FOUNDATIONS OF PHYSIOLOGICAL PSYCHOLOGY, 6/e

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Structure of the Nervous System

chapter 3

CHAPTER OUTLINE:

LEARNING OBJECTIVES:

1. Describe the appearance of the brain and identify the terms used to indicate directions and planes of section.
2. Describe the divisions of the nervous system, the meninges, the ventricular system, and the production of cerebrospinal fluid and its flow through the brain.
3. Outline the development of the central nervous system.
4. Describe the telencephalon, one of the two major structures of the forebrain.
5. Describe the two major structures of the diencephalon.
6. Describe the major structures of the midbrain, the hindbrain, and the spinal cord.
7. Describe the peripheral nervous system, including the two divisions of the autonomic nervous system.

PROLOGUE:

The Left Is Gone

Miss S. was a sixty-year-old woman with a history of high blood pressure, which was not responding well to the medication she was taking. One evening she was sitting in her reclining chair reading the newspaper when the phone rang. She got out of her chair and walked to the phone. As she did, she began feeling giddy and stopped to hold onto the kitchen table. She has no memory of what happened after that.

The next morning, a neighbor, who usually stopped by to have coffee with Miss S., found her lying on the floor, mumbling incoherently. The neighbor called an ambulance, which took Miss S. to a hospital.

Two days after her admission, I visited her in her room, along with a group of people being led by the chief of neurology. The neurological resident in charge of her case had already told us that she had had a stroke in the back part of the right side of the brain. He had attached a CT scan to an illuminated viewer mounted on the wall and had showed us a white spot caused by the accumulation of blood in a particular region of her brain. (You can look at the scan yourself if you like; it is shown in Figure 5.17.)

About a dozen of us entered Miss S.'s room. She was awake but seemed a little confused. The resident greeted her and asked how she was feeling. "Fine, I guess," she said. "I still don't know why I'm here."

"Can you see the other people in the room?"

"Why, sure."

"How many are there?"

She turned her head to the right and began counting. She stopped when she had counted the people at the foot of her bed. "Seven," she reported. "What about us?" asked a voice from the left of her bed. "What?" she said, looking at the people she had already counted. "Here, to your left. No, toward your left!" the voice repeated. Slowly, rather reluctantly, she began turning her head to the left. The voice kept insisting, and finally, she saw who was talking. "Oh," she said, "I guess there are more of you."

The resident approached the left side of her bed and touched her left arm. "What is this?" he asked. "Where?" she said. "Here," he answered, holding up her arm and moving it gently in front of her face.

"Oh, that's an arm."

"An arm? Whose arm?"

"I don't know. . . . I guess it must be yours."

"No, it's yours. Look, it's a part of you." He traced with his fingers from her arm to her shoulder.

"Well, if you say so," she said, still sounding unconvinced.

When we returned to the residents' lounge, the chief of neurology said that we had seen a classic example of unilateral neglect, caused by damage to a particular part of the brain. "I've seen many cases like this," he explained. "People can still perceive sensations from the left side of their body, but they just don't pay attention to them. A woman will put makeup on only the right side of her face, and a man will shave only half of his beard. When they put on a shirt or a coat, they will use their left hand to slip it over their right arm and shoulder, but then they'll just forget about their left arm and let the garment hang from one shoulder. They also don't look at things located toward the left or even the left halves of things. Once I saw a man who had just finished eating breakfast. He was sitting in his bed, with a tray in front of him. There was half of a pancake on his plate. 'Are you all done?' I asked. 'Sure,' he said. I turned the plate around so that the unearten part was on his right. He gave a startled look and said, 'Where the hell did that come from?'"

The goal of neuroscience research is to understand how the brain works. To understand the results of this research, you must be acquainted with the basic structure of the nervous system. The number of terms introduced in this chapter is kept to a minimum (but as you will see, the minimum is still a rather large number). (See ***Chapter 3 Animations: Figures and Diagrams.***) With the framework you will receive from this chapter and from the animations, you should have no trouble learning the material presented in subsequent chapters.

The exercise on the CD-ROM for Chapter 3 entitled "Figures and Diagrams" will help you learn the names and locations of the major structures of the nervous system.

Basic Features of the Nervous System

Before beginning a description of the nervous system, I want to discuss the terms that are used to describe it. The gross anatomy of the brain was described long ago, and everything that could be seen without the aid of a microscope was given a name. Early anatomists named most brain structures according to their similarity to commonplace objects: amygdala, or “almond-shaped object”; hippocampus, or “sea horse”; genu, or “knee”; cortex, or “bark”; pons, or “bridge”; uncus, or “hook,” to give a few examples. Throughout this book I will translate the names of anatomical terms as I introduce them, because the translation makes the terms more memorable. For example, knowing that *cortex* means “bark” (like the bark of a tree) will help you to remember that the cortex is the outer layer of the brain.

When describing features of a structure as complex as the brain, we need to use terms denoting directions. Directions in the nervous system are normally described relative to the **neuraxis,** an imaginary line drawn through the spinal cord up to the front of the brain. For simplicity’s sake, let’s consider an animal with a straight neuraxis. Figure 3.1 shows an alligator and two humans. This alligator is certainly laid out in a linear fashion; we can draw a straight line that starts between its eyes and continues down the center of its spinal cord. (See ***Figure 3.1***.) The front end is **anterior,** and the tail is **posterior.** The terms **rostral** (toward the

neuraxis An imaginary line drawn through the center of the length of the central nervous system, from the bottom of the spinal cord to the front of the forebrain.

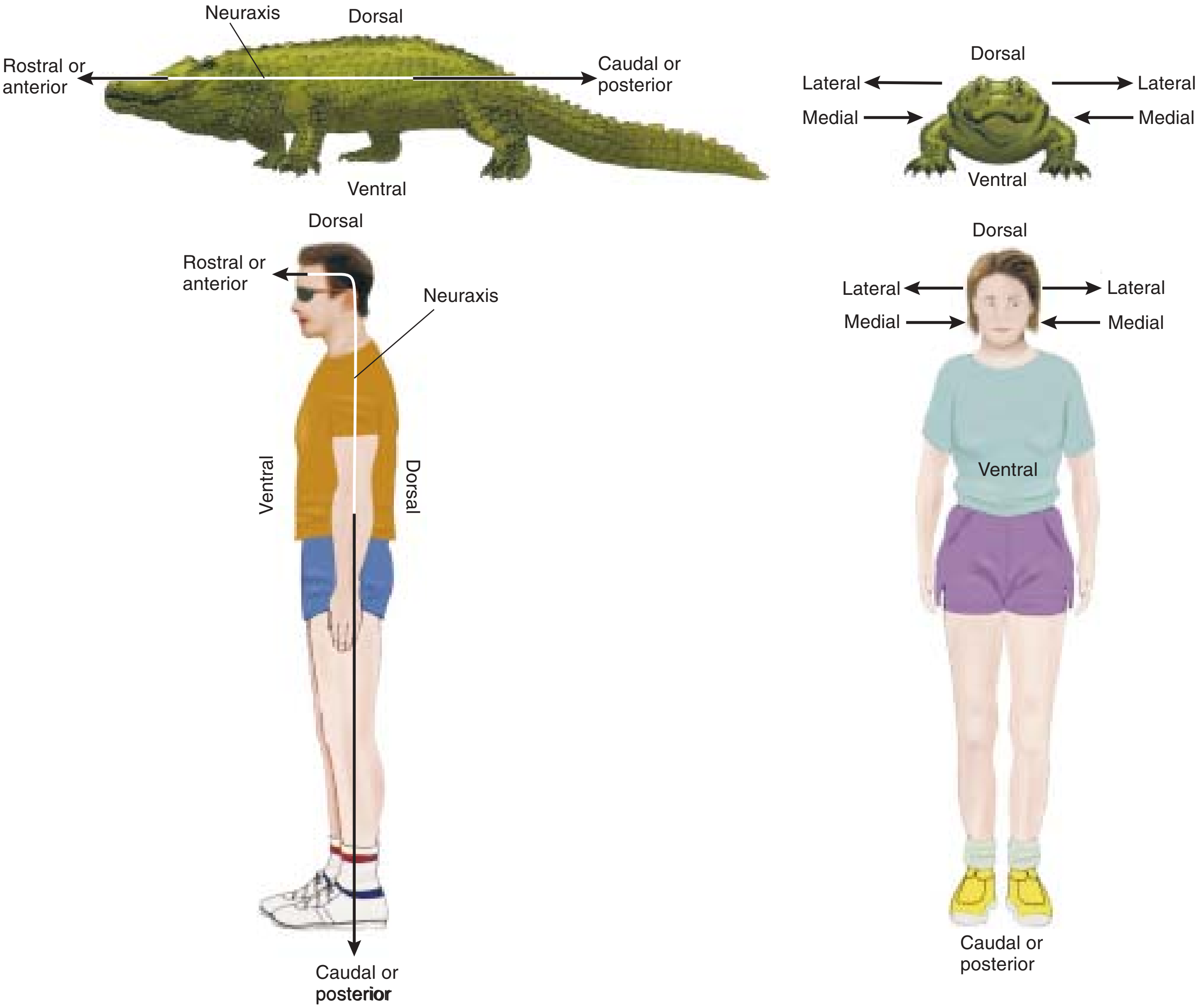
anterior With respect to the central nervous system, located near or toward the head.

posterior With respect to the central nervous system, located near or toward the tail.

rostral “Toward the beak”; with respect to the central nervous system, in a direction along the neuraxis toward the front of the face.

