On or toward the back or, in reference to brain nuclei, located above
Frontal	"Of the front" or, in reference to brain sections, a viewing orientation from the front
Inferior	Located below
Lateral	Toward the side of the body
Medial	Toward the middle; sometimes written as *mesial*
Posterior	Located near or toward the tail
Rostral	"Toward the beak"; located toward the front
Sagittal	Parallel to the length (from front to back) of the skull; used in reference to a plane
Superior	Located above
Ventral	On or toward the belly or side of the animal in which the belly is located or, in reference to brain nuclei, located below

On the CD, visit the module on the Central Nervous System to better visualize the various planes of the brain.

The Brain's Surface Features

Returning to the brain in the open skull, you are now ready to examine its structures more closely. The first thing to notice is that the brain is covered by a tough material known as the **meninges** [*men **in** jeez* (the accented syllable is in boldface type)], which is a three-layered structure, as illustrated in Figure 2-5. The outer layer is known as the *dura mater* (from Latin, meaning "hard mother"). It is a tough double layer of fibrous tissue enclosing the brain in a kind of loose sack. The middle layer is the *arachnoid* layer (from Greek, meaning "like a spider's web"). It is a very thin sheet of delicate

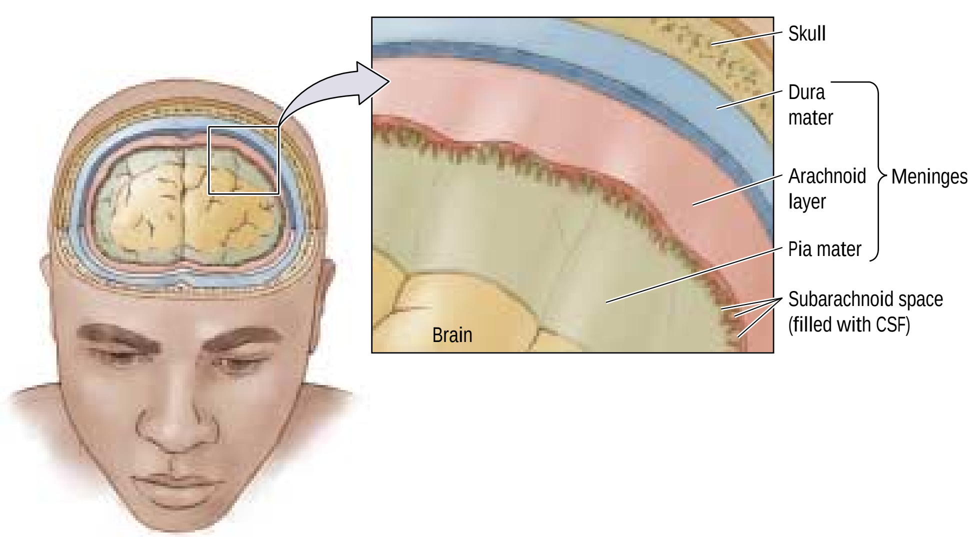


Figure 2-5
The brain is covered by thick coverings known as the meninges and is cushioned by a fluid known as the cerebrospinal fluid (CSF).

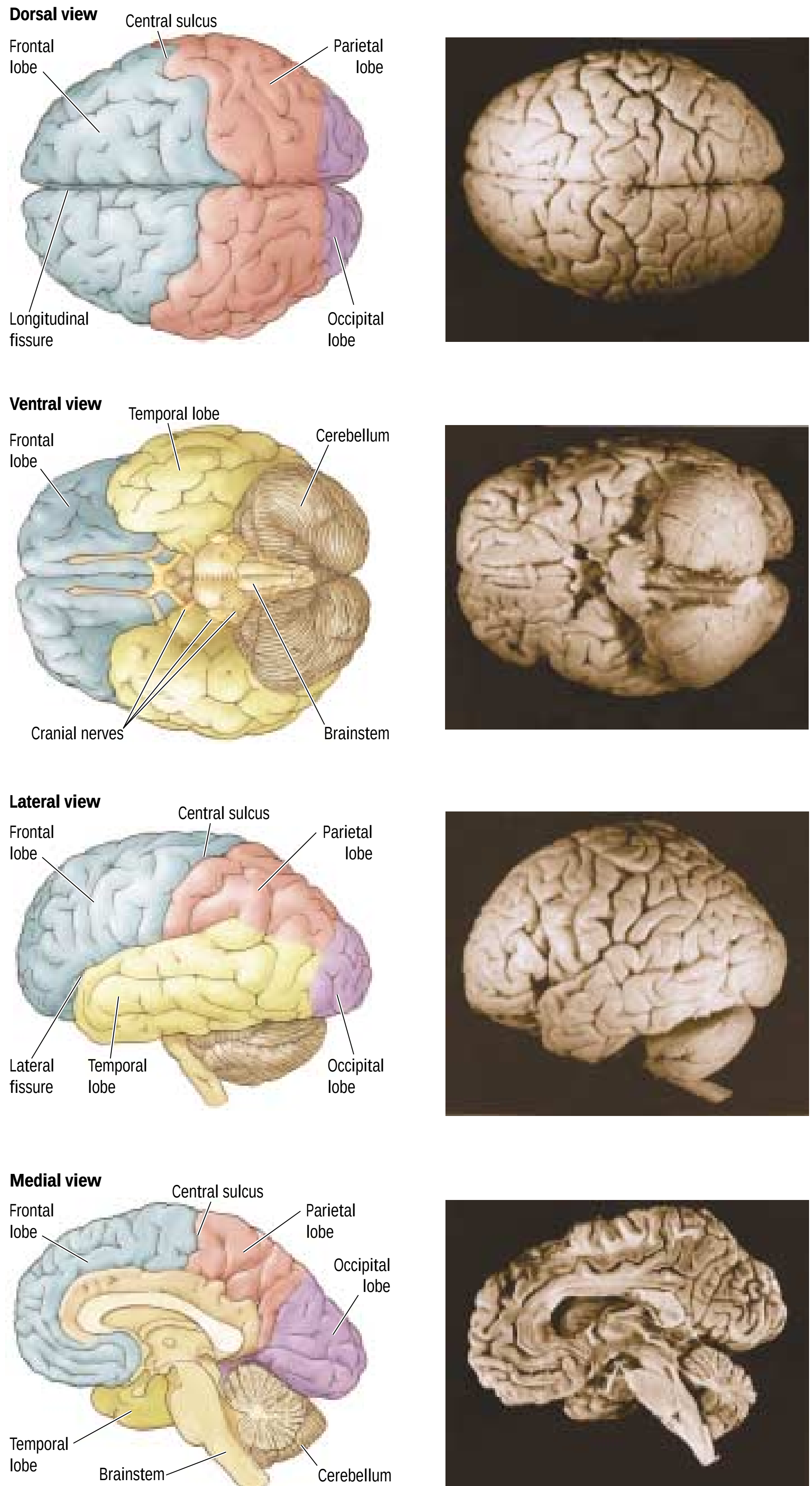


Figure 2-6

In these views of the human brain (from the top, bottom, side, and middle), the locations of the frontal, parietal, occipital, and temporal lobes of the cerebral hemispheres are shown, as are the cerebellum and the three major sulci (the central sulcus, lateral fissure, and longitudinal fissure) of the cerebral hemispheres.

Photos courtesy of Yakolev Collection/AFIP.

connective tissue that follows the brain's contours. The inner layer is the *pia mater* (from Latin, meaning "soft mother"). It is a moderately tough membrane of connective-tissue fibers that cling to the surface of the brain. Between the arachnoid and pia mater is a fluid, known as **cerebrospinal fluid (CSF),** which is a colorless solution of sodium chloride and other salts. It provides a cushion so that the brain can move or expand slightly without pressing on the skull. (Meningitis is an infection of the meninges. Its symptoms are described in "Meningitis and Encephalitis" on page 46.)

If we remove the meninges, we can now remove the brain from the skull and examine its various parts. As we look at the brain from the top or the side, it appears to have two major parts, each wrinkly in appearance. The larger part is the **cerebrum** [*sa* ***ree*** *brum*], which consists of two cerebral hemispheres, the left and the right, and the smaller part is the **cerebellum** [*sair a* ***bell*** *um*]. Both the cerebrum and the cerebellum are visible in the brains shown in Figure 2-2. Each of these structures is wrinkled in large-brained animals because its outer surface is made of a relatively thin sheet of tissue, the cortex, that has been pushed together to make it fit into the skull. To see why the cortex is wrinkled, force a piece of writing paper, $8^1/_2$ by 11 inches, into a cup. The only way is to crinkle the paper up into a ball. Essentially the same crinkling-up has been done to the cortex of the cerebrum and the cerebellum. Like a crinkled piece of paper, much of the cortex is invisible from the surface. All we can see from the surface are bumps and cracks. The bumps are known as **gyri** [***jye*** *rye;* singular: gyrus (***jye*** *russ*)], whereas the cracks are known as **sulci** [***sul*** *sigh;* singular: sulcus (***sul*** *kus*)]. Some of the sulci are very deep and so are often called *fissures.* The two best-known fissures are the longitudinal fissure and the lateral fissure, both of which are shown in Figure 2-6, along with the central sulcus.

If we now look at the bottom of the brain, we see something completely different. The cerebrum is still the wrinkled part, but now there is also a whitish structure down the middle with little tubes attached. This middle structure is known as the **brainstem,** and the little tubes are **cranial nerves** that run to and from the head.

One final gross feature is obvious: the brain appears to be covered in blood vessels. As in other parts of the body, the brain receives blood through arteries and sends it back through veins to the kidneys and lungs for cleaning and oxygenation. The arteries come up the neck and then wrap around the outside of the brainstem, cerebrum, and cerebellum, finally piercing the brain's surface to get to its inner regions. Figure 2-7 shows the three major arteries that feed blood to the cerebrum—namely, the anterior, middle, and posterior cerebral arteries. Because the brain is very sensitive to loss of blood, a blockage or break in a cerebral artery is likely to lead to the death of the affected region, a condition known as a **stroke** (see "Stroke" on page 48). Because the three cerebral arteries service different parts of the brain, strokes disrupt different brain functions, depending on the artery affected.

Cerebrum. The major structure of the forebrain, consisting of two equal hemispheres (left and right).

Cerebellum. Major structure of the hindbrain specialized for motor coordination; in large-brained animals, it may also have a role in the coordination of other mental processes.

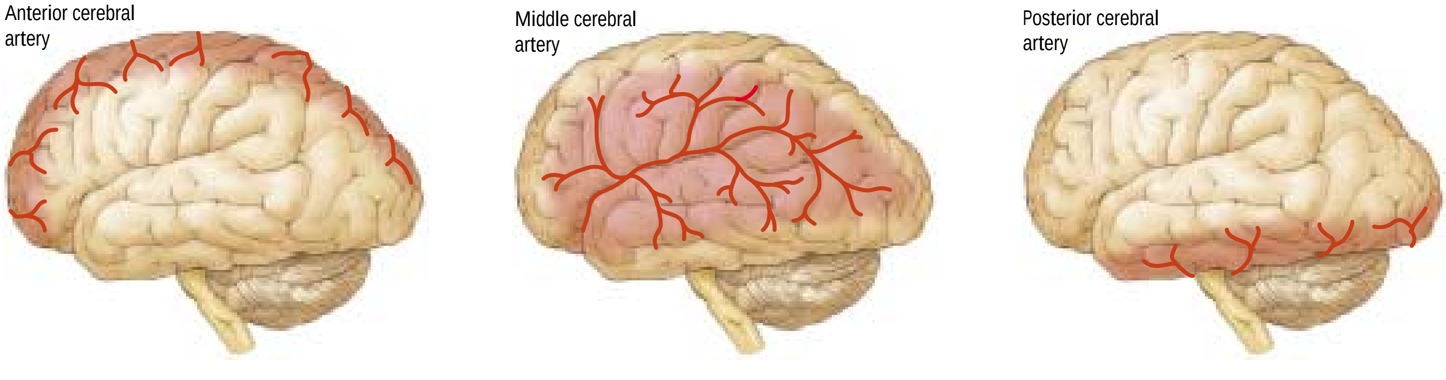
Brainstem. Central structures of the brain including the hindbrain, midbrain, thalamus, and hypothalamus.

Cranial nerve. One of a set of nerves that control sensory and motor functions of the head; includes senses of smell, vision, audition, taste, and touch on the face and head.

Plug in the CD to examine, locate, and rotate the parts of the brain in the section on the subdivisions of the CNS in the module on the Central Nervous System.

Figure 2-7

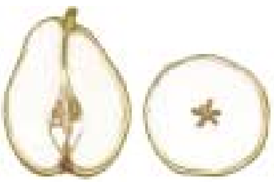
Each of the three major arteries of the cerebral hemispheres—the anterior, middle, and posterior—provides blood to a different region of the cerebrum.



White matter. Those areas of the nervous system rich in axons, leading to a white appearance.

Gray matter. Those areas of the nervous system composed predominantly of cell bodies, leading to a gray appearance.

Reticular matter. Area composed of intermixed cell bodies and axons that produce a mottled gray and white, or netlike, appearance.



Look at the CD to examine a three-dimensional model of the ventricular system in the section on subcortical structures in the module on the Central Nervous System.

The Brain's Internal Features

The simplest way to examine what is inside something—be it an engine, a pear, or a brain—is to cut it in half. The orientation in which we cut makes a difference in what we see, however. Consider what happens when we slice through a pear held in different orientations. If we cut a pear from side to side, we cut across the core; whereas, if we cut it from top to bottom, we cut parallel to the core. Our impression of what the inside of a pear looks like is clearly influenced by the way in which we slice it. The same is true of the brain.

We can begin by cutting the brain in half, slicing it downward through the middle. The result is shown in Figure 2-8. This view of the brain is known as a *frontal section* because we can now see the inside of the brain from the front.

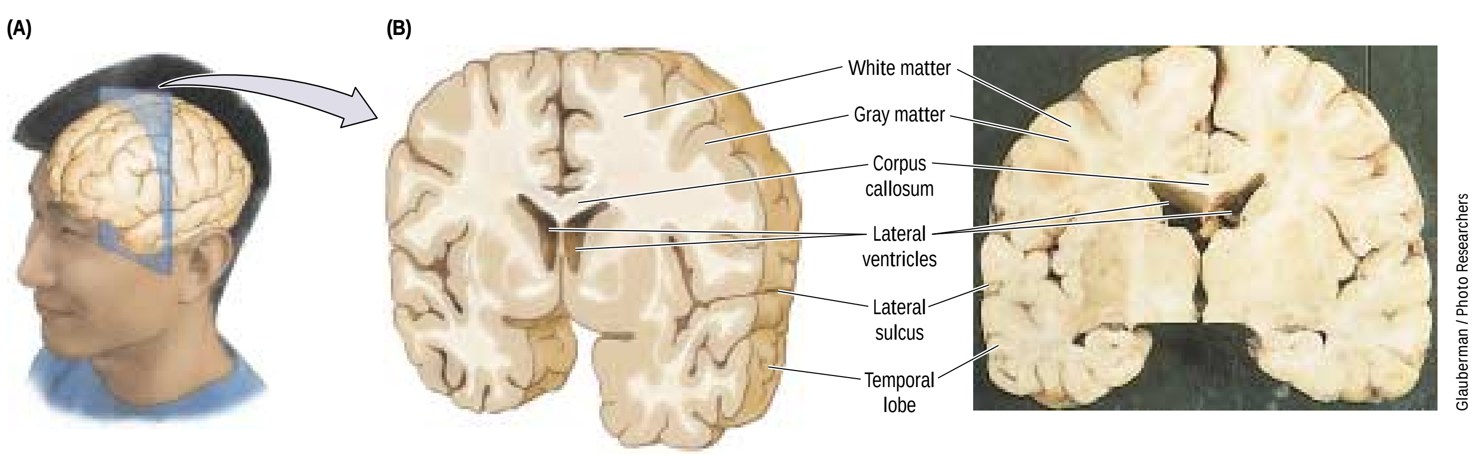
Several features of the brain's interior are immediately apparent. First, it contains four cavities, known as **ventricles** [***ven*** *trik uls*], which are shown in Figure 2-9. Cells that line the ventricles make the cerebrospinal fluid that fills them. The ventricles are connected, so CSF flows from the two lateral ventricles to the ventricles that lie on the brain's midline, eventually flowing into the space between the lower layers of the meninges as well as into the spinal-cord canal. Although the function of the ventricles is not well understood, they are thought to play an important role in maintaining the brain. The CSF may allow certain compounds access to the brain, and it probably helps the brain excrete metabolic wastes. Very likely, too, the CSF produced in the ventricles acts as a kind of shock absorber. The CSF surrounds the brain; so, if there is a blow to the head, this fluid cushions the movement of the brain within the skull.

A second feature apparent in our frontal section of the brain is that the brain's interior is not homogeneous. There are both light and dark regions. These light and dark regions may not seem as distinct as the different parts of a car's engine, but nevertheless they represent different components. The light regions, called **white matter,** are mostly fibers with fatty coverings. The fatty coverings produce the white appearance, much as fat droplets in milk make it appear white. The dark regions, called **gray matter** because of their gray-brown color, are areas where capillary blood vessels and cell bodies predominate. Some regions of the brain have a mottled gray and white, or netlike, appearance. These regions, which have both cell bodies and fibers mixed together, are called **reticular matter** (from the Latin word *rete,* meaning "net").

Another way to cut the brain is from front to back. The result is a side view, called a *sagittal* [***sadj*** *i tal*] section. If we make our cut down the brain's midline, we divide the cerebrum into its two hemispheres. Figure 2-10 shows such a sagittal section.

Figure 2-8

This frontal section through the brain shows the internal features. The brain is **(A)** cut and then **(B)** viewed at a slight angle. This section displays regions that are relatively white and gray. The white areas are largely composed of fibers, whereas the gray areas are composed of cell bodies. The large bundle of fibers joining the two areas is the corpus callosum. Each ventricle is a fluid-filled tube.