Figure 3.1

Side and frontal views of alligator and human, showing the terms used to denote anatomical directions.



beak) and **caudal** (toward the tail) are also employed, especially when referring specifically to the brain. The top of the head and the back are part of the **dorsal** surface, while the **ventral** (front) surface faces the ground. (*Dorsum* means "back," and *ventrum* means "belly.") These directions are somewhat more complicated in the human; because we stand upright, our neuraxis bends, so the top of the head is perpendicular to the back. (You will also encounter the terms *superior* and *inferior*. In referring to the brain, *superior* means "above," and *inferior* means "below." For example, the *superior colliculi* are located above the *inferior colliculi*.) The frontal views of both the alligator and the human illustrate the terms **lateral** and **medial:** toward the side and toward the midline, respectively. (See ***Figure 3.1.***)

Two other useful terms are *ipsilateral* and *contralateral*. **Ipsilateral** refers to structures on the same side of the body. If we say that the olfactory bulb sends axons to the *ipsilateral* hemisphere, we mean that the left olfactory bulb sends axons to the left hemisphere and the right olfactory bulb sends axons to the right hemisphere. **Contralateral** refers to structures on opposite sides of the body. If we say that a particular region of the left cerebral cortex controls movements of the *contralateral* hand, we mean that the region controls movements of the right hand.

To see what is in the nervous system, we have to cut it open; to be able to convey information about what we find, we slice it in a standard way. Figure 3.2 shows a human nervous system. We can slice the nervous system in three ways:

1. Transversely, like a salami, giving us **cross sections** (also known as **frontal sections** when referring to the brain)
2. Parallel to the ground, giving us **horizontal sections**
3. Perpendicular to the ground and parallel to the neuraxis, giving us **sagittal sections.** The **midsagittal plane** divides the brain into two symmetrical halves. The sagittal section in Figure 3.2 lies in the midsagittal plane.

Note that because of our upright posture, cross sections of the spinal cord are parallel to the ground. (See ***Figure 3.2.***)

caudal "Toward the tail"; with respect to the central nervous system, in a direction along the neuraxis away from the front of the face.

dorsal "Toward the back"; with respect to the central nervous system, in a direction perpendicular to the neuraxis toward the top of the head or the back.

ventral "Toward the belly"; with respect to the central nervous system, in a direction perpendicular to the neuraxis toward the bottom of the skull or the front surface of the body.

lateral Toward the side of the body, away from the middle.

medial Toward the middle of the body, away from the side.

ipsilateral Located on the same side of the body.

contralateral Located on the opposite side of the body.

cross section With respect to the central nervous system, a slice taken at right angles to the neuraxis.

frontal section A slice through the brain parallel to the forehead.

horizontal section A slice through the brain parallel to the ground.

sagittal section (***sadj*** *i tul*) A slice through the brain parallel to the neuraxis and perpendicular to the ground.

midsagittal plane The plane through the neuraxis perpendicular to the ground; divides the brain into two symmetrical halves.

An Overview

The nervous system consists of the brain and spinal cord, which make up the *central nervous system (CNS)*, and the cranial nerves, spinal nerves, and peripheral ganglia, which constitute the *peripheral nervous system (PNS)*. The CNS is encased in bone: The brain is covered by the skull, and the spinal cord is encased by the vertebral column. (See ***Table 3.1.***)

Figure 3.3 shows the relation of the brain and spinal cord to the rest of the body. Do not be concerned with unfamiliar labels on this figure; these structures will be described later. (See ***Figure 3.3*** on page 68.) The brain is a large mass of neurons, glia, and other supporting cells. It is the most protected organ of the body, encased in a tough, bony skull and floating in a pool of cerebrospinal fluid. The brain receives a copious supply of blood and is chemically guarded by the blood–brain barrier.

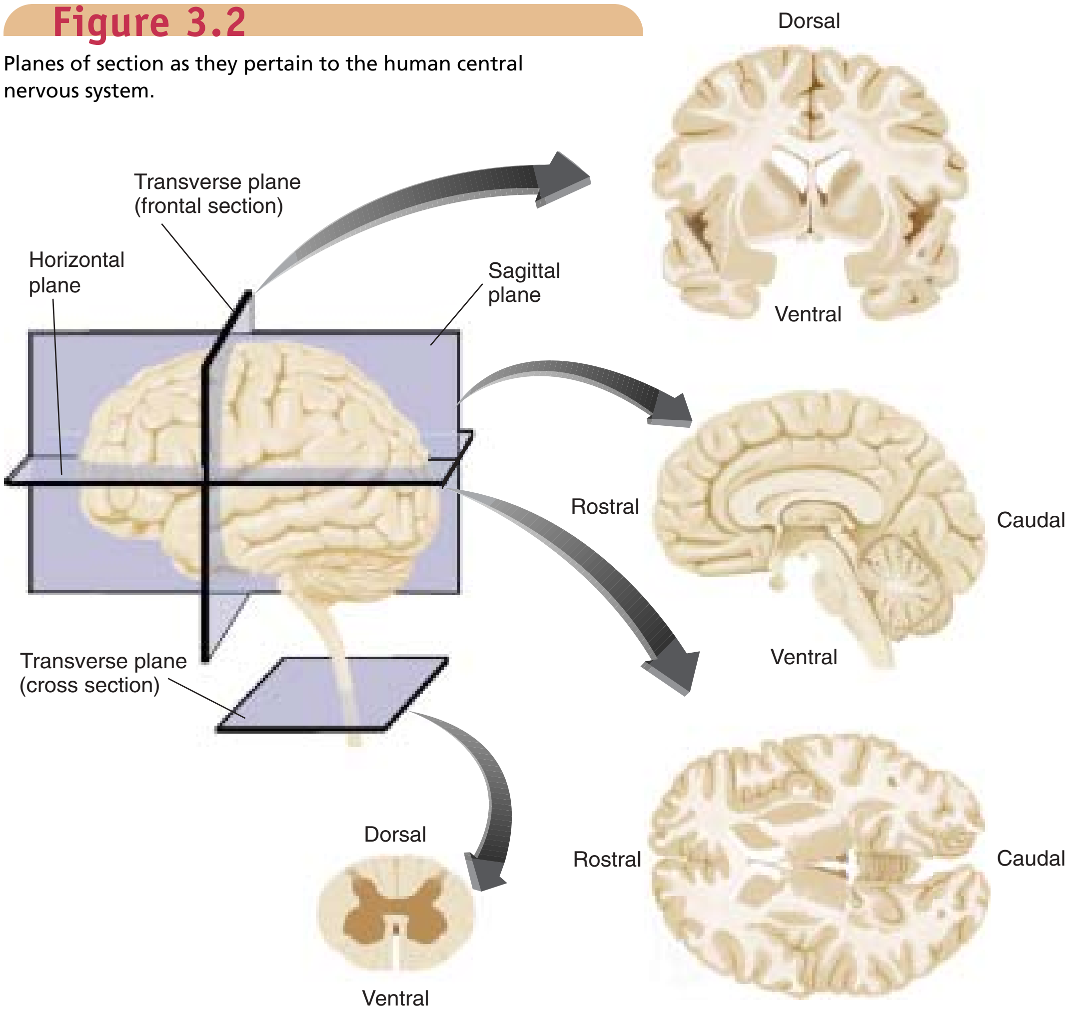
Table 3.1

The Major Divisions of the Nervous System

Central Nervous System (CNS)	Peripheral Nervous System (PNS)
Brain	Spinal cord
Nerves	Peripheral ganglia

Figure 3.2

Planes of section as they pertain to the human central nervous system.



Meninges

The entire nervous system—brain, spinal cord, cranial and spinal nerves, and peripheral ganglia—is covered by tough connective tissue. The protective sheaths around the brain and spinal cord are referred to as the **meninges** (singular: *meninx*). The meninges consist of three layers, which are shown in Figure 3.3. The outer layer is thick, tough, and flexible but unstretchable; its name, **dura mater,** means "hard mother." The middle layer of the meninges, the **arachnoid membrane,** gets its name from the weblike appearance of the *arachnoid trabeculae* that protrude from it (from the Greek *arachne,* meaning "spider"; *trabecula* means "track"). The arachnoid membrane, soft and spongy, lies beneath the dura mater. Closely attached to the brain and spinal cord, and following every surface convolution, is the **pia mater** ("pious mother"). The smaller surface blood vessels of the brain and spinal cord are contained within this layer. Between the pia mater and the arachnoid membrane is a gap called the **subarachnoid space.** This space is filled with a liquid called **cerebrospinal fluid (CSF).** (See ***Figure 3.3.***)

The peripheral nervous system (PNS) is covered with two layers of meninges. The middle layer (arachnoid membrane), with its associated pool of CSF, covers only the brain and spinal cord. Outside the central nervous system, the outer and inner layers (dura mater and pia mater) fuse and form a sheath that covers the spinal and cranial nerves and the peripheral ganglia.

meninges (singular: **meninx**) (*men **in** jees*) The three layers of tissue that encase the central nervous system: the dura mater, arachnoid membrane, and pia mater.

dura mater The outermost of the meninges; tough and flexible.

arachnoid membrane (*a **rak** noyd*) The middle layer of the meninges, located between the outer dura mater and inner pia mater.

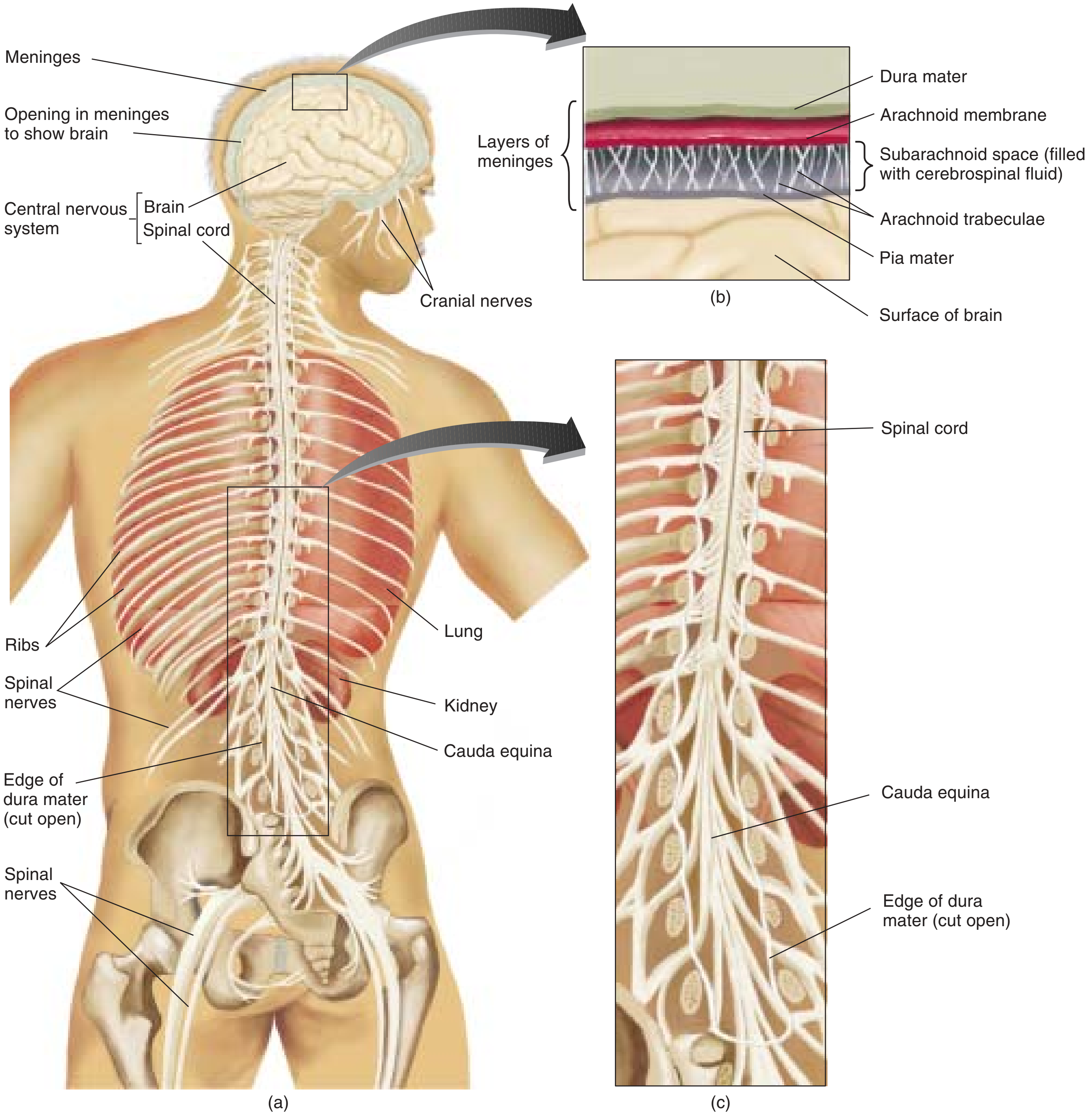
pia mater The layer of the meninges that clings to the surface of the brain; thin and delicate.

subarachnoid space The fluid-filled space that cushions the brain; located between the arachnoid membrane and the pia mater.

cerebrospinal fluid (**CSF**) A clear fluid, similar to blood plasma, that fills the ventricular system of the brain and the subarachnoid space surrounding the brain and spinal cord.

Figure 3.3

(a) The relation of the nervous system to the rest of the body. (b) Detail of the meninges that cover the central nervous system. (c) A closer view of the lower spinal cord and cauda equina.

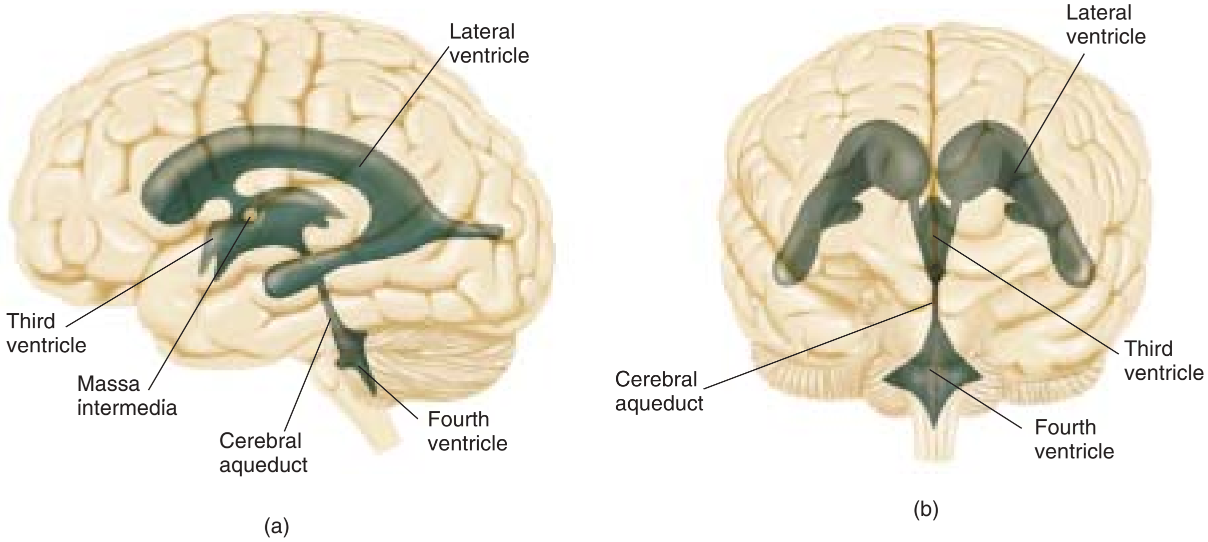


The Ventricular System and Production of Cerebrospinal Fluid

The brain is very soft and jellylike. The considerable weight of a human brain (approximately 1400 g), along with its delicate construction, necessitates that it be protected from shock. A human brain cannot even support its own weight well; it is

Figure 3.4

The ventricular system of the brain. (a) Lateral view of the left side of the brain. (b) Frontal view.



difficult to remove and handle a fresh brain from a recently deceased human without damaging it.