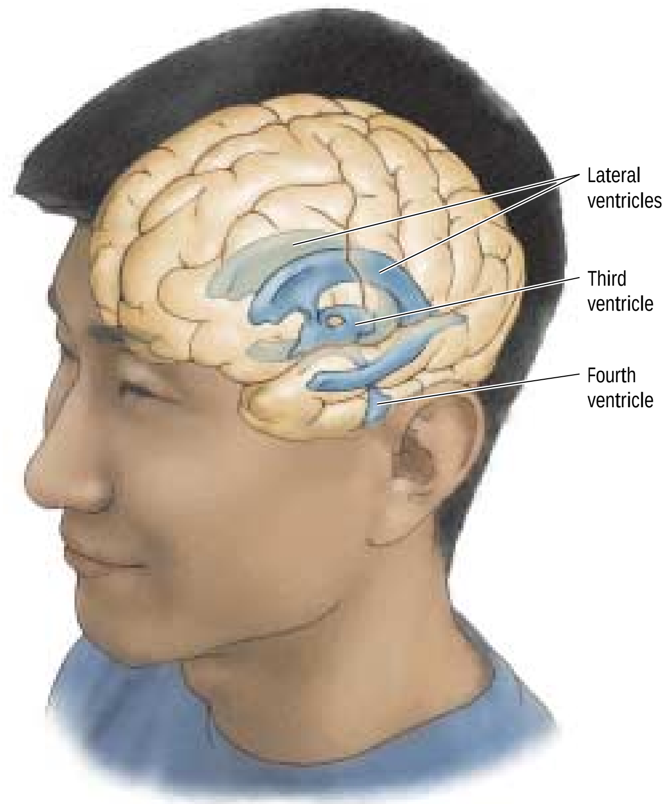
One feature seen from this viewing angle is a long band of white matter that runs much of the length of the cerebral hemispheres. This band is called the **corpus callosum [*ka* *loh* *sum*]**. The corpus callosum contains about 200 million fibers that join the two hemispheres and allow communication between them. It is also clear in Figure 2-10 that the cortex covers the cerebral hemispheres above the corpus callosum, whereas below the corpus callosum are various internal structures of the brain. Owing to their location below the cortex, these structures are known as **subcortical regions.**

We can see the internal structures of the brain in much more detail by coloring them with special stains. For example, if we use a dye that selectively stains cell bodies, we can see that the distribution of cells within the gray matter is not homogeneous, as shown in Figure 2-11. In particular, it becomes apparent that the cerebral cortex is composed of layers, each of which contains similarly staining cells. Furthermore, subcortical regions are now seen to be composed of clusters, known as **nuclei,** of similarly stained cells. Although layers and nuclei are very different in appearance, they both form functional units within the brain. Whether a particular brain region has layers or nuclei is largely an accident of evolution.

If you were to compare the two sides of the brain in sagittal section, you would be struck by their symmetry. The brain, in fact, has two of nearly every structure, one on each side. The few structures that are one of a kind are found along the brain's midline. Examples are the third and fourth ventricles and the pineal gland, mentioned in Chapter 1 in reference to Descartes's theory about how the brain works.

Figure 2-9

There are two lateral cerebral ventricles, one in each hemisphere, and a third and fourth cerebral ventricle, each of which lies in the midline of the brain.



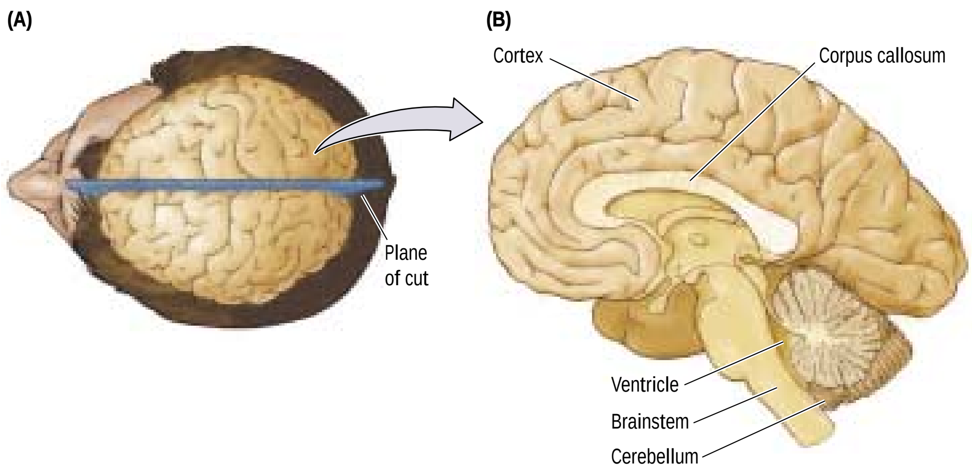


Figure 2-10

In this sagittal section through the brain, the brain is **(A)** cut and then **(B)** viewed from the side. This particular plane of cut separates the hemispheres, allowing a view of the midline structures of the brain, including the corpus callosum, which connects the two hemispheres. You can see the subcortical structures (ventricle, brainstem, and cerebellum) that lie below the corpus callosum.

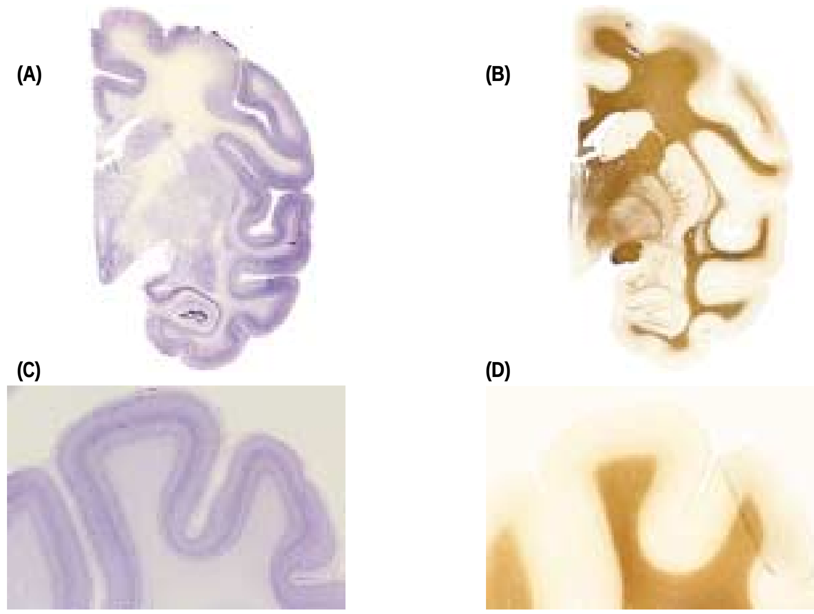
Subcortical regions. All of the regions of the brain that are located beneath the neocortex; the term is usually used to distinguish regions of the brain that control basic functions from those regions controlling cognitive functions, which are mediated by the neocortex.

Microscopic Inspection: Cells and Fibers

Although the parts of a car engine are all large enough to be seen with the naked eye, the fundamental units of the brain—its cells—are so small that they can be viewed only with the aid of a microscope. By using a microscope, we quickly discover that the

Figure 2-11

When brain sections are stained, various regions become clearly demarcated. These brain sections from the left hemisphere of a monkey (midline is to the left in each photograph) are stained with **(A)** a selective cell-body stain, known as a Nissl stain, and **(B)** a selective fiber stain, staining for myelin. It is immediately apparent that the two stains reveal a very different picture of the brain. **(C** and **D)** Higher-power micrographs through the Nissl- and myelin-stained sections show different cortical regions. Notice the difference in appearance.



Focus on Disorders

Meningitis and Encephalitis

A large number of harmful organisms can invade the linings, or meninges, of the brain, particularly the pia mater and the arachnoid layer, as well as the cerebrospinal fluid between them. Such infections are called *meningitis.* One symptom is inflammation, which, because the skull is solid, places pressure on the brain. This pressure often leads to delirium and, if the infection progresses, to drowsiness, stupor, and even coma.

Meningitis usually begins with severe headache and a stiff neck (known as cervical rigidity). Head retraction is an extreme form of cervical rigidity. Convulsions are a common symptom in children. They indicate that the brain also is affected by the inflammation.

Infection of the brain itself is called *encephalitis*. There are many forms of encephalitis, some of which have great historical significance. In World War I, a form of encephalitis referred to as sleeping sickness (encephalitis lethargica) reached epidemic proportions. The first symptoms were disturbances of sleep. People slept all day and became wakeful, even excited, at night. Subsequently, they showed symptoms of Parkinson's disease, characterized by severe tremors and difficulty in controlling body movements. Many were completely unable to make any voluntary movements, such as walking or even combing their hair. (These patients were immortalized in the movie *Awakenings*.) The cause of these symptoms is death of the brain nucleus known as the substantia nigra (black substance). Other forms of encephalitis may have different effects on the brain. For example, Rasmussen's encephalitis attacks one cerebral hemisphere in children. In most cases, the only effective treatment is a radical one: removal of the entire affected hemisphere. Surprisingly, some young children who lose a hemisphere adapt rather well. They may even complete college, literally with half a brain. But, unfortunately, retardation is a more common outcome of hemispherectomy after encephalitis.

Biophoto Associates / Science Source / Photo Researchers

In this photograph of the right hemisphere of a brain infected with meningitis, there is pus visible over the surface of the brain.

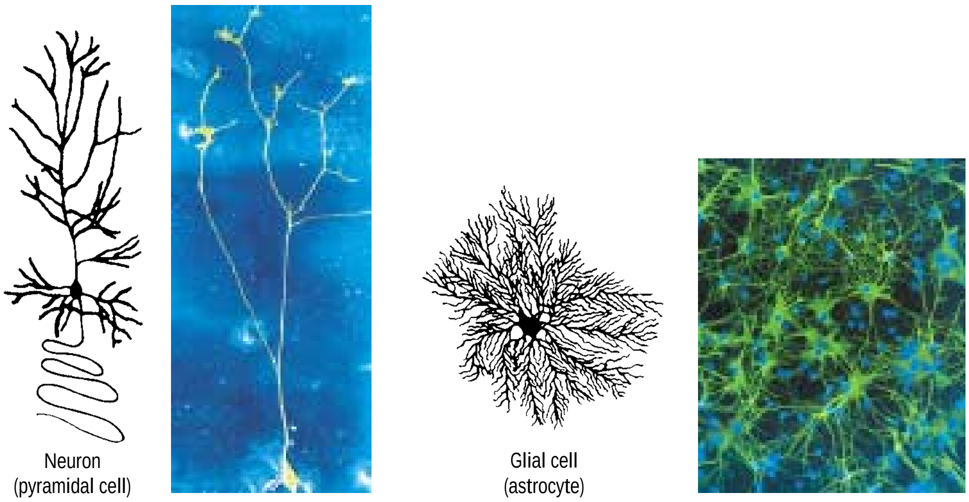


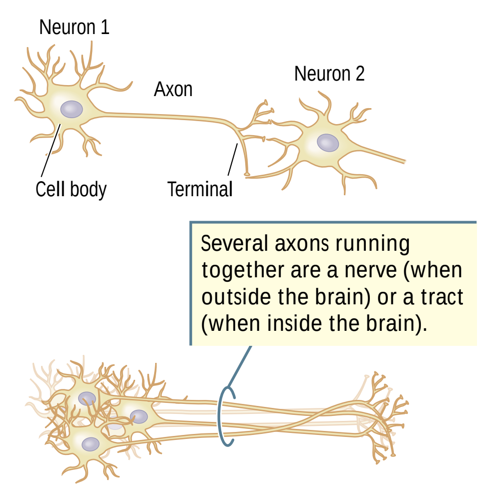
Figure 2-12

These examples of a prototypical neuron and glial cell show that both the neuron and the astrocyte have branches emanating from the cell body. This branching organization increases the surface area of the cell membrane. The neuron is a pyramidal cell, so called because the cell body is shaped somewhat like a pyramid; the glial cell is an astrocyte, so called because of its star-shaped appearance.

Photos: *left,* CNRI/ Science Photo Library; *right,* N. Kedesha/ Science Photo Library.

brain has two main types of cells: *neurons* and *glia,* illustrated in Figure 2-12. There are about 80 billion neurons and 100 billion glia in a human brain. Neurons are the cells that carry out the brain's major functions, whereas glia play a supporting role to aid and modulate the neurons' activities. Both neurons and glia come in many forms, each determined by the work done by particular cells. We return to neurons and glia in Chapter 3.

A key feature of neurons is that they are connected to one another by fibers known as *axons***.** When axons run along together, much like the wires that run from a car engine to the dashboard, they form a **nerve tract.** By convention, the term *tract* is usually used to refer to collections of nerve fibers found within the brain (or within the brain and spinal cord), whereas bundles of fibers located outside these central structures are typically referred to simply as *nerves*. Thus, the pathway from the eye to the brain is known as the optic nerve, whereas the pathway from the cerebral cortex to the spinal cord is known as the corticospinal tract.



In Review

We began this chapter by looking at the brain as we would a car engine. Inside the skull and under the meninges, we find two main structures: the cerebral hemispheres and the cerebellum. Both have many gyri and sulci covering their surfaces. At the base of the brain, we see the brainstem, of which the cerebellum is a part. Cutting open the brain, we observe the fluid-filled ventricles, the corpus callosum that connects the two hemispheres, and the cortex and subcortical regions below it. We also see that brain tissue is of three basic types: white matter, gray matter, and reticular matter. The question is how this jumble of parts produces behaviors as complex as human thought.

Focus on Disorders

Stroke

Stroke is the sudden appearance of neurological symptoms when severe interruption of blood flow to the brain kills brain cells. Stroke is a serious and common illness that occurs approximately every minute in the United States. This rate of occurrence produces about 500,000 new stroke victims in the United States every year.

The effects of stroke are illustrated by the case of Mr. Anderson, an electrical engineer who was 45 years old at the time of his stroke. He and his wife had three children and a comfortable middle-class life style. One Saturday afternoon in early 1998, Mr. Anderson was at a movie theater with his children when he suddenly collapsed. He was rushed to the hospital, where he was diagnosed with a massive stroke of the middle cerebral artery of his left hemisphere. A year after his stroke, Mr. Anderson was still unable to speak, although he could understand simple conversations. He had severe difficulties in moving his right leg, which required him to use a walker. Because he could not move the fingers of his right hand, he had difficulty in feeding himself. It is unlikely that Mr. Anderson will ever return to his old job or be able to drive or to get around on his own. In addition, the lost income and stroke-related medical bills have had a significant effect on the Andersons' standard of living.

The prognosis for many other stroke victims is equally grave. For every ten people who have a stroke, two die, six have varying degrees of disability, and two achieve some neurological recovery but still have a diminished quality of life. The survivors risk suffering further strokes, with the annual rate of recurrence being about 10 percent a year. Strokes, then, have significant consequences, both for the people who have them and for their families. Most stroke survivors require help to perform everyday tasks. Their caregivers are usually female, either a wife or a daughter, and most of them must give up work or other activities to care for the stroke victims. One year after a stroke occurs, half the caregivers develop an emotional illness, primarily depression or anxiety or both.

The hopeful news regarding stroke is that it may now be treatable with a new drug called tissue plasminogen activator (t-PA). The results of clinical trials showed that, when patients were given t-PA within 3 hours of a stroke, the number who made a nearly complete recovery increased by 32 percent, compared with those who were given a placebo (Chiu et al., 1998). In addition, impairments were reduced in the remaining patients who survived the stroke. Other drugs offering an even better outcome will likely become avail-able in the future. These drugs may extend the 3-hour window for administering treatment after a stroke. But, even with the best and fastest medical attention, most stroke victims will still suffer some residual motor, sensory, or cognitive deficit.

A CLOSER LOOK AT NEUROANATOMY

When we look at the parts of a car engine, we can make some pretty good guesses about what each part does. For example, we can guess that the battery must provide electrical power to run the radio and lights, and, because batteries need to be charged, we can infer that there must be some mechanism for charging them. The same approach can be taken to deduce the functions of the parts of the brain. For example, we can guess that the part of the brain connected to the optic nerve coming from an eye must have something to do with vision. Similarly, we can guess that brain structures connected to the auditory nerve coming from an ear must have something to do with hearing. With these simple observations, we can begin to understand how the brain is organized. The real test of inferences about the brain is analysis of actual brain function. Nevertheless, the place to start is with brain anatomy.

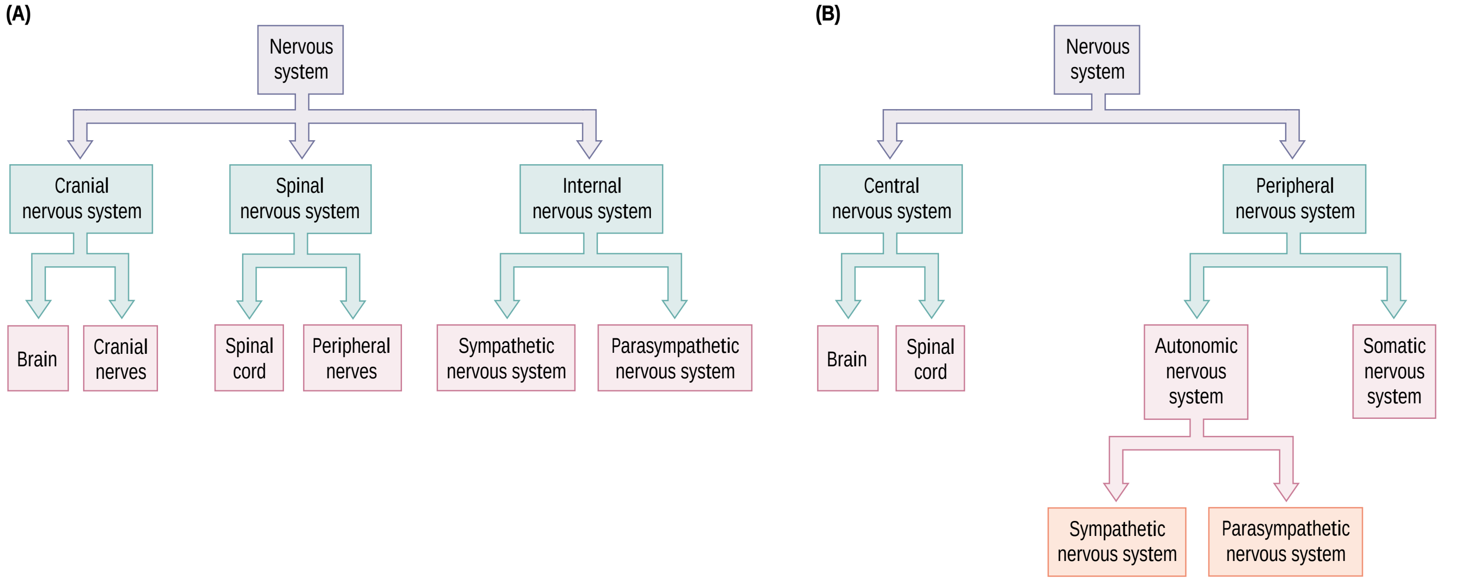


Figure 2-13

In a conceptualization of the nervous system, the nervous system can be **(A)** divided into three gross divisions: cranial, spinal, and internal. Each of these divisions can in turn be subdivided into smaller component parts. In a more traditional division of the nervous system, it is **(B)** divided into the central and peripheral nervous systems. Again, each division is subdivided into smaller components. The diagram in **(A)** is based on a practical functional distinction, whereas the diagram in **(B)** is based on a purely anatomical distinction. The internal nervous system **(A)** is equivalent to the autonomic nervous system **(B).** The peripheral nerves **(A)** are equivalent to the somatic nervous system **(B).**

One traditional way of categorizing the parts of the nervous system is to group them into two major divisions: the central nervous system (CNS) and the peripheral nervous system (PNS). These two major divisions were introduced in Chapter 1. The CNS consists of the brain and the spinal cord, and the PNS encompasses everything else. This way of dividing up the nervous system is shown in Figure 2-13B.

The CNS–PNS distinction, however, is based more on anatomy than on function. It is not very helpful for investigating how the nervous system actually works. A better approach for a functional analysis is shown in Figure 2-13A, which depicts three major divisions: the cranial, the spinal, and the internal nervous systems. The **cranial nervous system** includes the brain and its connections to parts of the head, such as to the eyes and ears. Because this system can control the other two systems, it can regulate all of behavior. The **spinal nervous system** includes the spinal cord and its connections to and from the body's muscles, as well as its connections from the joints and the skin. This system produces movements of the body (excluding movements of the head and face). It also receives incoming sensory information about such things as touch on the body's surface and the position and movement of limbs. Finally, the **internal nervous system** (also called the autonomic nervous system, discussed in Chapter 1) controls the body's internal organs and is composed of two subdivisions: the sympathetic and the parasympathetic. In the following sections, we explore the anatomy of the human nervous system by using this three-division approach. We begin with the master control center: the cranial nervous system.

The Cranial Nervous System

The cranial nervous system includes the brain and all of the nerves that connect the brain to the muscles and sensory organs of the head. There are literally thousands of parts to the cranial nervous system. Learning the name of a particular part is pointless without also learning something about its function. In this section, therefore, we focus on the names and functions of the major components of the cranial nervous system. We divide this system into the three subdivisions outlined in Table 2-2: the cranial nerves, the brainstem, and the forebrain.

These three subdivisions introduce a concept known as levels of function. This concept means that something is organized into functional levels, with newer levels partly replicating the work of older ones. A simple example is learning to read. When

Table 2-2 Anatomical Divisions of the Cranial Nervous System

Anatomical divisions	Functional divisions	Principal structures
Forebrain	Forebrain	Cerebral cortex
		Basal ganglia
		Limbic system
Brainstem	Diencephalon	Thalamus
		Hypothalamus
	Midbrain	Tectum
		Tegmentum
	Hindbrain	Cerebellum
		Pons
		Medulla oblongata
		Reticular formation
Cranial nerves	Cranial nerves	12 cranial nerves

you began to read in grade 1, you learned simple words and sentences. Then, as you progressed to higher levels, you mastered new, more challenging words and longer, more complicated sentences, but you still retained the simpler skills that you had learned before. Much later, you encountered Shakespeare, with a complexity and subtlety of language unimagined in grade school. Each new level of training added new abilities that overlapped and built on previously acquired skills. Yet all the levels dealt with reading. In much the same way, the brain has functional levels that overlap each other in purpose but allow for a growing complexity of behavior. For instance, the brain has functional levels that control movements. With the addition of each new level, the complexity of movements becomes increasingly refined. We return to this concept of levels of function at the end of this chapter.

THE CRANIAL NERVES

The cranial nerves are all the nerves that link the brain to various parts of the head, as illustrated in Figure 2-14, as well as to the internal organs. Cranial nerves can have either afferent functions, such as inputs to the brain from the eyes, ears, mouth, and nose, or efferent functions, such as control of the facial muscles, tongue, and eyes. There are 12 pairs of cranial nerves. One set of 12 controls the left side of the head, whereas the other set controls the head's right side. This arrangement makes sense for innervating duplicated parts of the head (such as the eyes), but it is not so clear why separate nerves should control the right and left sides of a singular structure (such as the tongue). Yet this is how the cranial nerves work. If you have ever received novocaine for dental work, you know that usually just one side of your tongue becomes anesthetized because the dentist injects the drug into only one side of your mouth. The rest of the skin and muscles on each side of the head are similarly controlled by cranial nerves located on that side.

We consider many of the cranial nerves in some detail later when we deal with topics such as vision and hearing. For now, you simply need to know that cranial nerves form part of the cranial nervous system, providing inputs to the brain from the head's sensory organs and muscles and controlling head and face movements.

On the CD, visit the module on the Central Nervous System for a detailed, three-dimensional view of the brainstem.

THE BRAINSTEM

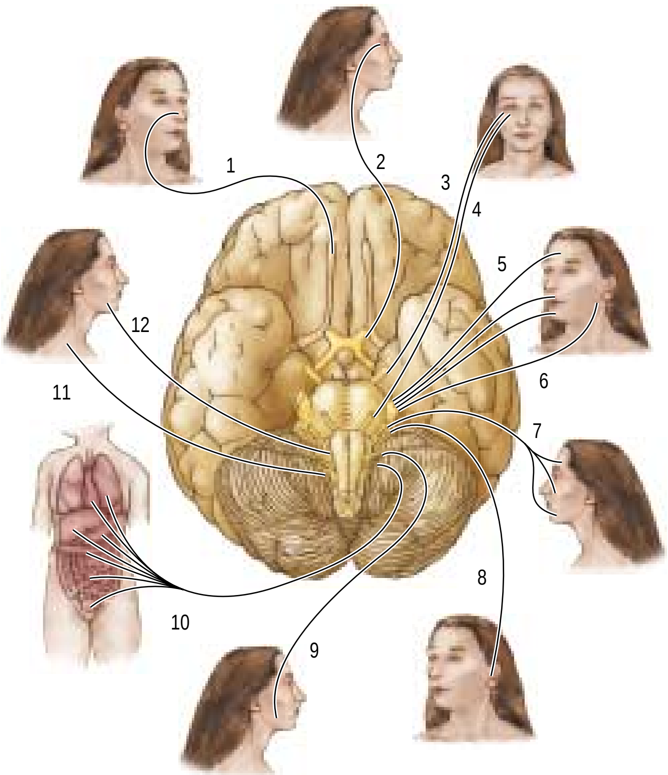
It is now time to look at the brain itself, starting at its base with the region called the brainstem. The brainstem begins where the spinal cord enters the skull and extends upward to the lower areas of the forebrain. The brainstem receives afferent nerves from all of the body's senses, and it sends efferent nerves to control all of the body's movements except the most complex movements of the fingers and toes. The brainstem, then, both produces movements and creates a sensory world. In some animals, such as frogs, the entire brain is largely equivalent to the brainstem of mammals or birds. With this kind of brain, frogs get along quite well, indicating that the brainstem must be a relatively sophisticated piece of machinery. If we had only a brainstem, we would still be able to create a world, but it would be a far simpler world, more like what a frog experiences.

The brainstem can be divided into three regions: the **hindbrain,** the **midbrain,** and the **diencephalon** [*dye en* ***seff*** *a lon*], which is also sometimes called the "between brain" because it borders upper parts of the brain. Figure 2-15 illustrates these three

Hindbrain. The embryonic part of the brain that contains the brainstem and cerebellum; thought to coordinate movements and support movements of walking and posture.

Midbrain. The middle part of the embryonic brain, which, in the adult, contains circuits for hearing and seeing as well as walking.

Diencephalon. The part of the brain that contains the hypothalamus, thalamus, and epithalamus; thought to coordinate many basic instinctual behaviors, including temperature regulation, sexual behavior, and eating.



Cranial nerve	Name	Functions
1	Olfactory	Smell
2	Optic	Vision
3	Oculomotor	Eye movement
4	Trochlear	Eye movement
5	Trigeminal	Masticatory movements and facial sensation
6	Abducens	Eye movement
7	Facial	Facial movement and sensation
8	Auditory vestibular	Hearing and balance
9	Glossopharyngeal	Tongue and pharynx movement and sensation
10	Vagus	Heart, blood vessels, viscera, movement of larynx and pharynx
11	Spinal accessory	Neck muscles
12	Hypoglossal	Tongue muscles

Figure 2-14

Each of the 12 pairs of cranial nerves has a different function. A common device for learning the order of the cranial nerves is: On old Olympus's towering top, a Finn and German vainly skip and hop. The first letter of each word (except the last *and*) is, in order, the first letter of the name of each nerve.

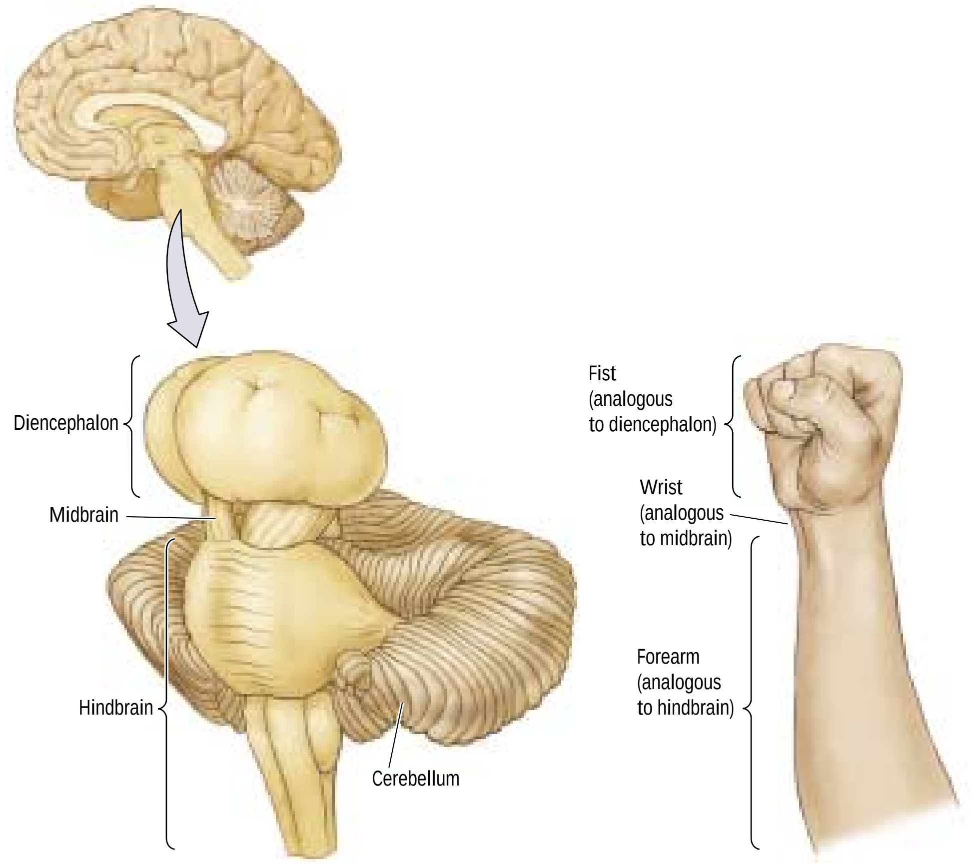
brainstem regions, all of which lie under the cerebral hemispheres. As Figure 2-15 shows, the shape of the brainstem can be compared to the lower part of your arm held upright. The hindbrain is long and thick like your forearm, the midbrain is short and compact like your wrist, and the diencephalon at the end is bulbous like your hand forming a fist.

Each of these three major regions of the brainstem performs more than a single task. Each contains various subparts, made up of groupings of nuclei, that serve different purposes. All three regions, in fact, have both sensory and motor functions. However, the hindbrain is especially important in various kinds of motor functions, the midbrain in sensory functions, and the diencephalon in integrative tasks. Here we consider the central functions of these three regions; later chapters will contain more information about them.

The Hindbrain The hindbrain, shown in Figure 2-16, controls various types of motor functions ranging from breathing to balance to the control of fine movements, such as those used in dancing. The most distinctive structure in the hindbrain is the cerebellum, which looks much like a cauliflower. Actually, the cerebellum is a separate structure lying above the rest of the hindbrain. In humans, it is one of the largest structures of the brain. As Figure 2-17 illustrates, the size of the cerebellum increases with the physical speed and dexterity of a species. Animals that move slowly (such as a sloth) have rather small cerebellums, whereas animals that can perform rapid, acrobatic movements (such as a hawk or a cat) have very large cerebellums. The cerebellum is apparently important in controlling complex movements.

Figure 2-15

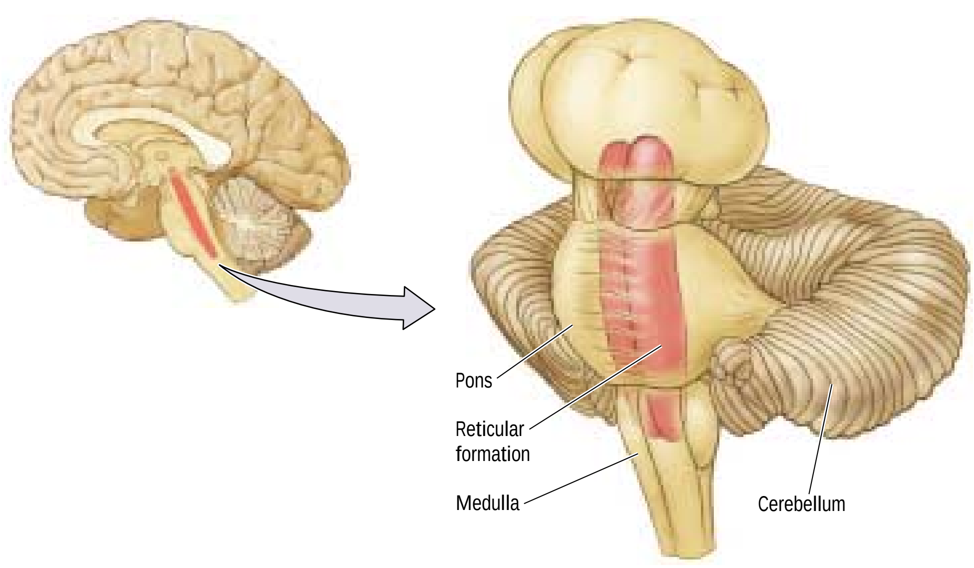
This medial view of the brain (*upper left*) shows the brainstem and its relation to the cerebral hemisphere. The shapes and relative sizes of the parts of the brainstem can be imagined to be like a hand and forearm, with the diencephalon being the fist, the midbrain being the wrist, and the hindbrain being the forearm.



As we look below the cerebellum at the rest of the hindbrain, we find that it is composed of three subparts: the *reticular formation*, the *pons*, and the *medulla*. The **reticular formation** is a mixture of neurons and nerve fibers that gives this structure the mottled appearance from which its name comes (the term *reticular*, as stated earlier, comes from the Latin word for "net"). We can visualize the reticular formation as being formed by a stack of poker chips lying on its side. Each chip has a special function in stimulating the forebrain, such as in awakening from sleep. Not surprisingly,

Figure 2-16

The principal structures of the hindbrain are the cerebellum, pons, medulla, and reticular formation.



Reticular formation. A part of the midbrain in which nuclei and fiber pathways are mixed, producing a netlike appearance; associated with sleep–wake behavior and behavioral arousal.

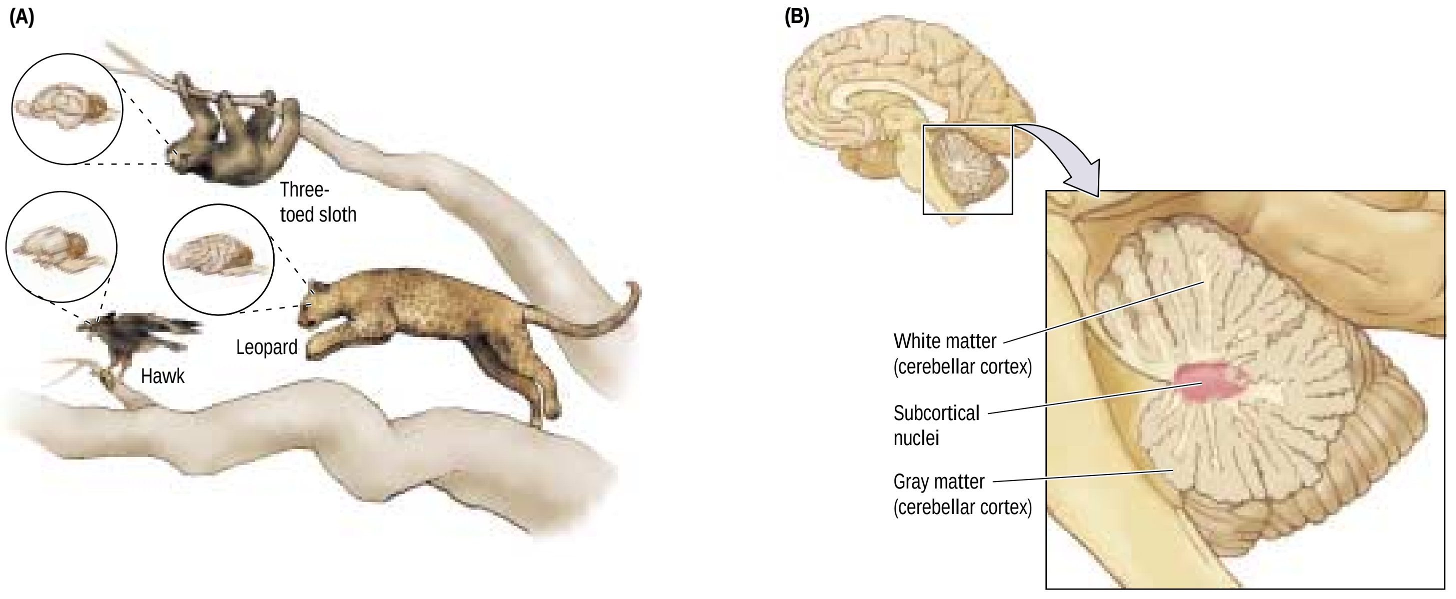


Figure 2-17

(A) The cerebellum is necessary for fine, coordinated movements such as flight and landing in birds and prey catching in cats. Like the sloth, animals that have slow movements have relatively smaller cerebellums. **(B)** Like the cerebrum, the cerebellum has a cortex, which has gray and white matter, and subcortical nuclei, as shown in this gross structure of the cerebellum.

the reticular formation is sometimes also called the *reticular activating system*. The other two structures in the hindbrain, the pons and medulla, contain substructures that control many vital movements of the body. The pons has nuclei that receive inputs from the cerebellum and provide a key bridge (the word *pons* means "bridge") between the cerebellum and the rest of the brain. The medulla has several nuclei that control such vital functions as the regulation of breathing and the cardiovascular system. For this reason, a blow to the back of the head can kill you—your breathing stops if the control centers in the hindbrain are injured.