Fortunately, the intact brain within a living human is well protected. It floats in a bath of CSF contained within the subarachnoid space. Because the brain is completely immersed in liquid, its net weight is reduced to approximately 80 g; thus, pressure on the base of the brain is considerably diminished. The CSF surrounding the brain and spinal cord also reduces the shock to the central nervous system that would be caused by sudden head movement.

The brain contains a series of hollow, interconnected chambers called **ventricles** ("little bellies"), which are filled with CSF. (See ***Figure 3.4.***) The largest chambers are the **lateral ventricles,** which are connected to the **third ventricle.** The third ventricle is located at the midline of the brain; its walls divide the surrounding part of the brain into symmetrical halves. A bridge of neural tissue called the *massa intermedia* crosses through the middle of the third ventricle and serves as a convenient reference point. The **cerebral aqueduct,** a long tube, connects the third ventricle to the **fourth ventricle.** The lateral ventricles constitute the first and second ventricles, but they are never referred to as such. (See ***Figure 3.4.***)

Cerebrospinal fluid is extracted from the blood and resembles blood plasma in its composition. It is manufactured by special tissue with an especially rich blood supply called the **choroid plexus,** which protrudes into all four of the ventricles. CSF is produced continuously; the total volume of CSF is approximately 125 ml, and the half-life (the time it takes for half of the CSF present in the ventricular system to be replaced by fresh fluid) is about 3 hours. Therefore, several times this amount is produced by the choroid plexus each day.

Cerebrospinal fluid is produced by the choroid plexus of the lateral ventricles and flows into the third ventricle. More CSF is produced in this ventricle, which then flows through the cerebral aqueduct to the fourth ventricle, where still more CSF is produced. The CSF leaves the fourth ventricle through small openings that connect with the subarachnoid space surrounding the brain. The CSF then flows through the subarachnoid space around the central nervous system, where it is reabsorbed into the blood supply. (See ***Animation 3.1, Meninges and CSF.***)

ventricle (***ven*** *trik ul*) One of the hollow spaces within the brain, filled with cerebrospinal fluid.

lateral ventricle One of the two ventricles located in the center of the telencephalon.

third ventricle The ventricle located in the center of the diencephalon.

cerebral aqueduct A narrow tube interconnecting the third and fourth ventricles of the brain, located in the center of the mesencephalon.

fourth ventricle The ventricle located between the cerebellum and the dorsal pons, in the center of the metencephalon.

choroid plexus The highly vascular tissue that protrudes into the ventricles and produces cerebrospinal fluid.

See Animation 3.1, Meninges and CSF, for an interactive tutorial on the meninges, the ventricular system, and the production, circulation, and reabsorption of CSF.

INTERIM SUMMARY

Basic Features of the Nervous System

Anatomists have adopted a set of terms to describe the locations of parts of the body. *Anterior* is toward the head, *posterior* is toward the tail, *lateral* is toward the side, *medial* is toward the middle, *dorsal* is toward the back, and *ventral* is toward the front surface of the body. In the special case of the nervous system, *rostral* means toward the beak (or nose), and *caudal* means toward the tail. *Ipsilateral* means "same side," and *contralateral* means "other side." A cross section (or, in the case of the brain, a frontal section) slices the nervous system at right angles to the neuraxis, a horizontal section slices the brain parallel to the ground, and a sagittal section slices it perpendicular to the ground, parallel to the neuraxis.

The central nervous system (CNS) consists of the brain and spinal cord, and the peripheral nervous system (PNS) consists of the spinal and cranial nerves and peripheral ganglia. The CNS is covered with the meninges: dura mater, arachnoid membrane, and pia mater. The space under the arachnoid membrane is filled with cerebrospinal fluid, in which the brain floats. The PNS is covered with only the dura mater and pia mater. Cerebrospinal fluid is produced in the choroid plexus of the lateral, third, and fourth ventricles. It flows from the two lateral ventricles into the third ventricle, through the cerebral aqueduct into the fourth ventricle, then into the subarachnoid space, and finally back into the blood supply through the arachnoid granulations. If the flow of CSF is blocked by a tumor or other obstruction, the result is hydrocephalus: enlargement of the ventricles and subsequent brain damage.

The Central Nervous System

Although the brain is exceedingly complicated, an understanding of the basic features of brain development makes it easier to learn and remember the location of the most important structures. With that end in mind, I introduce these features here in the context of development of the central nervous system. Two animations will help you learn and remember the structure of the brain. ***Animation 3.2, The Rotatable Brain*** is just what the title implies: a drawing of the human brain that you can rotate in three dimensions. You can choose whether to see some internal structures or see specialized regions of the cerebral cortex. ***Animation 3.3, Brain Slices*** is even more comprehensive. It consists of two sets of photographs of human brain slices, taken in the transverse (frontal) and horizontal planes. As you move the cursor across each slice, brain regions are outlined, and their names appear. If you want to know how to pronounce these names, you can click on the region. You can also see magnified views of the slices and move them around by clicking and dragging. Finally, you can test yourself: The computer will present names of the regions shown in each slice, and you try to click on the correct region.

See Animation 3.2, The Rotatable Brain, for an interactive examination of the human brain.

See Animation 3.3, Brain Slices, for a chance to examine and learn the names of internal structures of actual human brains.

Development of the Central Nervous System

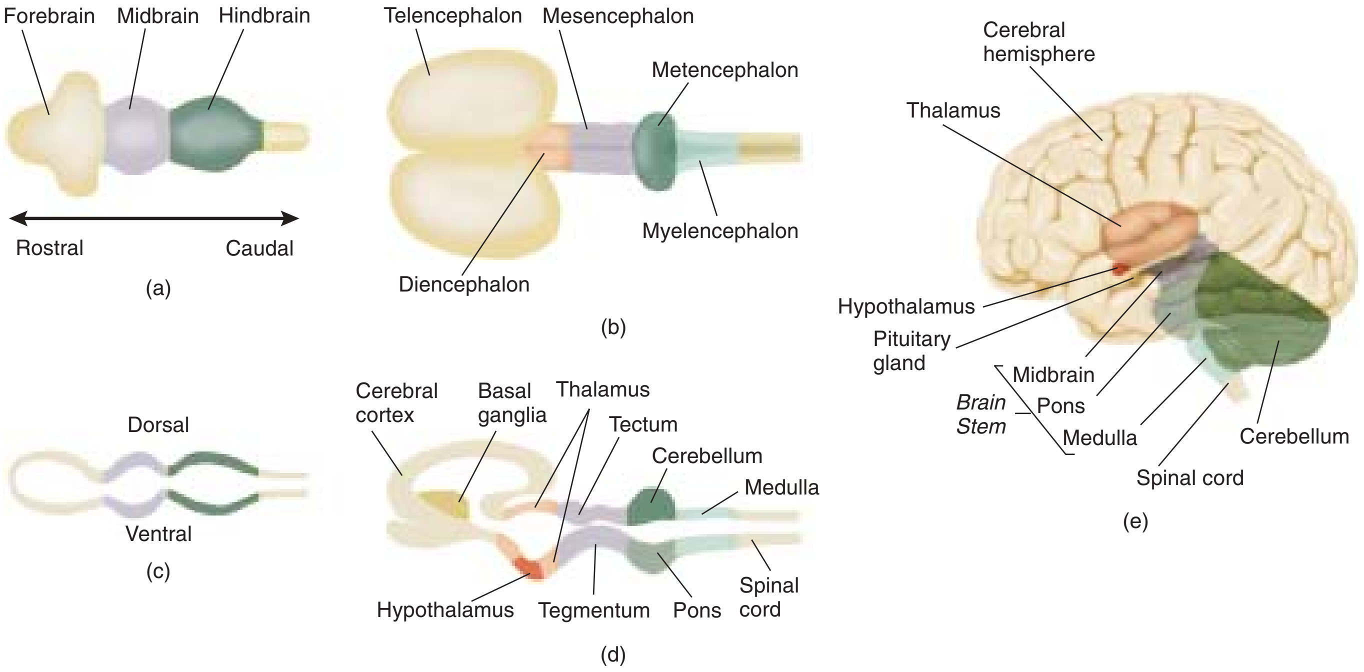
The central nervous system begins early in embryonic life as a hollow tube, and it maintains this basic shape even after it is fully developed. During development, parts of the tube elongate, pockets and folds form, and the tissue around the tube thickens until the brain reaches its final form.