The Midbrain In the midbrain, shown in Figure 2-18, a specialized structure known as the **tectum** receives a massive amount of information from the eyes and ears. The tectum consists of two principal parts, the *superior* and *inferior colliculi* [*kuh **lik** yew lee*], which have visual and auditory functions, respectively. The optic nerve sends a large bundle of nerve fibers to the superior colliculus, whereas the inferior colliculus receives much of its input from auditory pathways. But the colliculi

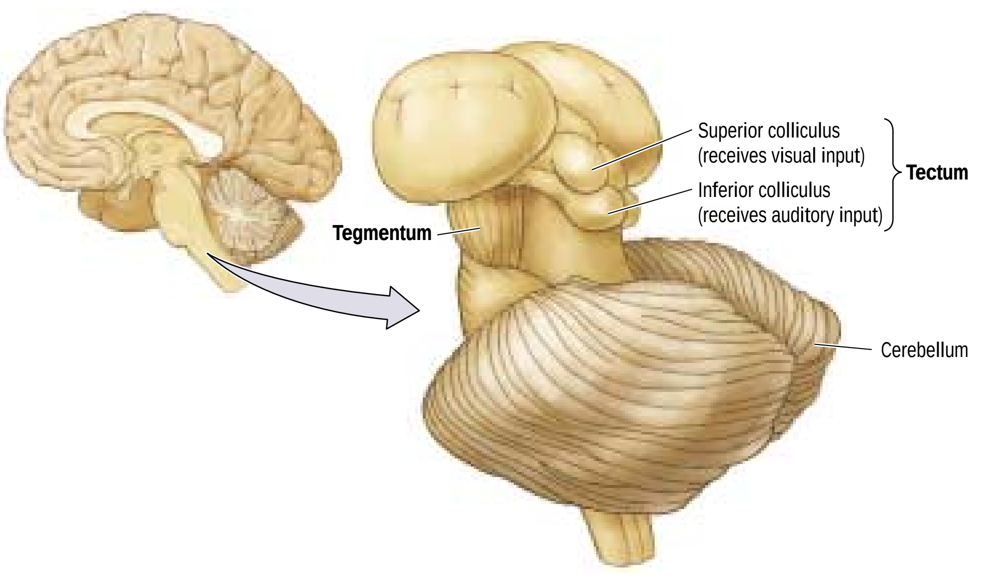


Figure 2-18

The major structures of the midbrain are the tectum and tegmentum. The tectum is made up of the superior colliculus, which receives visual input, and the inferior colliculus, which receives auditory input.

Tectum. The roof, or area above the ventricle, of the midbrain; its functions are sensory.

Tegmentum. The floor, or area below the ventricle, of the midbrain; has motor functions.

Hypothalamus. A part of the diencephalon that contains many nuclei associated with temperature regulation, eating and drinking, and sexual behavior.

Thalamus. A part of the diencephalon through which all of the sensory system projects to reach the neocortex and then projects, through one region of the neocortex, to relay messages to another region of the forebrain.

function not only to process sensory information. They also produce movements related to sensory inputs, such as turning your head to see the source of a sound. This orienting behavior is not as simple as it may seem. To produce it, the auditory and visual systems must share some sort of common "map" of the external world so that the ears can tell the eyes where to look. If the auditory and visual systems had different maps, it would be impossible to use the two systems together. In fact, the colliculi also have a tactile map. After all, if you want to look at the source of an itch on your leg, your visual and tactile systems need a common representation of where that place is.

Lying below the tectum is the **tegmentum.** The tegmentum is not a single structure but is composed of many nuclei, largely with movement-related functions. It has several nuclei that control eye movements, the so-called *red nucleus,* controlling limb movements, and the *substantia nigra*, connected to the forebrain; both the substantia nigra and the forebrain are especially important in initiating movements.

The Diencephalon The diencephalon, shown in Figure 2-19, has more structures than the hindbrain and midbrain have, owing to its role in both motor and sensory functions, as well as their integration. The two principal structures of the diencephalon are the **hypothalamus** and the **thalamus.** The hypothalamus is composed of about 22 small nuclei, as well as fiber systems that pass through it. Attached to the base of the hypothalamus is the pituitary gland. Although comprising only about 0.3 percent of the brain's weight, the hypothalamus takes part in nearly all aspects of behavior, including feeding, sexual behavior, sleeping, temperature regulation, emotional behavior, hormone function, and movement. The hypothalamus is organized more or less similarly in different mammals, largely because the control of feeding, temperature, and so on, is carried out similarly. But there are sex differences in the structures of some parts of the hypothalamus, which are probably due to differences between males and females

Plug in the CD to examine the hypothalamus and the thalamus in three dimensions in the module on the Central Nervous System in the subsection on subcortical structures.

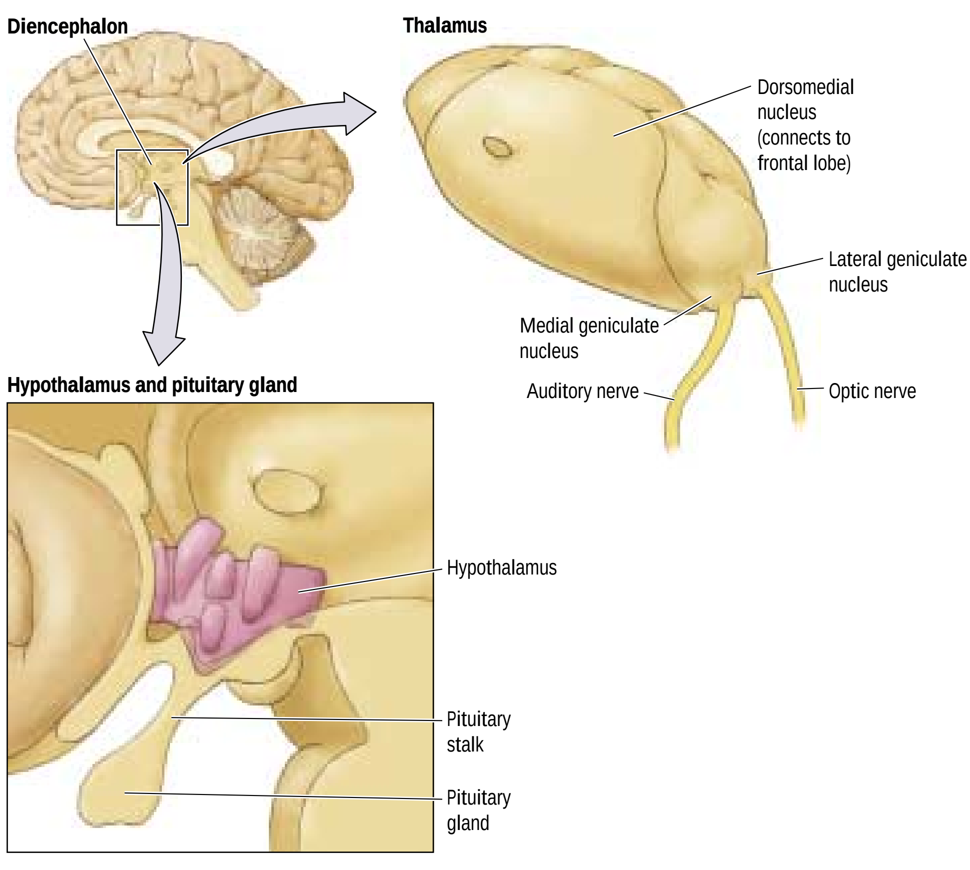


Figure 2-19

The diencephalon is composed of the thalamus, hypothalamus, and associated pituitary gland. The hypothalamus and pituitary are at the base of the brain and lie above the roof of the mouth. The pituitary gland lies adjacent to the optic chiasm, which is the place where the left and right optic nerves (originating from the eyes) cross over. The hypothalamus is composed of many nuclei, each with distinctly different functions. The thalamus lies above the hypothalamus. The connections of only three of the thalamic nuclei are shown, but every thalamic nucleus connects to a discrete region of cortex.

in activities such as sexual behavior and parenting. A critical function of the hypothalamus is to control the body's production of various hormones, which is accomplished by interactions with the pituitary gland.

The other principal structure of the diencephalon is the thalamus, which is much larger than the hypothalamus. Like the hypothalamus, the thalamus contains about 20 nuclei, although the nuclei in the thalamus are much larger than those in the hypothalamus. Perhaps the most distinctive function of the thalamus is to act as a kind of gateway for sensory information traveling to the cerebral cortex. All of the sensory systems send inputs to the thalamus, which then relays this information to the cortex. The optic nerve, for example, sends information through a large bundle of fibers to a region of the thalamus known as the *lateral geniculate nucleus*. In turn, the lateral geniculate nucleus processes some of this information and then sends it to the visual region of the cortex. Analogous regions of the thalamus receive auditory and tactile information, which is subsequently relayed to the respective auditory and tactile cortical regions. Some thalamic regions are not sensory in function. These regions have motor functions or perform some sort of integrative task. An example of a region with an integrative function is the *dorsomedial thalamic nucleus*. It has connections to most of the frontal lobe of the cortex. We return to the thalamic sensory nuclei in Chapters 8 through 10, where we examine how sensory information is processed. Other thalamic regions are considered in Chapters 11 and 13, where we explore motivation and memory.

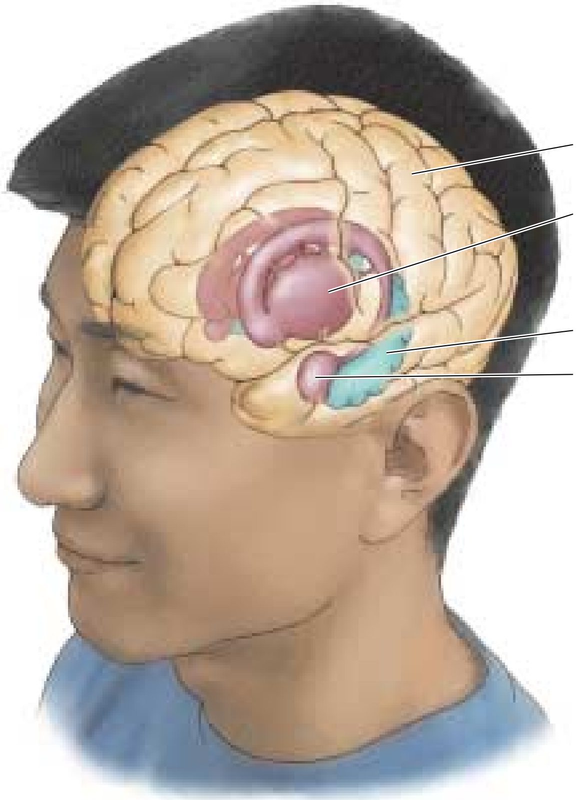


Figure 2-20

The major structures of the forebrain include the cerebral cortex, the basal ganglia, and the limbic system of which the amygdala and hippocampus are shown.

THE FOREBRAIN

The **forebrain,** shown in Figure 2-20, is the largest region of the mammalian brain. Its three principal structures are the **cortex,** the **limbic system,** and the **basal ganglia.** Extending our analogy between the brainstem and your forearm, imagine that the "fist" of the brainstem (the diencephalon) is thrust inside a watermelon. The watermelon represents the forebrain, with the rind being the cortex and the fruit inside being the limbic system and the basal ganglia. By varying the size of the watermelon, we can vary the size of the brain. In a sense, this is what evolution has done. The forebrain varies considerably in size across species.

The three principal structures of the forebrain are the largest parts of the mammalian brain, and each has multiple functions. To summarize these functions briefly, the cortex regulates mental activities such as perception and planning, the basal ganglia control movement, and the limbic system regulates emotions and behaviors that require memory. Because we encounter each of these structures in detail later in this book, they are only briefly presented here.

The Cortex There are actually two types of cortex. The first type, called **neocortex,** has six layers of gray matter on top of a layer of white matter. The neocortex is the tissue that is visible when we view the brain from the top or the side, as in two of the views in Figure 2-6. This cortex is unique to mammals, and its primary function is to create a perceptual world. The second type of cortex, sometimes called **limbic cortex,** has three or four layers of gray matter on top of a layer of white matter. This tissue is not easily observed on the outside surface of the human brain, except for where it forms the *cingulate cortex,* which lies just above the corpus callosum (see Figure 2-24).

Forebrain. The most anterior part of the embryonic brain; contains the basal ganglia and the neocortex and is therefore thought to coordinate advanced cognitive functions such as thinking, planning, and language.

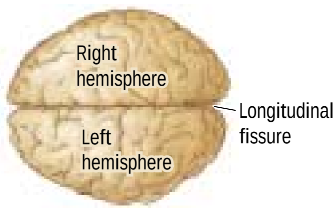
Cortex (neocortex). Newest layer of the forebrain, forming the outer layer or "new bark" and composed of about six layers.

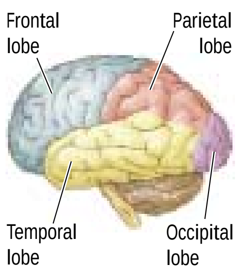
Limbic system. Consists of structures that lie between the neocortex and the brainstem and form a hypothetical functional system that controls affective behavior and certain forms of memory; includes the cingulate cortex and hippocampus.

Basal ganglia. A group of structures in the forebrain that are located just beneath the neocortex and have connections to the thalamus and to the midbrain; thought to have motor functions that coordinate the movements of the limbs and the body.

Look at the CD for a three-dimensional model of the cortex along with photographs of cortical sections in the module on the Central Nervous System.

Click onto the Web site to see how the cortex looks in other animals at **www.worthpublishers.com/kolb/chapter2.**





The limbic cortex is more primitive than the neocortex. It is found in the brains of other animals in addition to mammals, especially in birds and reptiles. This cortex is thought to play a role in controlling motivational states. Although anatomical and functional differences exist between the neocortex and the limbic cortex, the distinctions are not critical for most discussions in this book. Therefore, we will usually refer to both types of tissue simply as cortex.

Measured by volume, the cortex makes up most of the forebrain, comprising 80 percent of the brain overall. It is the brain region that has expanded the most during mammalian evolution. The human neocortex has an area as large as 2500 square centimeters but a thickness of only 1.5 to 3.0 millimeters. This area is equivalent to about four pages of this book. (In contrast, a chimpanzee has a cortical area equivalent to about one page.) The pattern of sulci and gyri formed by the folding of the cortex varies across species. Some species, such as rats, have no sulci or gyri, whereas carnivores have gyri that form a longitudinal pattern (look back at Figure 2-2). In humans, the sulci and gyri form a more diffuse pattern.

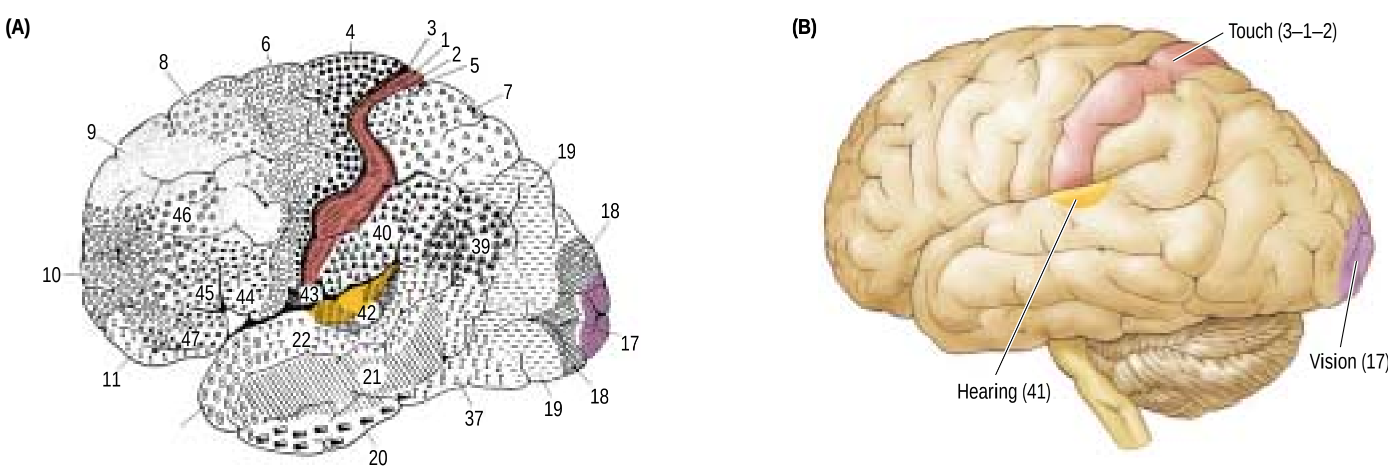
As Figure 2-6 shows, the human cortex consists of two nearly symmetrical hemispheres, the left and the right, which are separated by the longitudinal fissure. Each hemisphere is subdivided into the four lobes introduced in Chapter 1: the frontal, the temporal, the parietal, and the occipital. These names correspond to the skull bones overlying each hemisphere. Unfortunately, there is little relation between bone location and brain function. As a result, the lobes of the cortex are rather arbitrarily defined regions that include many different functional zones.

Fissures and sulci often establish the boundaries of cortical lobes. For instance, in humans, the central sulcus and lateral fissure form the boundaries of each frontal lobe. They also form the boundaries of each parietal [*pa* ***rye*** *i tul*] lobe, but in this case the lobes lie *behind* the central sulcus, not in front of it (refer again to Figure 2-6). The lateral fissure demarcates each temporal [***tem*** *por ul*] lobe as well, forming its dorsal (top) boundary. The occipital [*ok* ***sip*** *i tul*] lobes are not so clearly separated from the parietal and temporal lobes, because there is no large fissure to mark their boundaries. Traditionally, the occipital lobes are defined on the basis of other anatomical features, which are presented in Chapter 8.