An Overview of Brain Development

Development of the nervous system begins around the eighteenth day after conception. Part of the *ectoderm* (outer layer) of the back of the embryo thickens and

Figure 3.5

A schematic outline of brain development, showing its relation to the ventricles. (a) and (c) Early development. (b) and (d) Later in development. (e) A lateral view of the left side of a semitransparent human brain, showing the brain stem "ghosted in." The colors of all figures denote corresponding regions.



forms a plate. The edges of this plate form ridges that curl toward each other along a longitudinal line, running in a rostral–caudal direction. By the twenty-first day these ridges touch each other and fuse together, forming a tube—the **neural tube**—that gives rise to the brain and spinal cord.

By the twenty-eighth day of development the neural tube is closed, and its rostral end has developed three interconnected chambers. These chambers become ventricles, and the tissue that surrounds them becomes the three major parts of the brain: the forebrain, the midbrain, and the hindbrain. (See ***Figures 3.5a*** and ***3.5c.***) As development progresses, the rostral chamber (the forebrain) divides into three separate parts, which become the two lateral ventricles and the third ventricle. The region around the lateral ventricles becomes the telencephalon ("end brain"), and the region around the third ventricle becomes the diencephalon ("interbrain"). (See ***Figures 3.5b*** and ***3.5d.***) In its final form, the chamber inside the midbrain (mesencephalon) becomes narrow, forming the cerebral aqueduct, and two structures develop in the hindbrain: the metencephalon ("afterbrain") and the myelencephalon ("marrowbrain"). (See ***Figure 3.5e.***)

Table 3.2 summarizes the terms I have introduced here and mentions some of the major structures found in each part of the brain. The colors in the table match those in Figure 3.5. These structures will be described in the remainder of the chapter, in the order in which they are listed in Table 3.2. (See ***Table 3.2.***)

Details of Brain Development

Brain development begins with a thin tube and ends with a structure weighing approximately 1400 g (about 3 lb) and consisting of several hundreds of billions of cells. Where do these cells come from, and what controls their growth?

neural tube A hollow tube, closed at the rostral end, that forms from ectodermal tissue early in embryonic development; serves as the origin of the central nervous system.

Table 3.2

Anatomical Subdivisions of the Brain

Major Division	Ventricle	Subdivision	Priciple Structures
Forebrain	Lateral	Telencephalon	Cerebral cortex Basal ganglia Limbic system
	Third	Diencephalon	Thalamus Hypothalamus
Midbrain	Cerebral aqueduct	Mesencephalon	Tectum Tegmentum
Hindbrain	Fourth	Metencephalon	Cerebellum Pons
		Myelencephalon	Medulla oblongata

The cells that line the inside of the neural tube—the **ventricular zone**—give rise to the cells of the central nervous system. These cells divide, producing neurons and glia, which then migrate away from the center. Ten weeks after conception the brain of the human fetus is about 1.25 cm (0.5 in.) long and, in cross section, is mostly ventricle—in other words, hollow space. By 20 weeks the brain is about 5 cm (2 in.) long and has the basic shape of the mature brain. In cross section we see more brain tissue than ventricle.

Let's consider the development of the cerebral cortex, about which most is known. *Cortex* means "bark," and the **cerebral cortex**, approximately 3 mm thick, surrounds the cerebral hemispheres like the bark of a tree. Corrected for body size, the cerebral cortex is larger in humans than in any other species. As we will see, circuits of neurons in the cerebral cortex play a vital role in cognition and control of movement.

The cerebral cortex develops from the inside out. That is, the first cells to be produced by the ventricular zone migrate a short distance and establish the first layer. The next cells pass through the first layer and form the second one. The last cells to be produced must pass through all the ones born before them.

What guides neurons to their final resting place? Rakic (1972, 1988) discovered that a special form of glial cell provides pathways that neurons follow during their migration. These cells, **radial glia,** extended fibers radially outward from the ventricular zone, like spokes in a wheel. These fibers end in cuplike feet that attach to the surface of the cortex, and as the cortex grows thicker, these fibers grow along with it.

The cells in the ventricular zone that give rise to neurons are known as **founder cells.** During the first phase of development, founder cells divide, making new founder cells and increasing the size of the ventricular zone. This phase is referred to as **symmetrical division,** because the division of each founder cell produces two identical cells. Then, seven weeks after conception, founder cells receive a signal to begin a period of **asymmetrical division.** During this phase founder cells divide asymmetrically, producing another founder cell, which remains in place, and a neuron, which travels outward into the cerebral cortex, guided by the fiber of a radial glial cell. Neurons crawl along radial fibers like amoebas, pushing their way through neurons that were born earlier and finally coming to rest. (See ***Figure 3.6.***)

ventricular zone A layer of cells that line the inside of the neural tube; contains founder cells that divide and give rise to cells of the central nervous system.

cerebral cortex The outermost layer of gray matter of the cerebral hemispheres.

radial glia Special glia with fibers that grow radially outward from the ventricular zone to the surface of the cortex; provide guidance for neurons migrating outward during brain development.

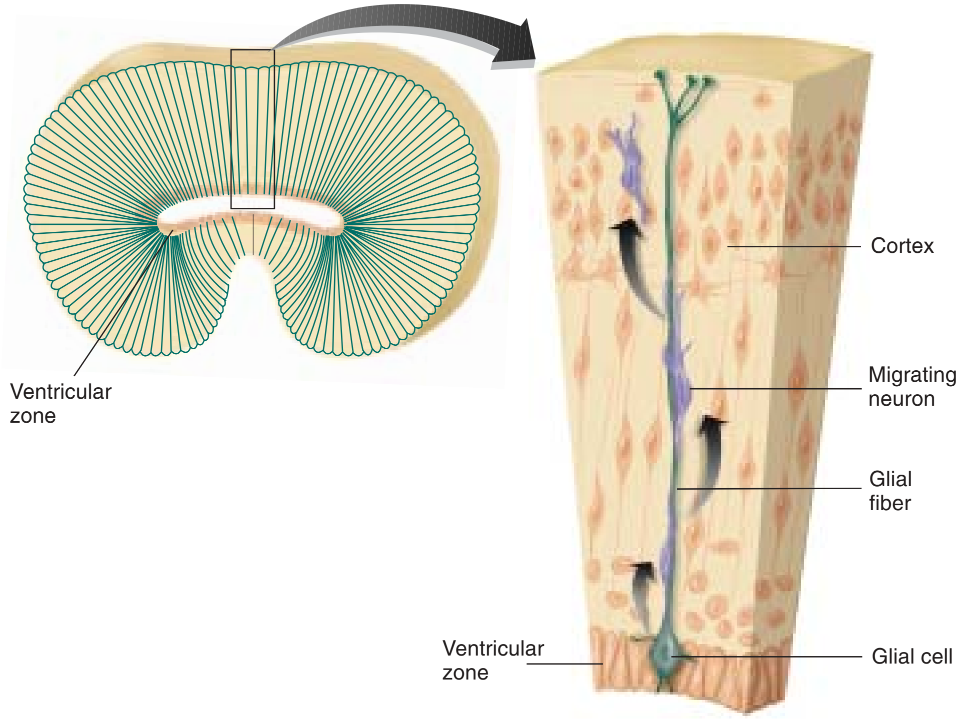
founder cells Cells of the ventricular zone that divide and give rise to cells of the central nervous system.

symmetrical division Division of a founder cell that gives rise to two identical founder cells; increases the size of the ventricular zone and hence the brain that develops from it.

asymmetrical division Division of a founder cell that gives rise to another founder cell and a neuron, which migrates away from the ventricular zone toward its final resting place in the brain.

Figure 3.6

A cross section through the nervous system early in its development. Radially oriented glial cells help to guide the migration of newly formed neurons.



Adapted from Rakic, P. A small step for the cell, a giant leap for mankind: A hypothesis of neocortical expansion during evolution. *Trends in Neuroscience,* 1995, *18,* 383–388.