The layers of the cortex have several distinct characteristics. First, different layers have different cell types, as shown in Figure 2-11. Second, the density of the cells varies, ranging from virtually no cells in layer I (the top layer) to very dense cell packing in layer IV. Third, there are other differences in appearance related to the functions of cortical layers in different regions. These visible differences led neuroanatomists of the early twentieth century to make maps of the cortex, like the one in Figure 2-21A.

Figure 2-21

(A) In his cytoarchitectonic map of the cortex, Brodmann defined areas by the organization and characteristics of the cells. A few numbers are missing from the original sources, including 12 through 16 and 48 through 51. **(B)** This schematic map shows the regions associated with the simplest sensory perceptions of touch, vision, and audition. As we shall see, the areas of the cortex processing sensory information are far greater than these basic areas.



Because these maps are based on cell characteristics, the subject of cytology, they are called **cytoarchitectonic maps.** As the early neuroanatomists suspected, the characteristics of cells in a particular region of the cortex are related to that region's function. For example, sensory regions of the parietal lobe, shown in red in Figure 2-22, have a distinct layer IV, whereas motor regions of the frontal lobe, shown in blue in the same illustration, have a more distinctive layer V. Layer IV is an afferent layer, whereas layer V is an efferent one. It makes sense that a sensory region would have a large input layer, whereas a motor region would have a large output layer. Finally, there are chemical differences in the cells in different regions of the cortex. These differences can be revealed by coloring cortical tissue with stains that have affinities for specific chemicals. Some regions are rich in one chemical, whereas others are rich in another. These differences are presumably related to functional specialization of different areas of the cortex.

There is one significant difference between the organization of the cortex and the organization of other parts of the brain. Unlike most brain structures that connect to only selective brain regions, the cortex is connected to virtually all other parts of the brain. The cortex, in other words, is the ultimate meddler. It takes part in everything. This fact not only makes it difficult to identify specific functions of the cortex, but also complicates our study of the rest of the brain because the cortex's role in other brain regions must always be considered.

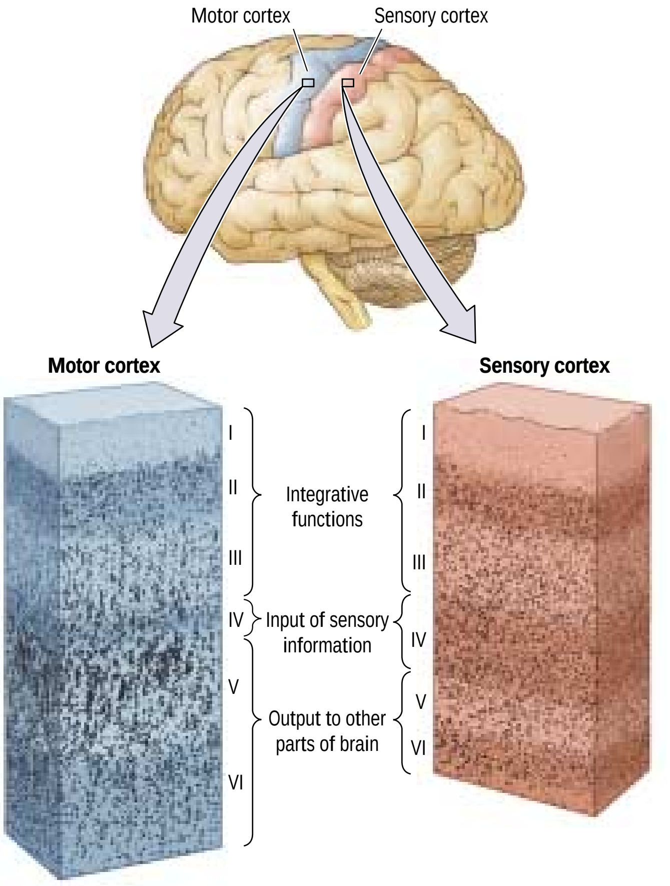


Figure 2-22

As this comparison of cortical layers in the sensory and motor cortices shows, layer IV is relatively thick in the sensory cortex and relatively thin in the motor cortex. Afferents go to layer IV (from the thalamus) as well as to layers II and III. Efferents go to other parts of the cortex and to the motor structures.

To illustrate, consider your perception of clouds. Undoubtedly, you have gazed up at clouds on a summer's day and imagined that they look like familiar shapes. You see in them galleons, elephants, faces, and countless other objects. Although a cloud does not really look exactly like an elephant, you can concoct an image of one if you impose your cortex's imagination on the sensory inputs. This kind of cortical activity is known as *top-down processing* because the top level of the nervous system, the cortex, is influencing how information is processed in lower regions—in this case the midbrain and hindbrain. The cortex influences many things besides the perception of objects. It influences our cravings for foods, our lust for things (or people), and how we interpret the meaning of abstract concepts such as words. The cortex is the ultimate creator of our reality, and one reason that it serves this function is that it is so well connected.

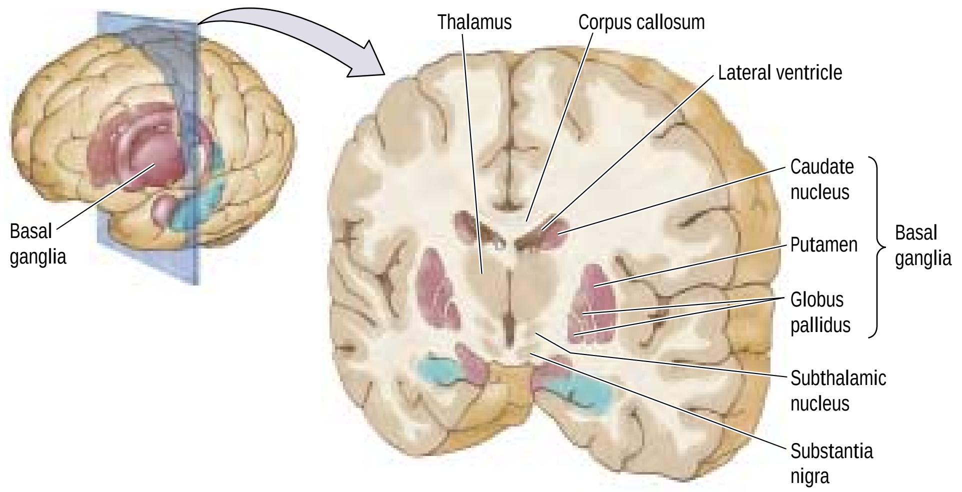
The Basal Ganglia The basal ganglia are a collection of nuclei that lie within the forebrain just below the white matter of the cortex. The three principal structures of the basal ganglia, shown in Figure 2-23 on page 58, are the *caudate nucleus*, the *putamen*, and the *globus pallidus*. Together with the thalamus and two closely associated structures, the *substantia nigra* and *subthalamic nucleus*, the basal ganglia form a system that functions primarily to control certain aspects of movement.

Visit the CD for a three-dimensional model of the basal ganglia in the section on subcortical structures in the module on the Central Nervous System.

We can observe the functions of the basal ganglia by analyzing the behavior of people who have one of the many diseases that interfere with the normal functioning of these nuclei. For instance, people afflicted with Parkinson's disease, one of the most common disorders of movement in the elderly, take short, shuffling steps, have bent posture, and often require a walker to get around. Many have an almost continual tremor of the hands and sometimes of the head as well. (We return to this disorder in Chapter 10.) Another example of a disorder of the basal ganglia is Tourette's syndrome, characterized by various forms of tics, involuntary noises (including curse

Figure 2-23

This frontal section of the cerebral hemispheres shows the basal ganglia relative to the surrounding structures. Two associated structures, the substantia nigra and subthalamic nucleus, also are illustrated.

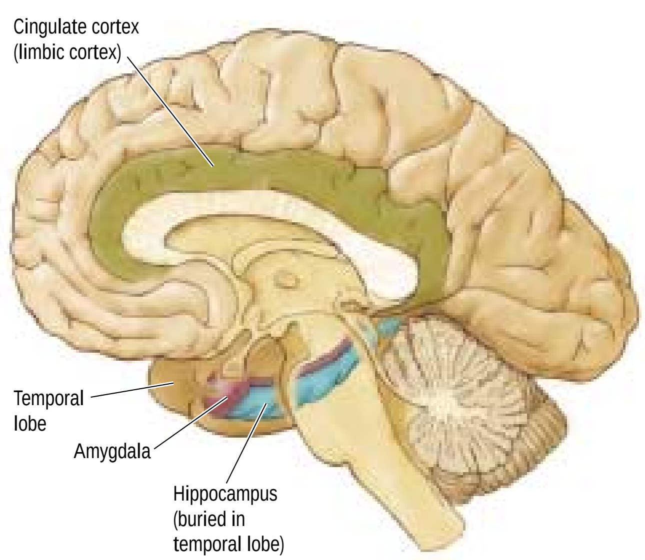


words and animal sounds), and odd, involuntary movements of the body, especially of the face and head. Neither Parkinson's disease nor Tourette's syndrome is a disorder of *producing* movements, as in paralysis. Rather they are disorders of *controlling* movements. The basal ganglia, therefore, must play a role in the control and coordination of movement patterns, not in activating the muscles.

The Limbic System In the 1930s, psychiatry was dominated by the theories of Sigmund Freud, who emphasized sexuality and emotion in understanding human behavior. At the time, regions controlling these behaviors had not been identified in the brain, but there was a group of brain structures, collectively called the limbic system, that as yet had no known function. It was a simple step to thinking that perhaps the limbic system played a central role in sexuality and emotion. One sign that this hypothesis might be right came from James Papez, who discovered that people with rabies had infections of limbic structures, and one of the symptoms of rabies is emotional blunting. We now know that such a simple view of the limbic system is inaccurate. In fact, the limbic system is not a unitary system at all, and, although some limbic structures have roles in emotion and sexual behaviors, limbic structures serve other functions, too, including memory.

Figure 2-24

This medial view of the right hemisphere illustrates the principal structures of the limbic system, including the cingulate cortex, the hippocampus, and the amygdala.



The principal structures of the limbic system are shown in Figure 2-24. They include the *amygdala* [*a* ***mig*** *da la*], the *hippocampus,* and the *cingulate cortex,* which lies in the cingulate gyrus. Removal of the amygdala produces truly startling changes in emotional behavior. For example, a cat with the amygdala removed will wander through a colony of monkeys, completely undisturbed by their hooting and threats. No self-respecting cat would normally be caught anywhere near such bedlam. The hippocampus, the cingulate cortex, and associated structures have roles in certain memory functions, as well as in the control of navigation in space.

The Olfactory System At the very front of the brain are the *olfactory bulbs,* the organs responsible for our sense of smell. The olfactory system is unique among the senses, as Figure 2-25 shows, because it is almost entirely a forebrain structure. Unlike the other sensory systems, which send most of their inputs from the sensory receptors to the midbrain and thalamus, the olfactory bulb sends most of its inputs to a specialized region of the cortex lying on the bottom of the brain. This region is known as the *pyriform cortex.* Compared with the olfactory bulbs of animals such as rats and dogs, which depend more heavily on the sense of smell than we do, the human olfactory bulb is relatively small. Because the sense of smell tends to be less important in humans than the senses of vision, hearing, and touch, we will not consider the olfactory system in any detail.

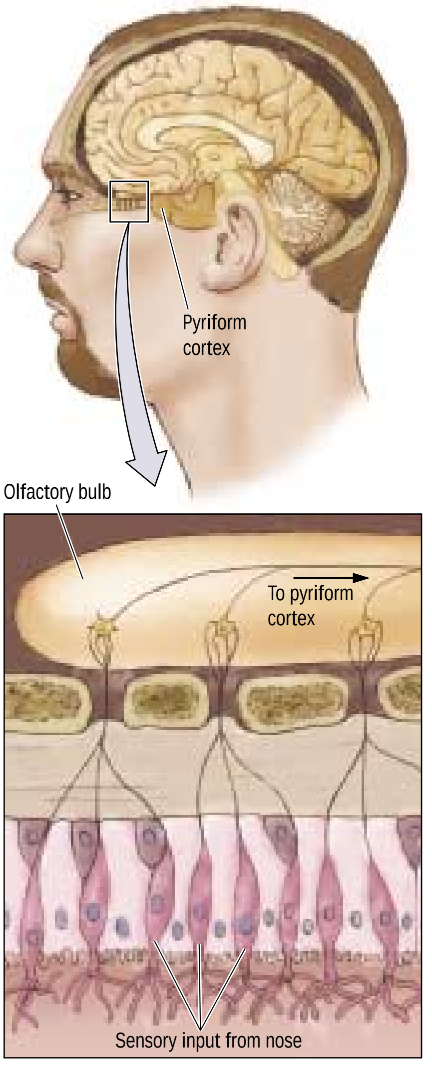


Figure 2-25

The olfactory bulb lies at the base of the human brain and is connected to receptor cells that lie in the nasal cavity. Although relatively small in humans, the olfactory bulb is larger in animals, such as rats or cats, that rely more heavily on the sense of smell.

The Spinal Nervous System

Although producing movements of the body is one of the functions of the brain, it is ultimately the spinal nervous system that controls these movements. To understand how important the spinal nervous system is, think of the old saying "running around like a chicken with its head cut off." This saying refers to the spinal nervous system at work. When a chicken's head is lopped off to provide dinner for the farmer's family, the chicken is still capable of running around the barnyard until it collapses from loss of blood. The chicken accomplishes this feat with its spinal nervous system, because that system can act independently of the brain.

You can demonstrate movement controlled by the spinal nervous system in your own body by tapping your patellar tendon, just below your kneecap (the patella), as shown in Figure 2-26 on page 60. Your lower leg kicks out and, try as you might, it is very hard to prevent the movement from occurring. Your brain, in other words, has trouble inhibiting the spinal nervous system reaction. This type of automatic movement is known as a *spinal reflex,* a topic we return to in Chapter 10.

The spinal nervous system is composed of both the spinal cord, which lies inside the bony spinal column, and the nerves running to and from the skin, joints, and muscles. As Figure 2-27 shows (see page 60), the spinal column is made up of a series of small bones called **vertebrae** that are categorized into five groups: the *cervical, thoracic, lumbar, sacral,* and *coccygeal.* You can think of each vertebra (the singular of *vertebrae*) within these five groups as a very short segment of the spinal column. The spinal cord within each vertebra functions as that segment's "minibrain."

This arrangement of having so many minibrains within the spinal column may seem a bit odd, but it has a long evolutionary history. Think of a simple animal, such as a worm, which evolved long before humans did. A worm's body is a tube divided into segments. Within that tube is another tube, this one of neurons, which also is segmented. Each of the worm's nervous system segments receives fibers from sensory receptors in the part of the body adjacent to it, and that nervous system segment sends fibers back to the muscles in that body part. Each segment, therefore, works

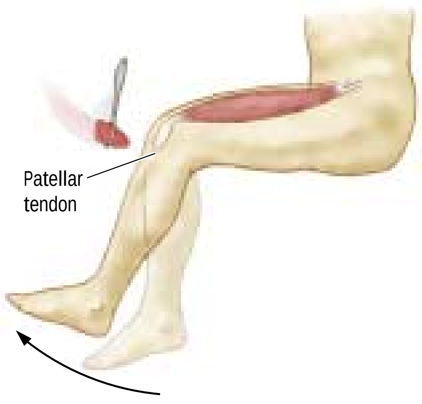


Figure 2-26

In the knee-jerk reflex (also known as the patellar reflex), when the patellar tendon is struck lightly, the lower leg flexes out "reflexively."

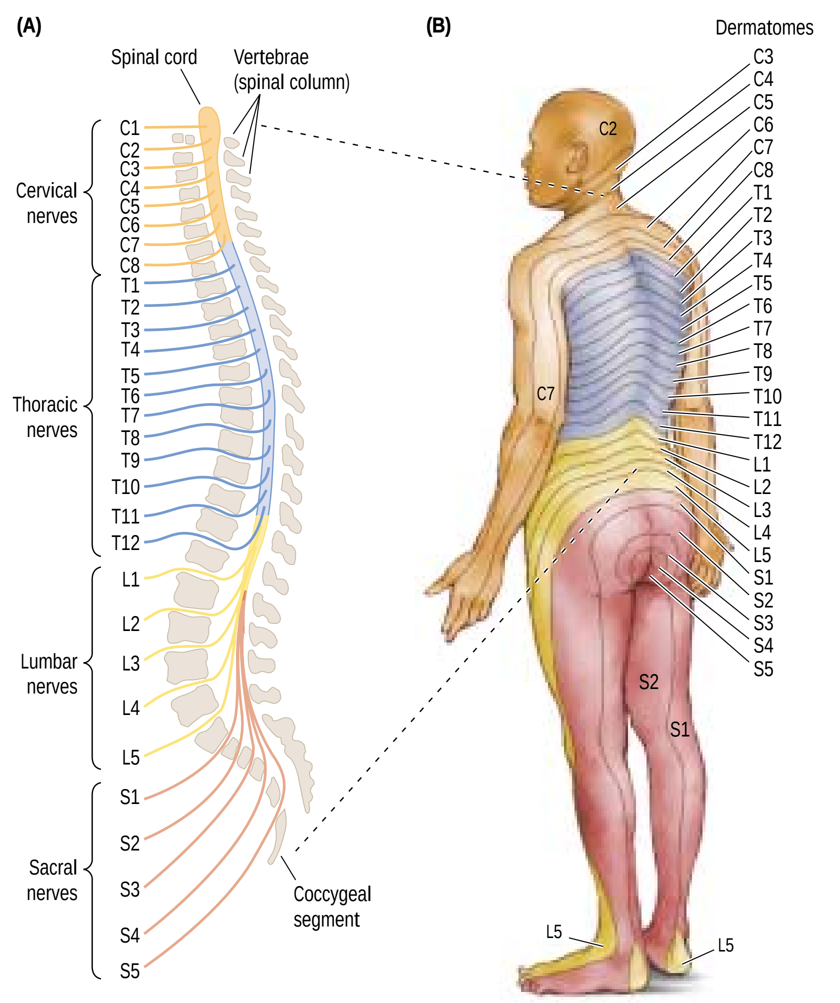
relatively independently, although fibers interconnect the segments and coordinate their activities. As vertebrates evolved a spinal column, this segmental organization was maintained. The vertebrae correspond to the segments of the worm's nerve tube, and the nerves running in and out of a vertebra's section of the spinal cord send information to and from muscles and sensory receptors at that particular level of the body.

A complication arises in animals that have limbs. The limbs may originate at one segment level, but they extend past other segments of the spinal column. Your shoulders, for example, may begin at C3 (cervical segment 3), but your arms hang down well past the sacral segments. So, unlike the worm, which has nerve-tube segments that connect to body segments directly adjacent to them, human body segments appear to be in a strange patchwork pattern, as shown in Figure 2-27B.

Regardless of their complex pattern, however, the segments of our bodies still correspond to segments of the spinal cord. Each of these body segments is called a **dermatome** (meaning "skin cut"). A dermatome has both a sensory nerve, which sends information from the skin, joints, and muscles to the spinal cord, and a motor nerve, which controls the movements of the muscles in that particular segment of the body. These sensory and motor nerves are known as **peripheral nerves,** and they are functionally equivalent to the cranial nerves of the head. Whereas the cranial nerves receive information from sensory receptors in the eyes, ears, facial skin, and so forth, the peripheral nerves receive information from sensory receptors in the rest of the

Figure 2-27

(A) The spinal column showing the vertebrae is illustrated in this saggital view. There are five segments: cervical (C), thoracic (T), lumbar (L), sacral (S), and coccygeal. **(B)** Each spinal segment corresponds to a region of body surface (dermatome) that is identified by the segment number (examples are C5 and L2).



Dermatome. Area of the skin supplied with afferent nerve fibers by a single spinal-cord dorsal root.

body. Similarly, whereas the cranial nerves move the muscles of the eyes, tongue, and face, the peripheral nerves move the muscles of the limbs and trunk. Like the cranial nervous system, the spinal nervous system is also two sided. The left side of the spinal cord controls the left side of the body, and the right side of the spinal cord controls the body's right side.

You are now ready to look inside the spinal cord to see how it is structured. Figure 2-28 shows a cross section of it. Look first at the fibers entering the spinal cord's dorsal side (in the body of a normally upright animal such as a human, the dorsal side means the back, as illustrated in Figure 2-3). These dorsal fibers carry information from the body's sensory receptors. The fibers collect together as they enter a spinal-cord segment, and this collection of fibers is called a *dorsal root*. Fibers leaving the spinal cord's ventral side (*ventral* here means the front) carry information from the spinal cord to the muscles. They, too, bundle together as they exit the spinal cord and so form a *ventral root*. As you can see in the cross section at the top of the drawing in Figure 2-28, the outer part of the spinal cord consists of white matter, or tracts. These tracts are arranged so that, with few exceptions, the dorsal tracts are sensory and the ventral tracts are motor. The inner part of the cord, which has a butterfly shape, is gray matter. It is composed largely of cell bodies.

Go to the CD and find the spinal cord area of the Central Nervous System module. There you can see various sections of the spinal cord as well as a rotatable model of a spinal cord.

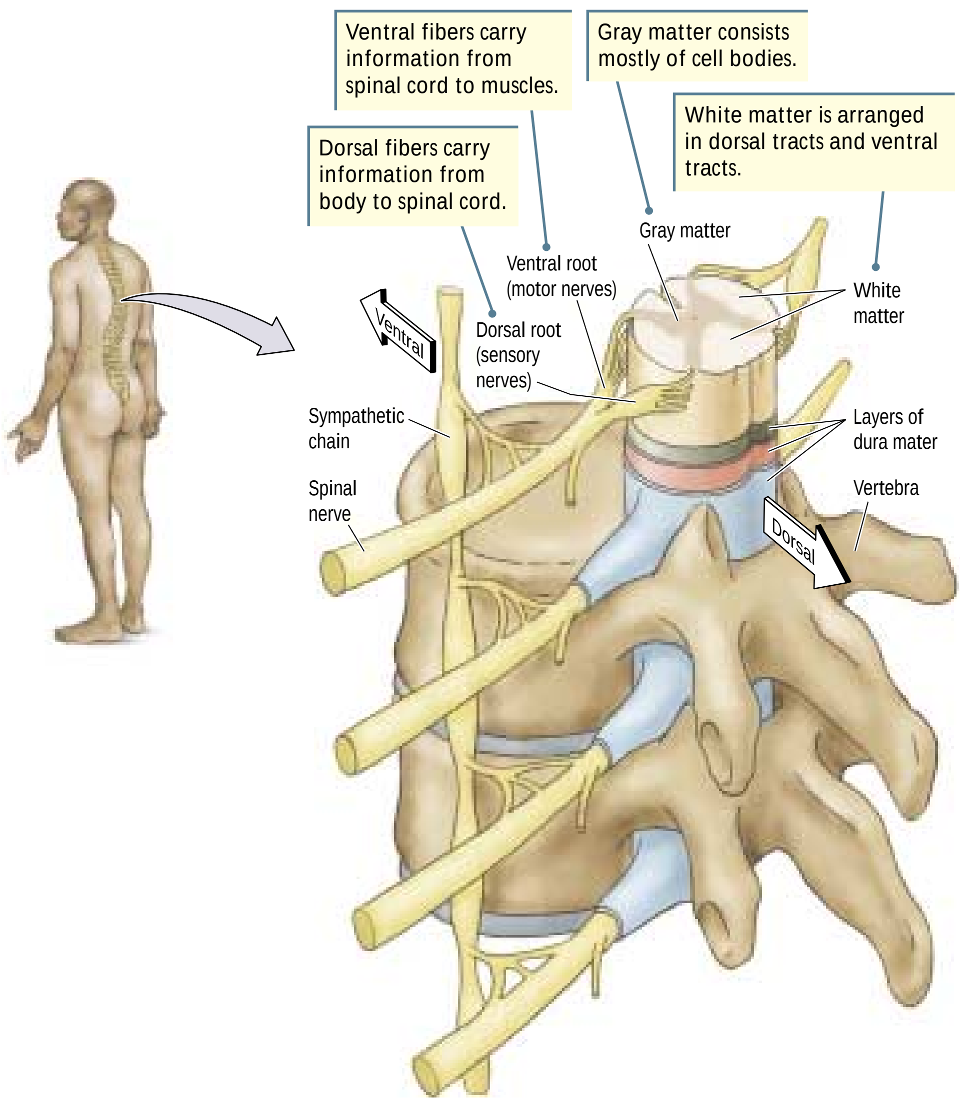


Figure 2-28

The spinal cord runs inside the vertebral column. Part of the internal nervous system (the sympathetic nerve chain) lies outside the spinal column. The gray matter is made up largely of cell bodies, whereas the white matter is made up of fiber tracts that ascend and descend to and from the brain, respectively. Note that dorsal is in front in this diagram so that you can imagine that the skin and muscles of the back have been removed to allow this view of the spinal cord and vertebral column. Below, a photo shows the exposed spinal column.

Bassett/Visuals Unlimited

The observation that the dorsal side of the spinal cord is sensory and the ventral side is motor is known as the **law of Bell and Magendie,** one of the nervous system's very few laws. The Bell and Magendie law, combined with an understanding of the spinal cord's segmental organization, enables neurologists to make quite accurate inferences about the location of spinal-cord damage or disease on the basis of changes in sensation or movement that patients experience. For instance, if a person experiences numbness in the fingers of the left hand but can still move the hand fairly normally, one or more of the dorsal nerves in spinal-cord segments C7 and C8 must be damaged. In contrast, if sensation in the hand is normal but the person cannot move the fingers, the ventral roots of the same segments must be damaged. The topic of diagnosing spinal-cord injury or disease is further discussed in "Magendie, Bell, and Bell's Palsy."

So far we have emphasized the segmental organization of the spinal cord, but the spinal cord must also somehow coordinate inputs and outputs across different segments. For example, many body movements require the coordination of muscles that are controlled by different segments, just as many sensory experiences require the coordination of sensory inputs to different parts of the spinal cord. How is this coordination of spinal-cord activities accomplished? The answer is that the spinal-cord segments are interconnected in such a way that adjacent segments can operate together to form rather complex coordinated movements.

The integration of spinal-cord activities does not require the brain's participation, which is why the headless chicken can run around in a reasonably coordinated way. Still, there must be a close working relation between the brain (and therefore the cranial nervous system) and the spinal nervous system. Otherwise, how could we consciously plan and execute our voluntary actions? Somehow information must be relayed back and forth between the cranial and the spinal systems. Examples of this sharing of information are numerous. For instance, tactile information from sensory nerves in the skin travels not just to the spinal cord, but also to the cerebral cortex through the thalamus. Similarly, the cerebral cortex and other brain structures can control movements because of their connections to the ventral roots of the spinal cord. So, even though the cranial and spinal nervous systems can function independently, the two are intimately connected in their functions.

The Internal Nervous System

The internal nervous system (which, as mentioned earlier, is another term for the autonomic nervous system) is a hidden partner in controlling behavior. Even without our conscious awareness, it stays on the job to keep the heart beating, the liver releasing glucose, the pupils of the eyes adjusting to light, and so forth. Without the internal nervous system, life would quickly cease, because the internal nervous system is in charge of regulating all the body's internal organs and glands. Although it is possible to learn to exert some conscious control over some of the internal nervous system's activities, such conscious interference is unnecessary. One important reason is that the internal nervous system must keep working during sleep, a time when conscious awareness is off-duty.

The internal nervous system is composed of two opposing subsystems: the **sympathetic** and the **parasympathetic.** These subsystems work in opposition to each other, with the sympathetic acting to arouse the body for action and the parasympathetic acting to quiet down the body. For example, the sympathetic system stimulates the heart to beat faster and inhibits digestion, whereas the parasympathetic system slows the heartbeat and stimulates digestion.

Focus on Disorders

Magendie, Bell, and Bell's Palsy

François Magendie, a volatile and committed French experimental physiologist, reported in a three-page paper in 1822 that he had succeeded in cutting the dorsal and ventral roots of puppies, animals in which the roots are sufficiently segregated to allow such surgery. Magendie found that cutting the dorsal roots caused loss of sensation, whereas cutting the ventral roots caused loss of movement. Eleven years earlier, however, a Scotsman named Charles Bell also had proposed functions for these nerve roots based on anatomical information and the results of somewhat inconclusive experiments on rabbits. Although Bell's findings were not identical with Magendie's, they were similar enough to ignite a controversy. Bell hotly disputed Magendie's claim to the discovery of dorsal and ventral root functions. As a result, the principle of sensory and motor segregation in the nervous system has been given both researchers' names: the law of Bell and Magendie.

Magendie's conclusive experiment on puppies was considered extremely important because it enabled neurologists for the first time to localize nervous system damage from the symptoms that a patient displays. Bell went on to describe an example of such localized motor-nerve dysfunction, which still bears his name—Bell's palsy. Bell's palsy is a facial paralysis that occurs when the motor part of the facial nerve on one side of the head becomes inflamed (see the accompanying photograph). The onset of Bell's palsy is typically sudden. Often the stricken person wakes up in the morning and is shocked to discover that the face is paralyzed on one side. He or she cannot open the mouth on that side of the head or completely close the eye on that side. Most people fully recover from Bell's palsy, although it may take several months. But, in rare instances, such as that of Jean Chretien, the Prime Minister of Canada, paralysis of the mouth is permanent.

Dr. P. Marazzi / Science Photo Library/ Photo Researchers

A young man suffering from Bell's palsy, a paralysis of the facial nerve that causes weakness over one side of the face. He was photographed during an involuntary tic (a nervous reaction) that affects the right side of the face, causing his right eye to close tightly.

The internal nervous system is connected to the rest of the nervous system, especially to the spinal nervous system. In fact, activation of the sympathetic system starts in the thoracic and lumbar spinal-cord regions. But the spinal nerves do not directly control the target organs. Rather, the spinal cord is connected to *autonomic control centers*, which are collections of cells called ganglia. It is the ganglia that actually control the organs. The sympathetic system ganglia are located near the spinal cord, forming a chain that runs parallel to the cord, as illustrated in Figure 2-29 on page 64. The parasympathetic system also is connected to the spinal cord—in this case, to the sacral region. But an even larger part of it derives from three cranial nerves: the *vagus nerve*, which controls most of the internal organs, and the *facial* and *oculomotor nerves*, which control salivation and pupil dilation, respectively. In contrast with the sympathetic system, the parasympathetic system connects with ganglia that are near the target organs, as shown in Figure 2-29.

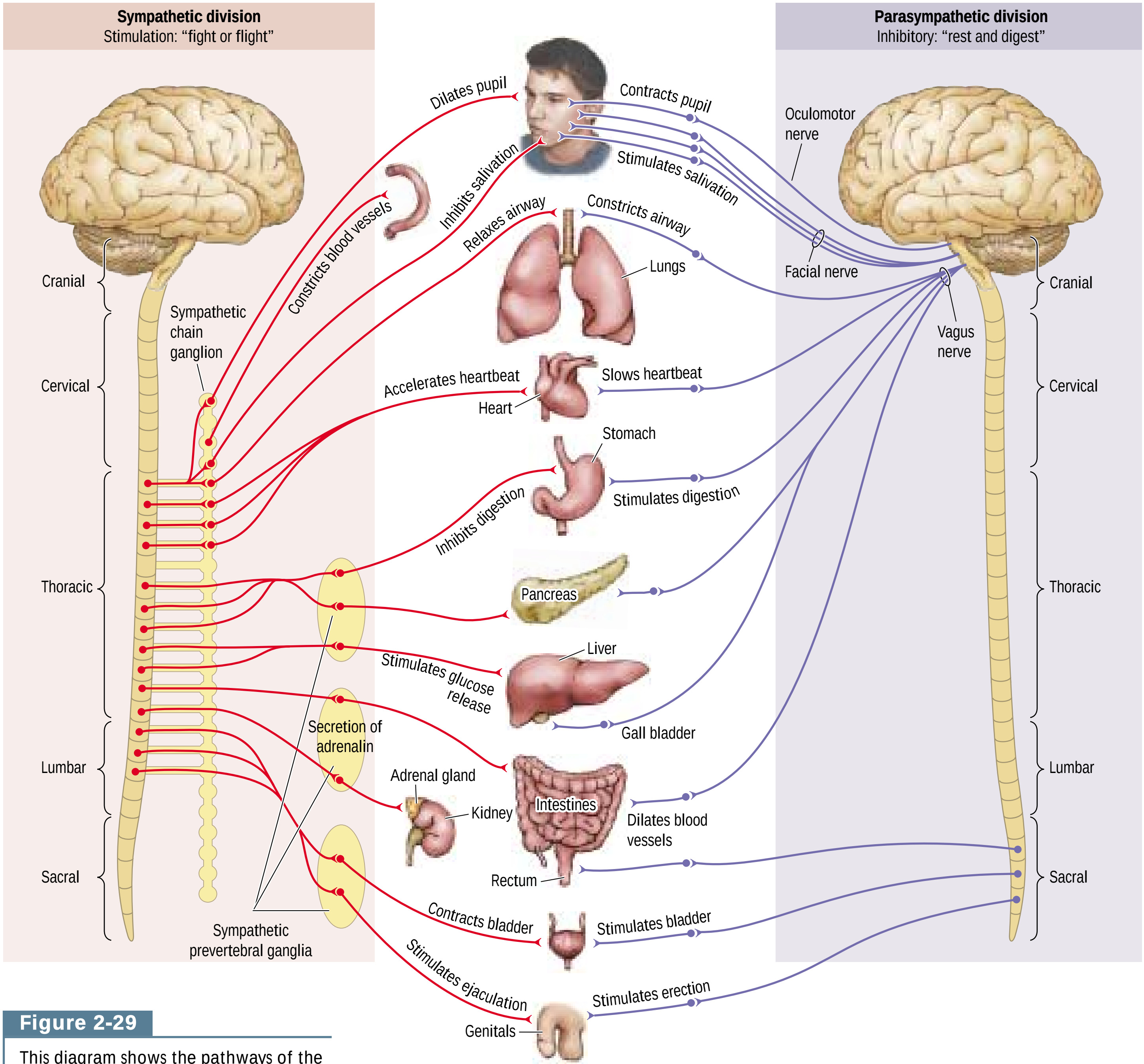


Figure 2-29

This diagram shows the pathways of the internal nervous system, also called the autonomic nervous system. The internal nervous system consists of two parts, the sympathetic and the parasympathetic, that exert opposing effects on the organs that they innervate. All of the autonomic fibers "stop" en route from the spinal cord to their target organs. For the sympathetic system, the fibers "stop" near the spinal cord in the celiac ganglion. For the parasympathetic system, the fibers "stop" on individual parasympathetic ganglia that are found near the target organs.

In Review

We began the chapter by taking a general look at the anatomy of the nervous system and then, in this section, we started to make some guesses about what different nervous system structures might do. Traditional discussions of the nervous system distinguish between the central nervous system, which consists of the brain and spinal cord, and the peripheral nervous system, which encompasses everything else. An alternative categorization is based more on function and divides the nervous system into the cranial nervous system (which includes the brain and its connections to parts of the head), the spinal nervous system (which includes the spinal cord and its connections to and from the body's muscles, joints, and skin), and the internal nervous system (which controls the body's internal organs). Each of these sections of the nervous system can be subdivided into large subsections that are functionally distinct, such as the forebrain and hindbrain of the cranial nervous system. Similarly, within each of the subsections, we find more functional subregions, such as the limbic system and the basal ganglia of the forebrain. Finally, each of these functional systems can be further divided into areas that have their own unique functions, such as the caudate nucleus, putamen, and globus pallidus of the basal ganglia. The process of learning the anatomy of the nervous system is to work from the general to the more specific in each part of the nervous system and, in each case, to remember to associate structure with function.

THE FUNCTIONAL ORGANIZATION OF THE BRAIN

Knowing the parts of a car engine is the place to start in understanding how an engine works. But knowing the parts, unfortunately, is not enough. You also need some principles concerning how the parts work together. For example, even though you know which part the carburetor is, you will not understand its function until you grasp the principle of air and fuel mixing and igniting in the cylinders. Similarly, although you now know the basic parts of the nervous system, you need some general principles to help you understand how these different parts work together. Table 2-3 lists eight such principles, which form the basis for many discussions later in this book. You should spend the time needed to understand these principles fully before moving on to the next chapters.