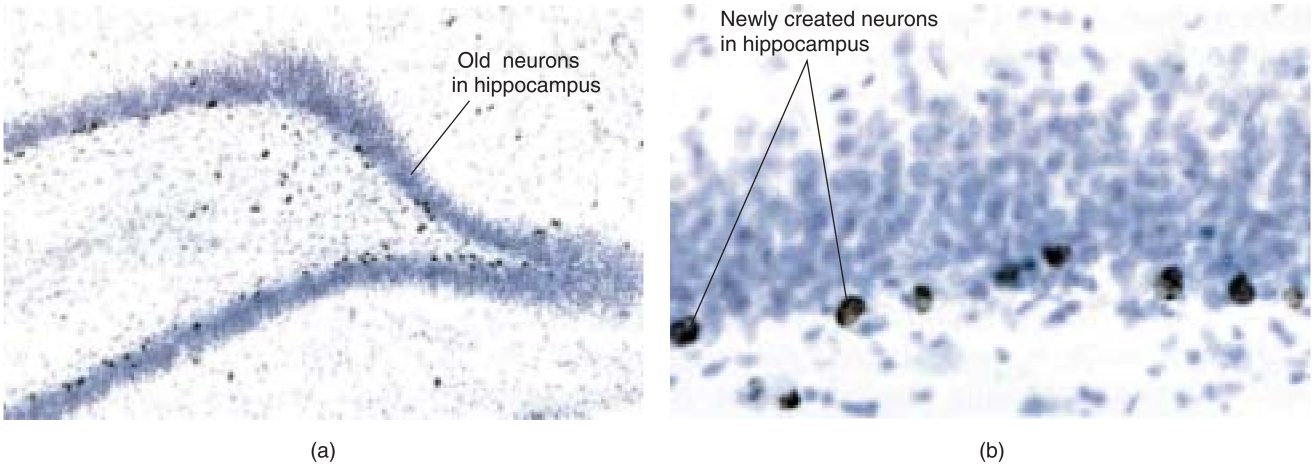
The period of asymmetrical division lasts about three months. Because the human cerebral cortex contains about 100 billion neurons, there are about one billion neurons migrating along radial glial fibers on a given day. The migration path of the earliest neurons is the shortest and takes about one day. The last neurons have the longest distance to go, because the cortex is thicker by then. Their migration takes about two weeks. The end of cortical development occurs when the founder cells receive a chemical signal that causes them to die—a phenomenon known as **apoptosis** (literally, a "falling away"). Molecules of the chemical that conveys this signal bind with receptors that activate killer genes within the cells. (All cells have these genes, but only certain cells respond to the chemical signal that turns them on.) Once neurons have migrated to their final locations, they begin forming connections with other neurons. They grow dendrites, which receive the terminal buttons from the axons of other neurons, and they grow axons of their own.

The ventricular zone gives rise to more neurons than are needed. In fact, these neurons must compete to survive. The axons of approximately 50 percent of these neurons do not find vacant postsynaptic cells of the right type with which to form synaptic connections, so they die by apoptosis. This phenomenon, too, involves a chemical signal; when a presynaptic neuron establishes synaptic connections, it receives a signal from the postsynaptic cell that permits it to survive. The neurons that come too late do not find any available space and therefore do not receive this life-sustaining signal. This scheme might seem wasteful, but apparently the evolutionary process found that the safest strategy was to produce too many neurons and let them fight to establish synaptic connections rather than try to produce exactly the right number of each type of neuron.

apoptosis (*ay po* ***toe*** *sis*) Death of a cell caused by a chemical signal that activates a genetic mechanism inside the cell.

Figure 3.7

Evidence of neurogenesis. (a) A section through a part of the hippocampus, showing cells containing DNA labeled with a radioactive nucleotide. (b) A magnified view of part of the same section.



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During development, thousands of different pathways—groups of axons that connect one brain region with another—develop in the brain. Within many of these pathways the connections are orderly and systematic. For example, the axons of sensory neurons from the skin form orderly connections in the brain; axons from the little finger form synapses in one region, those of the ring finger form synapses in a neighboring region, and so on. In fact, the surface of the body is "mapped" on the surface of the brain. Similarly, the surface of the retina of the eye is "mapped" on another region of the surface of the brain.

For many years researchers have believed that *neurogenesis* (production of new neurons) does not take place in the fully developed brain. However, recent studies have shown this belief to be incorrect—the adult brain contains some stem cells (similar to the founder cells that give rise to the cells of the developing brain) that can divide and produce neurons. Detection of newly produced cells is done by administering a small amount of a radioactive form of one of the nucleotide bases that cells use to produce the DNA that is needed for neurogenesis. The next day the animals' brains are removed and examined with methods described in Chapter 5. Such studies have found evidence for neurogenesis in the adult brain (Cameron and McKay, 2001.) (See ***Figure 3.7.***) However, although the mature brain can produce new neurons, there is no evidence yet that indicates that these neurons can establish connections to replace neural circuits that have been destroyed through injury, stroke, or disease (Horner and Gage, 2000).

Evolution of the Human Brain

The brains of the earliest vertebrates were smaller than those of later animals; they were simpler as well. The evolutionary process brought about genetic changes that were responsible for the development of more complex brains, with more parts and more interconnections.

The human brain is larger than that of any other primate when corrected for body size—more than three times larger than that of a chimpanzee, our closest relative. What types of genetic changes are required to produce a large brain? Considering that the difference between the genes of humans and those of chimpanzees is only 1.2 percent, the number of genes responsible for the differences between the chimpanzee brain and the human brain must be small. After all, only a small percentage of the 1.2 percent is devoted to brain development. In fact, Rakic (1988) suggests that the size differences between these two brains could be caused by a very simple process.

We just saw that the size of the ventricular zone increases during symmetrical division of the founder cells located there. The ultimate size of the brain is determined by the size of the ventricular zone. As Rakic notes, each symmetrical division doubles the number of founder cells and thus doubles the size of the brain. The human brain is ten times larger than that of a rhesus macaque monkey. Thus, between three and four additional symmetrical divisions of founder cells would account for the difference in the size of these two brains. In fact, the stage of symmetrical division lasts about two days longer in humans, which provides enough time for three more divisions. The period of asymmetrical division is longer, too, which accounts for the fact that the human cortex is 15 percent thicker. Thus, delays in the termination of the symmetrical and asymmetrical periods of development could be responsible for the increased size of the human brain. A few simple mutations of the genes that control the timing of brain development could be responsible for these delays.

The Forebrain

As we saw, the **forebrain** surrounds the rostral end of the neural tube. Its two major components are the telencephalon and the diencephalon.

Telencephalon

The telencephalon includes most of the two symmetrical **cerebral hemispheres** that make up the cerebrum. The cerebral hemispheres are covered by the cerebral cortex and contain the limbic system and the basal ganglia. The latter two sets of structures are primarily in the **subcortical regions** of the brain—those located deep within it, beneath the cerebral cortex.

Cerebral Cortex. As we saw, c*ortex* means "bark," and the cerebral cortex surrounds the cerebral hemispheres like the bark of a tree. In humans the cerebral cortex is greatly convoluted. These convolutions, consisting of **sulci** (small grooves), **fissures** (large grooves), and **gyri** (bulges between adjacent sulci or fissures), greatly enlarge the surface area of the cortex, compared with a smooth brain of the same size. In fact, two-thirds of the surface of the cortex is hidden in the grooves; thus, the presence of gyri and sulci triples the area of the cerebral cortex. The total surface area is approximately 2360 cm^2 (2.5 ft^2), and the thickness is approximately 3 mm.

The cerebral cortex consists mostly of glia and the cell bodies, dendrites, and interconnecting axons of neurons. Because cells predominate, the cerebral cortex has a grayish brown appearance, and it is called *gray matter.* (See ***Figure 3.8.***) Millions of axons run beneath the cerebral cortex and connect its neurons with those located elsewhere in the brain. The large concentration of myelin around these axons gives this tissue an opaque white appearance—hence the term *white matter.*

Different regions of the cerebral cortex perform different functions. Three regions receive information from the sensory organs. The **primary visual cortex,** which receives visual information, is located at the back of the brain, on the inner surfaces of the cerebral hemispheres—primarily on the upper and lower banks of the **calcarine fissure.** (*Calcarine* means "spur-shaped." See ***Figure 3.9.***) The **primary auditory cortex,** which receives auditory information, is located on the upper surface of a deep fissure in the side of the brain—the **lateral fissure.** (See inset, ***Figure 3.9.***) The **primary somatosensory cortex,** a vertical strip of cortex just caudal to the **central sulcus,** receives information from the body senses. As Figure 3.9 shows, different regions of the primary somatosensory cortex receive information from different regions of the body. In addition, the base of the somatosensory cortex receives information concerning taste. (See ***Figure 3.9.***)

forebrain The most rostral of the three major divisions of the brain; includes the telencephalon and diencephalon.

cerebral hemisphere (*sa **ree** brul*) One of the two major portions of the forebrain, covered by the cerebral cortex.

subcortical region The region located within the brain, beneath the cortical surface.

sulcus (**plural: sulci**) (***sul** kus**, sul** sigh*) A groove in the surface of the cerebral hemisphere, smaller than a fissure.

fissure A major groove in the surface of the brain, larger than a sulcus.

gyrus (**plural: gyri**) (***jye** russ**, jye** rye*) A convolution of the cortex of the cerebral hemispheres, separated by sulci or fissures.

primary visual cortex The region of the posterior occipital lobe whose primary input is from the visual system.

calcarine fissure (***kal** ka rine*) A fissure located in the occipital lobe on the medial surface of the brain; most of the primary visual cortex is located along its upper and lower banks.

primary auditory cortex The region of the superior temporal lobe whose primary input is from the auditory system.

lateral fissure The fissure that separates the temporal lobe from the overlying frontal and parietal lobes.

primary somatosensory cortex The region of the anterior parietal lobe whose primary input is from the somatosensory system.

central sulcus (***sul** kus*) The sulcus that separates the frontal lobe from the parietal lobe.

Figure 3.8

A slice of a human brain showing fissures and gyri and the layer of cerebral cortex that follows these convolutions.

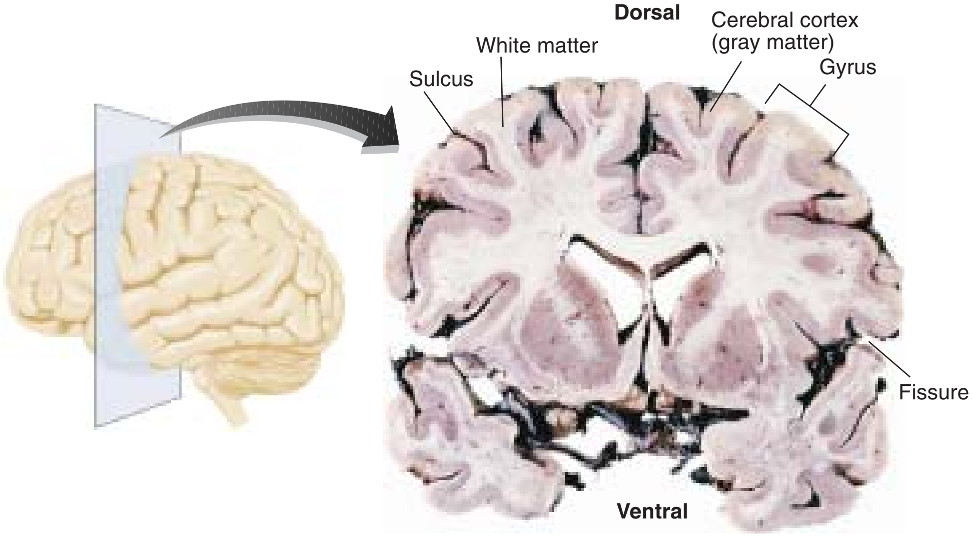
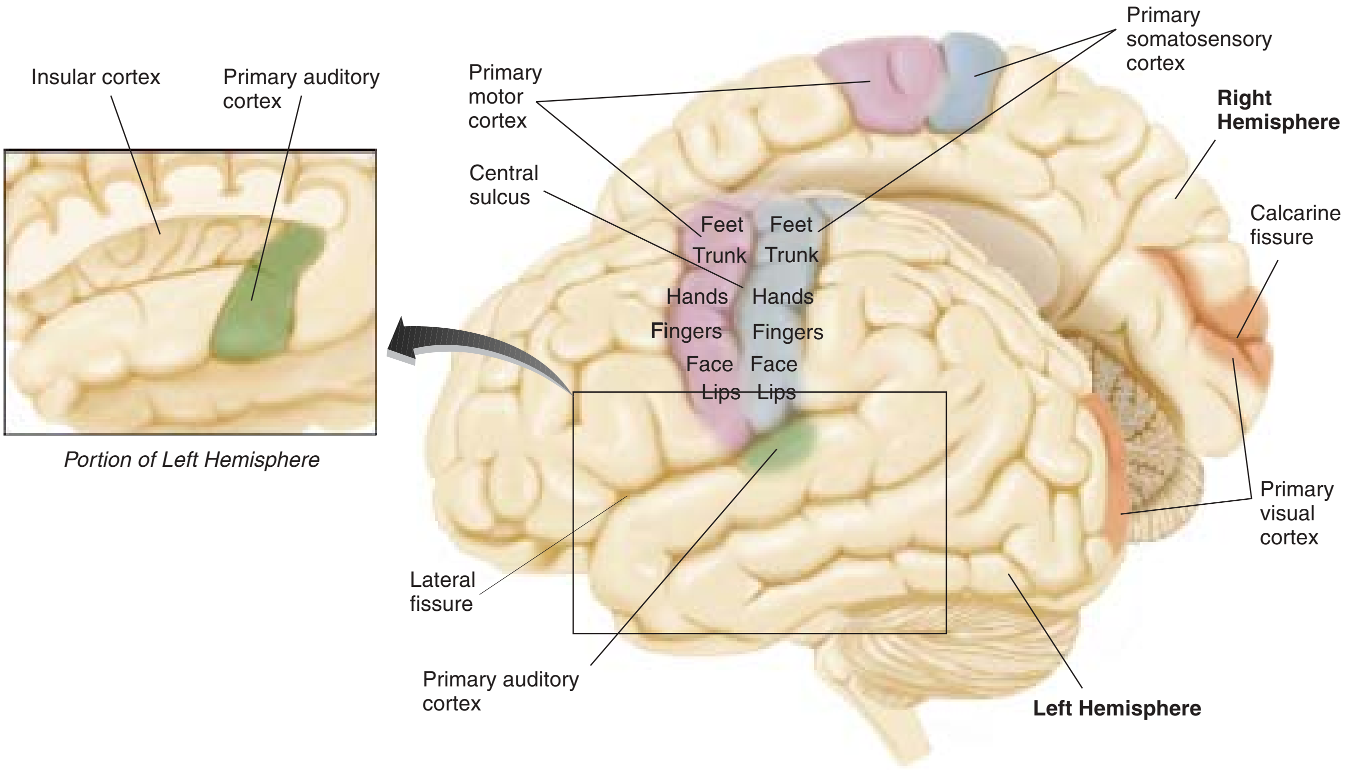


Figure 3.9

A lateral view of the left side of a human brain and part of the inner surface of the right side. The inset shows a cutaway of part of the frontal lobe of the left hemisphere, permitting us to see the primary auditory cortex on the dorsal surface of the temporal lobe, which forms the ventral bank of the lateral fissure.



With the exception of olfaction and gustation (taste), sensory information from the body or the environment is sent to primary sensory cortex of the contralateral hemisphere. Thus, the primary somatosensory cortex of the left hemisphere learns what the right hand is holding, the left primary visual cortex learns what is happening toward the person's right, and so on.

The region of the cerebral cortex that is most directly involved in the control of movement is the **primary motor cortex,** located just in front of the primary somatosensory cortex. Neurons in different parts of the primary motor cortex are connected to muscles in different parts of the body. The connections, like those of the sensory regions of the cerebral cortex, are contralateral; the left primary motor cortex controls the right side of the body and vice versa. Thus, if a surgeon places an electrode on the surface of the primary motor cortex and stimulates the neurons there with a weak electrical current, the result will be movement of a particular part of the body. Moving the electrode to a different spot will cause a different part of the body to move. (See ***Figure 3.9.***) I like to think of the strip of primary motor cortex as the keyboard of a piano, with each key controlling a different movement. (We will see shortly who the "player" of this piano is.)

The ability to navigate depends heavily on circuits of neurons in the parietal lobe.

The regions of primary sensory and motor cortex occupy only a small part of the cerebral cortex. The rest of the cerebral cortex accomplishes what is done between sensation and action: perceiving, learning and remembering, planning, and acting. These processes take place in the *association areas* of the cerebral cortex. The central sulcus provides an important dividing line between the rostral and caudal regions of the cerebral cortex. (See ***Figure 3.9.***) The rostral region is involved in movement-related activities, such as planning and executing behaviors. The caudal region is involved in perceiving and learning.