Principle 1: The Sequence of Brain Processing Is "In → Integrate → Out"

The parts of the brain make a great many connections with one another. Recall, for example, the meddling cerebral cortex that appears to be connected to everything. This connectivity of the brain is the key to its functioning. The points of connection, known as *synapses*, allow cells in different brain regions to influence one another. Chapter 5 explains the organization of the synapse. The key point here is that most

Table 2-3 Principles of Brain Functioning

1. Information is processed in a sequence of "in → integrate → out."
2. There is a functional division between sensory and motor throughout the nervous system.
3. Inputs and outputs to the brain are crossed.
4. There is both symmetry and asymmetry in brain anatomy and function.
5. The nervous system operates by a juxtaposition of excitation and inhibition.
6. The nervous system has multiple levels of function.
7. The nervous system operates as a series of systems arranged both in parallel and hierarchically.
8. Functions in the brain are both localized in specific regions and distributed.

neurons have afferent (incoming) connections with tens or sometimes hundreds of thousands of other neurons, as well as efferent (outgoing) connections to many other cells.

Figure 2-30 shows how these multiple connections enable neurons to integrate information, creating new information. The inputs to a neuron at any given moment are "summed up," and the neuron sends out signals to other neurons that incorporate this summation. The summation is more than just a matter of adding up equally weighted inputs. Some inputs have a greater influence than others on the receiving neuron, and the simultaneous occurrence of certain inputs may have effects that far exceed their simple sum. The summation of information, then, allows that information to be transformed in some way before being passed on to other neurons. This transformation makes the summation process partly one of creating new information.

Figure 2-31 gives a simple example of the creation of new information in the brain. This example begins with receptor cells that are located in the eyes' retinas and are maximally responsive to light of a particular wavelength: red, green, or blue. Now imagine a brain with neurons that receive inputs from one or more of these color-sensitive receptors. A neuron can receive inputs from only one receptor type, from two receptor types, or from all three receptor types. A neuron receiving input from green-type receptor cells would "know" only about green and would forward only green information. In contrast, a neuron receiving input from both green- and red-type receptors would "know" about two colors and would forward a very different message, as would a neuron receiving input from all three receptor types. Both neurons with more than one kind of input would sum the information that they get. In a sense, they would *create* new information that did not previously exist. Such a neuron

For an animation of how neurons integrate information, go to the section on neural integration in the CD module on Neural Communication.

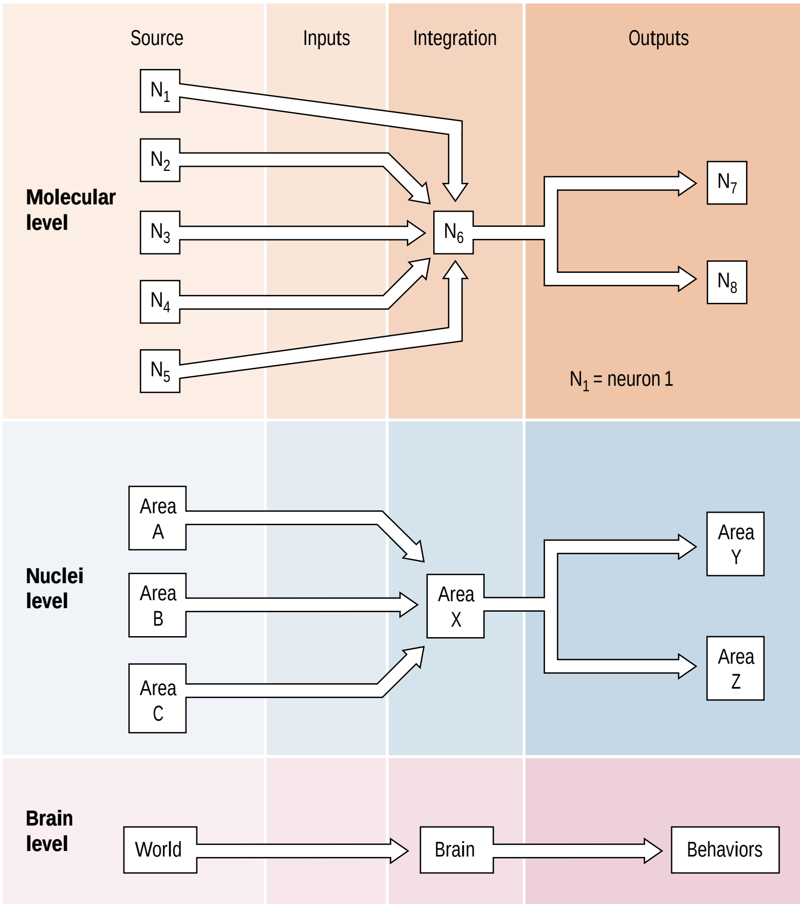


Figure 2-30

The neuron and the brain are devices for gathering, integrating, and sending information. At the cellular level, each of neurons 1 through 5 sends some message to neuron 6, which essentially now "knows" what neurons 1 through 5 signaled. This "knowledge" is a form of integration. The output from neuron 6 is sent to neurons 7 and 8, whose activity is affected by the "knowledge" of neuron 6. Similarly, three neural areas, A through C, send their signals to area X, which can combine (integrate) the information from areas A through C. The integrated information is then sent to areas Y and Z. A similar concept can be applied at the level of the brain as well. The world provides information to the brain, which produces behavior.

might know that an object is both green *and* red, whereas the inputs coming from each receptor contain information about one color only. This creation of new information is what is meant by the "integration operation" of the brain.

The same principle holds for the functioning of a nucleus within the brain or of a layer of brain tissue, as illustrated in Figure 2-30. In regard to a nucleus, the inputs to each neuron in a nucleus are not identical, so there are internal connections between the neurons. These internal connections are known as intrinsic connections. Several areas of the nucleus might each send different information to another area, which integrates that information and sends a combined message along to several other areas. This process is much like the summation of information in a single neuron, but, in this case, the summation takes place in a collection of neurons. As a result of the summation, the output of all of the cells in the nucleus is changed. Once again, there is integration.

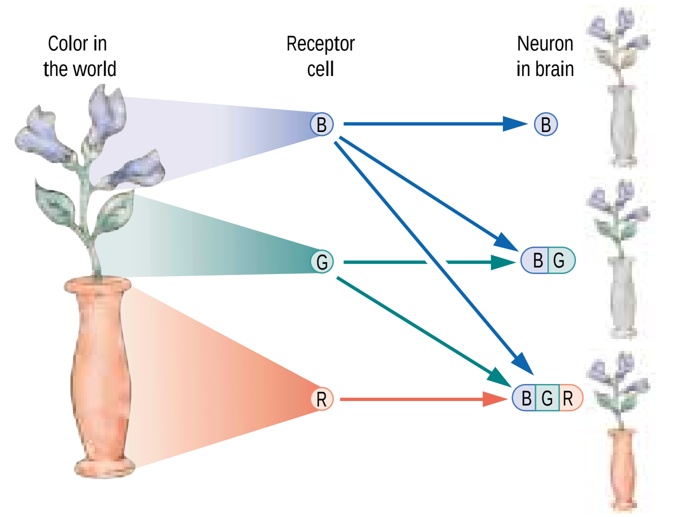


Figure 2-31

Input and output cells differ with respect to their knowledge about the world. Receptor cells B (blue), G (green), and R (red) each code information about one hue in the world. Neurons B, B/G, and B/G/R receive this information and alter it to send a new message that we understand to be color.

The logical extension of this discussion is to view the entire brain as an organ that receives inputs, creates information, and expresses thoughts about the world, as illustrated in Figure 2-30. To the animal whose brain is engaged in this process, the creation of information from inputs represents reality. The bigger the brain, the more complex the reality that can be created and, subsequently, the more complex the thoughts that can be expressed. The emergence of thought that enables consciousness may be the brain's ultimate form of integration.

Principle 2: Sensory and Motor Divisions Exist Throughout the Nervous System

You learned earlier that the spinal cord has separate sensory and motor structures, described in the Bell and Magendie law. This segregation of sensory and motor functions exists throughout the nervous system. However, distinctions between motor and sensory functions become more subtle in places such as the forebrain.

SENSORY AND MOTOR DIVISIONS AT THE PERIPHERY

The peripheral nerves going to and from the spinal cord can be divided into sensory and motor parts, as shown in Figure 2-28. In addition, the cranial nerves, too, have sensory and motor functions, although they are arranged somewhat differently from those in the peripheral nerves. Some of the cranial nerves are exclusively sensory; some are exclusively motor; and some have two parts, one sensory and one motor, much like the sensory and motor branches of peripheral nerves.

SENSORY AND MOTOR DIVISIONS IN THE BRAIN

The hindbrain and midbrain are essentially extensions of the spinal cord; they developed as simple animals evolved a brain at the anterior end of the body. It makes sense, therefore, that, in these lower brainstem regions, there should be a division between structures having sensory functions and those having motor functions, with sensory structures located dorsally and motor ones ventrally. Recall that an important function of the midbrain is to orient the body to stimuli. This orientation requires both sensory input and motor output. The midbrain's colliculi, which are located dorsally, are the sensory component, whereas the tegmentum, which is ventral (below the colliculi), is a motor structure that plays a role in controlling various types of movements, including orienting ones. Both these midbrain structures are illustrated in Figure 2-18.

Distinct sensory and motor nuclei are present in the thalamus, too, although they are no longer located dorsally. Because all sensory information reaches the forebrain through the thalamus, it is not surprising to find separate nuclei associated with vision, hearing, and touch. Separate thalamic nuclei also control movements. Other nuclei have neither sensory nor motor functions. They have connections to cortical areas, such as the frontal lobe, that perform more integrative tasks.

Finally, sensory and motor functions are divided in the cortex as well. This division exists in two ways. First, there are separate sensory and motor cortical regions. Some primarily process a particular sensory input, such as vision, hearing, or touch. Others control detailed movements of discrete body parts, such as the fingers. Second, the entire cortex can be viewed as being organized around the sensory and motor distinction. For instance, layer IV of the cortex always receives sensory inputs, whereas layers V and VI always send motor outputs, as shown in Figure 2-22. Layers I, II, and III are integrative, providing a connection between sensory and motor operations.

Principle 3: The Brain's Circuits Are Crossed

A most peculiar organizational feature of the brain is that its inputs and outputs are "crossed." Each of its halves receives sensory stimulation from the *opposite* (called *contralateral*) side of the body and controls muscles on the opposite side as well. Examples of this crossed organization are shown in Figure 2-32. Crossed organization explains why people with strokes in the left cerebral hemisphere may have difficulty in sensing stimulation to the right side of the body or in moving body parts on the right side. The opposite is true of people with strokes in the right cerebral hemisphere.

In humans, who have forward-facing eyes, the visual system is crossed in a more complex fashion than in animals with eyes on the sides of their head. This complexity is required because, if two eyes are facing forward instead of sideward, they inevitably see much the same thing, except on the far sides of the field of vision. The problem with this arrangement is that, to see an object, information about it must go to the same place in the brain. Duplicate information cannot be sent to two different places. Figure 2-32 (right) shows how the brain solves this problem by dividing each eye's visual field into a left half and a right half. The information that either eye receives from the left half of its visual field is sent to the right side of the brain, and the information that either eye receives from the right half of its visual field is sent to the left side of the brain. The visual system is still crossed, but in a more complicated way than are systems for other parts of the body.

For an animation and illustration of how the visual system is crossed, go to the section on the optic chiasm in the Visual System module on the CD.

One difficulty with a crossed nervous system is that the two sides of the world must be joined together somehow. This joining is accomplished by having numerous connections between the left and right sides of the brain. The most prominent connecting cable is the corpus callosum, shown in Figure 2-8. As stated earlier, the corpus callosum connects the left and right cerebral hemispheres with about 200 million fibers.

Principle 4: The Brain Is Both Symmetrical and Asymmetrical

You know that the brain has two halves, the left and the right hemispheres, which look like mirror images of each other. Although these two halves are symmetrical in many ways, they also have some asymmetrical features. This asymmetrical organization is essential for certain tasks. Consider speaking. If a language zone existed in both hemispheres, each connected to one side of the mouth, we would have the strange ability to talk out of both sides of the mouth at once. This would not make talking

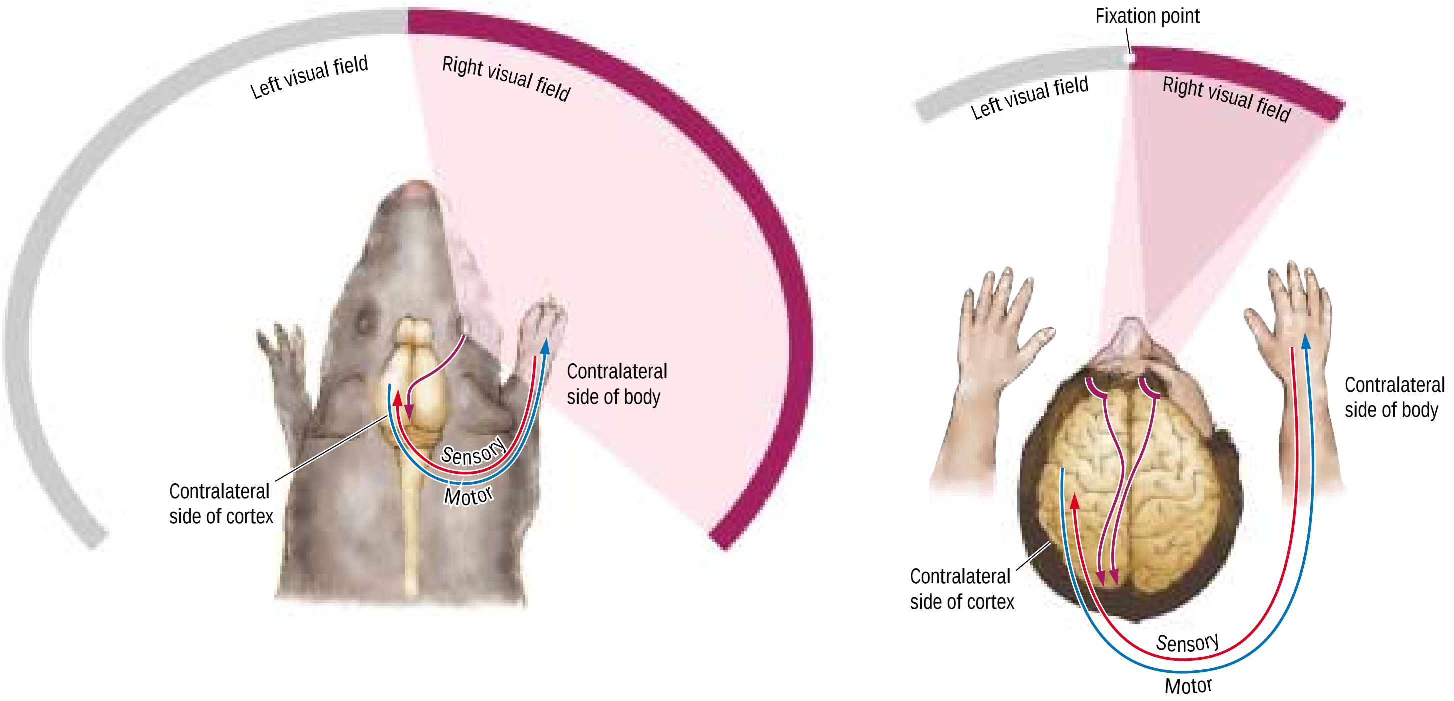


Figure 2-32

(*Left*) This schematic representation of a rat's brain from a dorsal view shows the projection of visual and somatosensory input to contralateral (opposite-side) areas of the cortex and the crossed projection of the motor cortex to the contralateral side of the body. The eyes of the rat are laterally placed, such that most of the input from each eye travels to the opposite hemisphere. (*Right*) In the human head, the two eyes are frontally placed. As a result, the visual input is split in two so that input from the right side of the world as seen by both eyes goes to the left hemisphere and input from the left side of the world as seen by both eyes goes to the right hemisphere. The somatosensory input of both rats and humans is completely crossed, so that information coming from the right paw or hand goes to the left hemisphere. Note that although the diagram as drawn shows activity as going directly to and from the brain, there are connectors en route.

easy, to say the least. One solution is to locate control of the mouth on one side of the brain only. Organizing the brain in this way would allow us to speak with a single voice. A similar problem arises in controlling the body's movement in space. We would not want the left and the right hemispheres each trying to take us to a different place. Again, the problem can be solved if a single brain area controls this sort of spatial processing.

In fact, processes such as language and spatial navigation *are* localized on only one side of the brain. Language is usually on the left side, and spatial functions are usually on the right. This asymmetrical organization is not unique to humans. Birds have developed a solution to producing song by locating the control of singing in one hemisphere. Curiously, like human language, bird song also is usually located on the brain's left side. Why this similarity exists is not completely clear. But the key point is that, in many species, the brain has both symmetrical and asymmetrical organization.

Principle 5: The Nervous System Works Through Excitation and Inhibition

Imagine that, while you are reading this page, the telephone rings. You stop reading, get up, walk to the telephone, pick it up, and talk to a friend who convinces you that going to a movie would be more fun than reading. To carry out this series of actions, not only must your brain produce certain behaviors, it must also stop other behaviors. When you were walking and talking, for example, you were not engaged in reading. To walk and talk, you had to first stop reading. Producing behavior, then, requires both initiating some actions and inhibiting others.

In talking about the nervous system, we refer to the initiation of an activity as **excitation** and the stoppage of an activity as **inhibition.** The juxtaposition of excitation and inhibition is a key principle of nervous system functioning. Recall, for example, that the sympathetic and parasympathetic systems produce opposite actions. The sympathetic system excites the heart, whereas the parasympathetic inhibits it. This general principle of excitation and inhibition is central to how the nervous system works.

The same principle can be seen in the activity of individual neurons. Neurons can pass on information to other neurons either by being active or by being silent. That is, they can be "on" or "off." Some neurons in the brain function primarily to excite other neurons, whereas others function to inhibit other neurons. These excitatory and inhibitory effects are produced by various chemicals that turn the neurons on or off.

Just as individual neurons can act to excite or inhibit other neurons, brain nuclei (or layers) can do the same to other nuclei (or layers). These actions are especially obvious in the motor systems. Inhibiting reading and initiating walking to the telephone, for example, result from the on and off actions of specific motor-system nuclei.

Now imagine that one of the nuclei that normally inhibits some type of movement is injured. The injury will result in an inability to inhibit that particular response. This symptom can be seen in people with frontal-lobe injury. Such people are often unable to inhibit behaviors, such as talking at inappropriate times or using certain words, such as curse words. In contrast, people with injury to the speech zones of the left hemisphere may be unable to talk at all, because the injury is in an area that normally initiates the behavior of speech. These contrasting symptoms lead to an important conclusion: brain injury can produce either a loss of behavior or a release of behavior. Behavior is lost when the damage prevents excitatory instructions; behavior is released when the damage prevents inhibitory instructions.

Principle 6: The Central Nervous System Has Multiple Levels of Function

You have seen that similar sensory and motor functions are carried out in various parts of the brain and spinal cord. But why are multiple areas with overlapping functions needed? After all, it would seem simpler to put all the controls for a certain function in a single place. Why bother with duplication?

The answer is that the mammalian brain is a product of evolution in which it changed according to the "descent with modification" rule. As the brain evolved, new areas were added, but old ones were retained. As a result, there was a problem of where to put the new regions. The simplest solution was to add them on top of the existing brain. We can see this solution in the evolution from primitive vertebrates to amphibians to mammals. For instance, primitive vertebrates, such as fish, make only whole-body movements to swim, movements that are controlled by the spinal cord and hindbrain. Amphibians developed legs and corresponding neural control areas in the brainstem. Mammals later developed new capacities with their limbs, such as independent limb movements and fine digit movements. These movements, too, required new control areas, which were added in the forebrain. We therefore find three distinct areas of motor control in mammals: the spinal cord, the brainstem, and the forebrain.

At the beginning of the twentieth century, John Hughlings-Jackson suggested that the addition of new brain structures in the course of evolution could be viewed as adding new levels of nervous system control. The lowest level is the spinal cord, the next level is the brainstem, and the highest level is the forebrain. These levels are not autonomous, however. To move the arms, the brainstem must use circuits in the spinal cord. Similarly, to make independent movements of the arms and fingers, such as in tying a shoelace, the cortex must use circuits in both the brainstem and the spinal cord. Each new level offers a refinement and elaboration of the motor control provided by one or more lower levels.

For more about the evolution of the brain, go to the Web site for a connection to the National Museum of Health and Medicine for photographs of brains from all sorts of creatures and discussion of brain evolution.

We can observe the operation of functional levels in the behavior of people with brain injuries. Someone whose spinal cord is disconnected from the brain cannot voluntarily move a limb because the brain has no way to control the movement. But the limb can still move automatically to withdraw from a noxious stimulus because the circuits for moving the muscles are still intact in the spinal cord. Similarly, if the forebrain is not functioning but the brainstem is still connected to the spinal cord, a person can still move, but the movements are relatively simple: there is limited limb use and no digit control.

The principle of multiple levels of function can also be applied to the cortex in mammals, which evolved by adding new areas, mostly sensory-processing ones. The newer areas essentially added new levels of control that provide more and more abstract analysis of inputs. Consider the recognition of an object, such as a car. The simplest level of analysis recognizes the features of this object such as its size, shape, and color. A higher level of analysis recognizes this object as a car. And an even higher level of analysis recognizes it as Susan's car with a dent in the fender. Probably the highest levels are cortical regions that substitute one or more words for the object (Honda Civic, for instance) and can think about the car in its absence.

When we consider the brain as a structure composed of multiple levels of function, it is clear that these levels must be extensively interconnected to integrate their processing and create unified perceptions or movements. The nature of this connectivity in the brain leads to the next principle of brain function: the brain has both parallel and hierarchical circuitry.

Principle 7: Brain Systems Are Organized Both Hierarchically and in Parallel

The brain and spinal cord are two semiautonomous nervous systems organized into functional levels, and, even within a single level, more than one area may take part in a given function. How then, with these different systems and levels, do we eventually obtain a unified conscious experience? Why, when we look at Susan's car, do we not have the sense that one part of the brain is processing features such as shape while another part is processing color? Or why, when we tie our shoelaces, are we not aware that different levels of motor control are at work to move our arms and fingers and coordinate their actions? These questions are part of what is called the "binding problem." It focuses on how the brain ties together its various activities into a whole. The solution to the problem must somehow be related to the ways in which the parts of the nervous system are connected.

There are two alternative possibilities for wiring the nervous system: serial or parallel circuits. A *serial circuit* hooks up in a series all the regions concerned with a given function. Consider Susan's car again. In a serial system, the information from the eyes would go first to a region (or regions) that performs the simplest analysis—for example, the detection of specific properties, such as color and shape. This information would then be passed on to another region that sums up the information and identifies a car. The information would next proceed to another region that compares this car with stored images and identifies it as Susan's car. Notice how the perceptual process entails the flow of information sequentially through the circuit. Because the regions in the chain range from simple to complex, this serial type of system is usually called a simple hierarchical model. It is illustrated in Figure 2-33A on page 72.

In the 1960s and 1970s, neuropsychologists proposed models of **hierarchical organization** to help in understanding how the brain might produce complex behaviors. One difficulty with such models, however, is that functionally related structures in the brain are not always linked serially. Although the brain has many serial connections, many expected connections are missing. For example, within the visual system, one group of cortical areas is not connected with what appears to be a parallel group of areas.

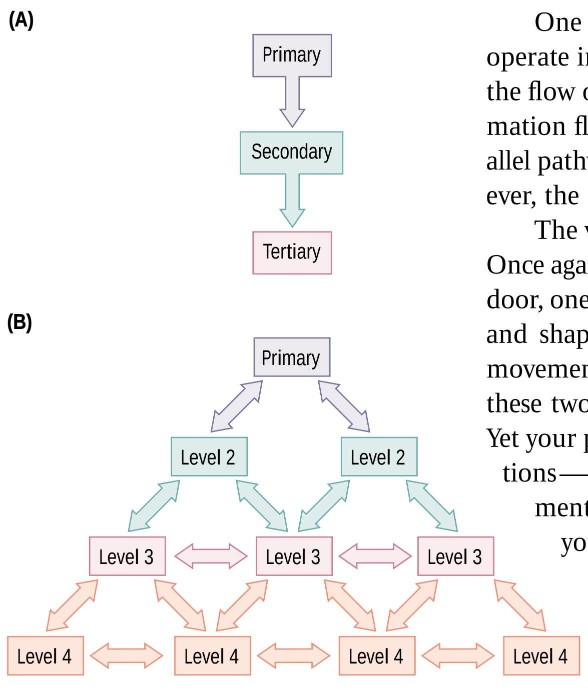


Figure 2-33

(A) This simple serial hierarchical model of cortical processing is similar to that first proposed by A. R. Luria. In Luria's scheme, information was conceptualized as being organized into three levels: primary, secondary, and tertiary. **(B)** In Daniel Felleman and David van Essen's distributed hierarchical model, there are multiple levels in each of several processing streams. Areas at each level are interconnected with one another.

One solution to this problem is to imagine multiple hierarchical systems that operate in parallel to one another but are also interconnected. Figure 2-33B illustrates the flow of information in such a distributed hierarchical model. If you trace the information flow from the primary area to levels 2, 3, and 4, you can see that there are parallel pathways. These multiple parallel pathways are also connected to each other. However, the connections are more selective than those that exist in a purely serial circuit.

The visual system provides a good example of such parallel hierarchical pathways. Once again we return to Susan's car—this time to one of its doors. As we look at the car door, one set of visual pathways processes information about its nature, such as its color and shape, while another set of pathways processes information about door-related movements, such as those required to open the door. It may surprise you to learn that these two systems are independent of each other, with no connections between them. Yet your perception when you pull the door open is not one of two different representations—the door's size, shape, and color, on the one hand, and the opening movements, on the other. When you open the door, you have the impression of unity in your conscious experience. Interestingly, the brain is organized into multiple parallel pathways in all of its subsystems. Yet our conscious experiences are always unified. We will return to this conundrum (and the binding problem) at the end of this book. For now, keep in mind that your common-sense impressions of how the brain works may not always be right.

Principle 8: Functions in the Brain Are Both Localized and Distributed

In our consideration of brain organization, we have so far assumed that functions can be localized in specific parts of the brain. This assumption makes intuitive sense, but it turns out to be controversial. One of the great debates in the history of brain research has been about what aspects of different functions are actually localized in specific brain regions.

Perhaps the fundamental problem is that of defining a function. Consider language, for example. Language includes the comprehension of spoken words, written words, signed words (as in American Sign Language), and even touched words (as in Braille). Language also includes processes of producing words, both orally and in writing, as well as constructing whole linguistic compositions, such as stories, poems, songs, and essays. Because the function that we call language has many aspects, it is not surprising that they reside in widely separated areas of the brain. We see evidence of this widespread distribution in language-related brain injuries. People with injuries in different locations may selectively lose the abilities to produce words, understand words, read words, write words, and so forth. Specific language-related abilities, therefore, are found in specific locations, but language itself is distributed throughout a wide region of the brain.

Memory provides another example of this same pattern. Memories can be extremely rich in detail and can include sensory material, feelings, words, and much more. Like language, then, memory is not located in just one brain region. Rather, it is distributed throughout a vast area of the brain.

Because many functions are both localized and distributed in the brain, damage to a small brain region produces only *focal symptoms*. Massive brain damage is required to completely remove some function. For instance, a relatively small injury could impair some aspect of language functioning, but it would take a very widespread injury to completely remove all language abilities. In fact, one of the characteristics of dementing diseases, such as Alzheimer's, is that people can have widespread deterioration of the cortex yet maintain remarkably normal language functions until late stages of the disease.

In Review

Knowing the parts of a car engine or a brain, and some general notions of what they might do, was only the beginning. The next step was to learn some principles concerning how the parts work together. We have identified eight such principles that will allow us to proceed to a closer look, in the chapters that follow, at how the brain produces behavior. You will benefit from reviewing each of these principles with an eye toward understanding the general concept being addressed, rather than simply memorizing the statement itself. For example, as you think about the principle stating that the nervous system works through excitation and inhibition, think about the balance created by this principle's application and what this balance means for the functioning brain. What would happen, say, if you could not inhibit behavior? When we encounter the rules that govern the operation of neurons in the next four chapters, you will want to revisit the inhibition–excitation principle and again think about how it can relate to the way in which individual cells work to produce behavior.

SUMMARY

1. *What are some of the larger external and internal features of the brain?* Under the tough, protective meninges that covers the brain lie its two major structures—the larger cerebrum, divided into two hemispheres, and the smaller cerebellum. Both structures are covered with gyri (bumps) and sulci (cracks), some of which are so deep that they are called fissures. At the base of the brain, where it joins the spinal cord, the brainstem is visible, as are the cranial nerves that run to the head. Cutting the brain in half reveals the fluid-filled ventricles inside it, as well as the white matter, gray matter, and reticular matter that make up its tissue. Also apparent is the corpus callosum, which joins the two hemispheres and the subcortical regions below the cerebral cortex.
2. *How can the nervous system be divided for functional analysis?* The nervous system is composed of subsystems that function semiautonomously. These subsystems are the cranial, spinal, and internal nervous systems. The cranial nervous system includes the brain and the cranial nerves, which link the brain to various parts of the head. The spinal nervous system consists of the spinal cord and the peripheral nerves that enter and leave it, going to and from muscles, skin, and joints in the body. The internal nervous system, which controls the body's internal organs, is also called the autonomic nervous system. It has two parts, the sympathetic and parasympathetic divisions. They work in opposition to each other, one arousing the body for action and the other calming the body down.
3. *What are the basic structures and functions of the lower part of the brain, called the brainstem?* The brainstem consists of three regions: the hindbrain, the midbrain, and the diencephalon. The cerebellum is important in controlling complex movements. Three other structures are the reticular formation (which serves to activate the forebrain), the pons (which provides a bridge from the cerebellum to the rest of the brain), and the medulla (which controls such vital functions as breathing). In the midbrain, the tectum processes information from the eyes and ears and produces movements related to these sensory inputs. Below it lies the tegmentum, which consists of many nuclei, largely with movement-related functions. Finally, the diencephalon consists of two main structures: the thalamus and the hypothalamus.

4. *What are some important structures in the upper part of the brain, called the forebrain?* The forebrain is the largest region of the brain. Its outer surface is the cortex. Sulci, especially deep ones called fissures, form the boundaries of the four lobes on each cerebral hemisphere: the frontal, the parietal, the temporal, and the occipital. The cells of the cortex form distinctive layers based on their specialized functions. Interconnections exist between these layers and virtually all other parts of the brain. These extensive connections to other brain regions are essential to the cortex with its directing role in top-down processing. The basal ganglia, lying just below the white matter of the cortex, are another important part of the forebrain that primarily play a role in movement. Also important in the forebrain is the limbic system. The part of the limbic system called the amygdala regulates emotional behavior, whereas the hippocampus and the cingulate cortex both have roles in memory and in navigating the body in space.
5. *How does the spinal nervous system work?* The spinal nervous system has sensory input from the skin, muscles, and joints of the body. It also has efferent connections to the skeletal muscles, which makes it responsible for controlling the body's movements. The spinal cord functions as a kind of minibrain for the nerves that enter and leave a particular spinal segment. Each segment works relatively independently, although fibers interconnect them and coordinate their activities. According to the law of Bell and Magendie, nerves entering a segment's dorsal side carry information from sensory receptors in the body, whereas nerves leaving a segment's ventral side carry information to the muscles.
6. *What are some basic principles related to the functional organization of the brain?* One principle is that the sequence of processing within the brain is "in → integrate → out," in which the term *integrate* refers to the creation of new information as cells, nuclei, and brain layers sum the inputs that they receive from different sources. A second principle is that sensory and motor functions are separated throughout the nervous system, not just in the spinal system but in the brain as well. A third principle is that the organization of the brain is *crossed*, meaning that the right hemisphere is connected to the left side of the body, whereas the left hemisphere is connected to the body's right side. Fourth is the principle that the brain, though largely symmetrical, also has asymmetrical organization appropriate for certain tasks, and fifth is the principle that the nervous system works through a combination of excitatory and inhibitory signals. The sixth principle is that the nervous system has multiple levels of function. Tasks are often duplicated in these multiple levels, which range from older, more primitive ones to higher levels that evolved more recently. Two final principles are that brain circuits are organized both hierarchically and in parallel and that functions are both localized and distributed in the brain.

KEY TERMS

basal ganglia, p. 55
brainstem, p. 43
cerebellum, p. 43
cerebrum, p. 43
cortex (neocortex), p. 55
cranial nerve, p. 43
dermatome, p. 60
diencephalon, p. 50
forebrain, p. 55
gray matter, p. 44
hindbrain, p. 50
hypothalamus, p. 54
limbic system, p. 55
midbrain, p. 50
reticular formation, p. 52
reticular matter, p. 44
subcortical regions, p. 45
tectum, p. 53
tegmentum, p. 54
thalamus, p. 54
white matter, p. 44

REVIEW QUESTIONS

1. What are the three primary functions of the brain?
2. What features of the brain are visible from the outside?
3. Contrast the anatomical and functional divisions of the nervous system.
4. Expand the Bell and Magendie law to include the entire nervous system.
5. In what sense is the nervous system crossed?
6. In what sense is the activity of the nervous system a summation of excitatory and inhibitory processes?
7. What does it mean to say that the nervous system is organized into levels?

FOR FURTHER THOUGHT

In the course of studying the effects of the removal of the entire cerebral cortex on the behavior of dogs, Franz Goltz noticed that the dogs were still able to walk, smell, bark, sleep, withdraw from pain, and eat. He concluded that functions must not be localized in the brain, reasoning that only widely distributed functions could explain how the dogs still performed all these behaviors despite so much lost brain tissue. On the basis of the principles introduced in this chapter, how would you explain why the dogs behaved so normally in spite of having lost about one-quarter of the brain?

RECOMMENDED READING

Diamond, M. C., Scheibel, A. B., & Elson, L. M. (1985). *The human brain coloring book.* New York: Barnes & Noble. Although a coloring book might seem an odd way to learn neuroanatomy, many students find this book to be a painless way to study the relations between brain structures.

Jerison, H. J. (1991). *Brain size and the evolution of mind*. New York: American Museum of Natural History. What is the mind and why do we have language? These questions and many more are discussed by the leading expert in brain evolution. This monograph is a fascinating introduction to the issues surrounding why the brain grew larger in the primate evolutionary branch and what advantage a large brain might confer in creating a richer sensory world.

Heimer, L. (1995). *The human brain and spinal cord: Functional neuroanatomy and dissection guide* (2nd ed.). New York: Springer Verlag. If coloring books aren't your thing, then Heimer's dissection guide to the human brain will provide a more traditional, and sophisticated, guide to human brain anatomy.

Luria, A. R. (1973). *The working brain*. Harmondsworth, England: Penguin. Luria was a Russian neurologist who studied thousands of patients over a long career. He wrote a series of books outlining how the human brain functions, of which *The Working Brain* is the most accessible. In fact, this book is really the first human neuropsychology book. Although many of the details of Luria's ideas are now outdated, his general framework for how the brain is organized is substantially correct.

Zeki, S. (1993). *A vision of the brain*. London: Blackwell Scientific. Humans are visual creatures. Zeki's book uses the visual system as a way of introducing the reader to how the brain is organized. It is entertaining and introduces the reader to Zeki's ideas about how the brain functions.

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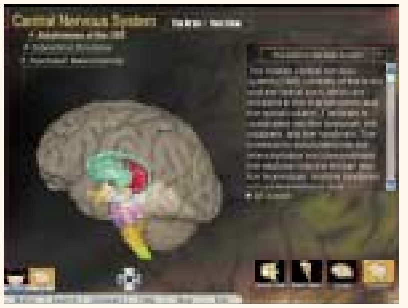

There are many resources available for expanding your learning on line:

■ **www.worthpublishers.com/kolb/chapter2**
Try some self-tests to reinforce your mastery of the material in Chapter 2. Look at some of the news updates reflecting current research on the brain. You'll also be able to link to some other sites which will reinforce what you've learned.

■ **www.neurophys.wisc.edu/brain**
Link to brain atlases that include photographs, stained sections, and movie clips from humans, monkeys, and even a dolphin. Note the differences among the brains (the increasing complexity as you move from mouse to human) as well as the similarities (try to find brain nuclei that are the same across species).

■ **www.williamcalvin.com/1990s/1998SciAmer.htm**
Read an article about the theory of brain evolution from *Scientific American.*

On your CD-ROM you'll be able to quiz yourself on your comprehension of Chapter 2. An entire module devoted to the Central Nervous System includes a rotatable, three-dimensional brain and many sections of the brain you can move through with the click of a mouse. In addition, the Research Methods module includes various CT and MRI images of the brain, including a video clip of a coronal MRI scan.