Discussing the various regions of the cerebral cortex is easier if we have names for them. In fact, the cerebral cortex is divided into four areas, or *lobes,* named for the bones of the skull that cover them: the frontal lobe, parietal lobe, temporal lobe, and occipital lobe. Of course, the brain contains two of each lobe, one in each hemisphere. The **frontal lobe** (the "front") includes everything in front of the central sulcus. The **parietal lobe** (the "wall") is located on the side of the cerebral hemisphere, just behind the central sulcus, caudal to the frontal lobe. The **temporal lobe** (the "temple") juts forward from the base of the brain, ventral to the frontal and parietal lobes. The **occipital lobe** (from the Latin *ob,* "in back of," and *caput,* "head") lies at the very back of the brain, caudal to the parietal and temporal lobes. Figure 3.10 shows these lobes in three views of the cerebral hemispheres: a ventral view (a view from the bottom), a midsagittal view (a view of the inner surface of the right hemisphere after the left hemisphere has been removed), and a lateral view. (See ***Figure 3.10.***)

Each primary sensory area of the cerebral cortex sends information to adjacent regions, called the **sensory association cortex.** Circuits of neurons in the sensory association cortex analyze the information received from the primary sensory cortex; perception takes place there, and memories are stored there. The regions of the sensory association cortex located closest to the primary sensory areas receive information from only one sensory system. For example, the region closest to the primary visual cortex analyzes visual information and stores visual memories. Regions of the sensory association cortex located far from the primary sensory areas receive

primary motor cortex The region of the posterior frontal lobe that contains neurons that control movements of skeletal muscles.

frontal lobe The anterior portion of the cerebral cortex, rostral to the parietal lobe and dorsal to the temporal lobe.

parietal lobe (*pa **rye** i tul*) The region of the cerebral cortex caudal to the frontal lobe and dorsal to the temporal lobe.

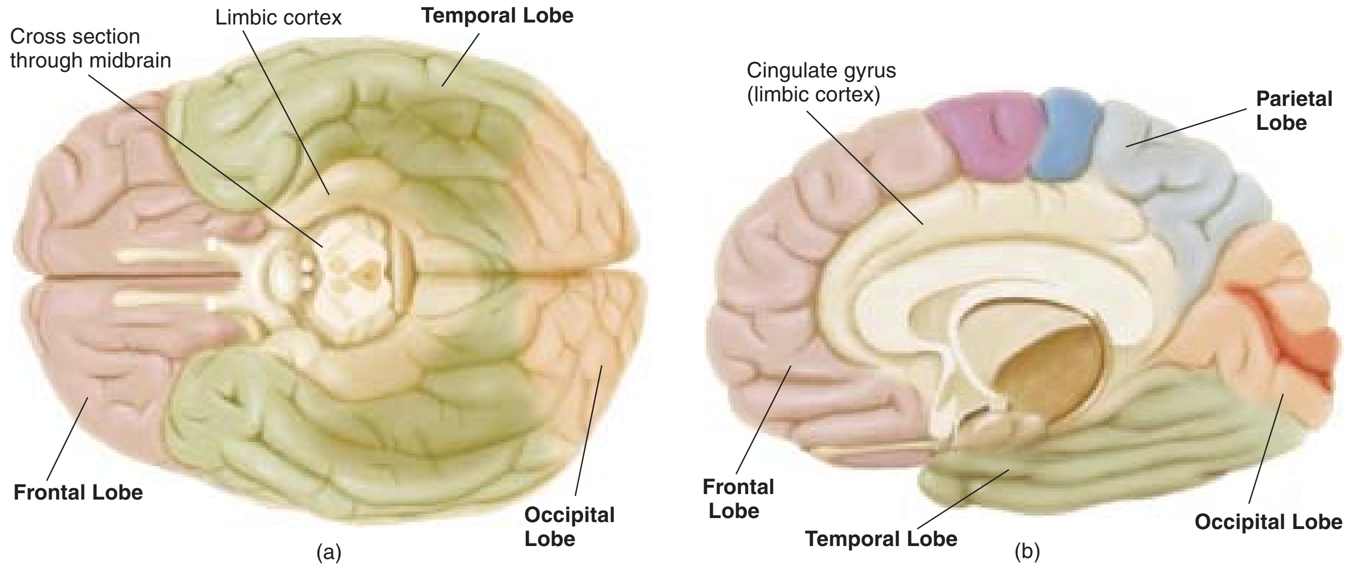
temporal lobe (***tem** por ul*) The region of the cerebral cortex rostral to the occipital lobe and ventral to the parietal and frontal lobes.

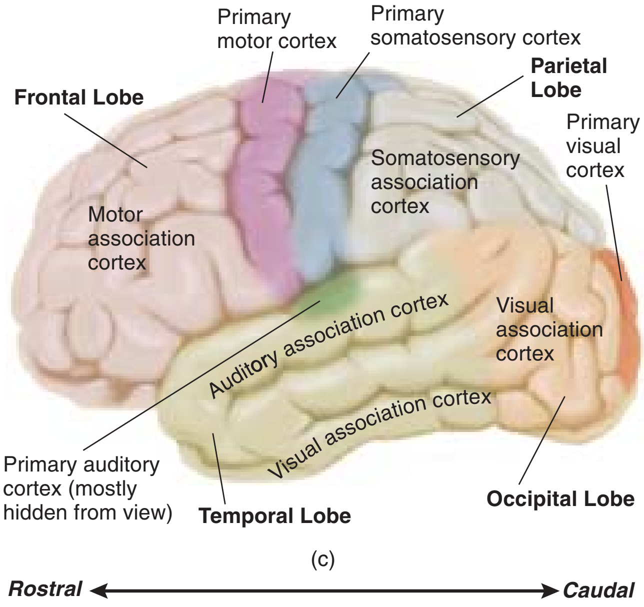
occipital lobe (*ok **sip** i tul*) The region of the cerebral cortex caudal to the parietal and temporal lobes.

sensory association cortex Those regions of the cerebral cortex that receive information from the regions of primary sensory cortex.

Figure 3.10

The four lobes of the cerebral cortex, the primary sensory and motor cortex, and the association cortex. (a) Ventral view, from the base of the brain. (b) Midsagittal view, with the cerebellum and brain stem removed. (c) Lateral view.





information from more than one sensory system; thus, they are involved in several kinds of perceptions and memories. These regions make it possible to integrate information from more than one sensory system. For example, we can learn the connection between the sight of a particular face and the sound of a particular voice. (See ***Figure 3.10.***)

If people sustain damage to the somatosensory association cortex, their deficits are related to somatosensation and to the environment in general; for example, they may have difficulty perceiving the shapes of objects that they can touch but not see, they may be unable to name parts of their bodies (see the case below), or they may have trouble drawing maps or following them. Destruction of the primary visual cortex causes blindness. However, although people who sustain damage to the visual association cortex will not become blind, they may be unable to recognize objects by sight. People who sustain damage to the auditory association cortex may have difficulty perceiving speech or even producing meaningful speech of their own. People who sustain damage to regions of the association cortex at the junction of the three posterior lobes, where the somatosensory, visual, and auditory functions overlap, may have difficulty reading or writing.

Just as regions of the sensory association cortex of the posterior part of the brain are involved in perceiving and remembering, the frontal association cortex is involved in the planning and execution of movements. The **motor association cortex** (also known as the *premotor cortex*) is located just rostral to the primary motor cortex. This region controls the primary motor cortex; thus, it directly controls behavior. If the primary motor cortex is the keyboard of the piano, then the motor association cortex is the piano player. The rest of the frontal lobe, rostral to the motor associa-

motor association cortex The region of the frontal lobe rostral to the primary motor cortex; also known as the premotor cortex.

tion cortex, is known as the **prefrontal cortex.** This region of the brain is less involved with the control of movement and more involved in formulating plans and strategies.

Although the two cerebral hemispheres cooperate with each other, they do not perform identical functions. Some functions are *lateralized*—located primarily on one side of the brain. In general, the left hemisphere participates in the *analysis* of information—the extraction of the elements that make up the whole of an experience. This ability makes the left hemisphere particularly good at recognizing *serial events*—events whose elements occur one after the other—and controlling sequences of behavior. (In a few people the functions of the left and right hemispheres are reversed.) The serial functions that are performed by the left hemisphere include verbal activities, such as talking, understanding the speech of other people, reading, and writing. These abilities are disrupted by damage to the various regions of the left hemisphere. (I will say more about language and the brain in Chapter 15.)

In contrast, the right hemisphere is specialized for *synthesis;* it is particularly good at putting isolated elements together to perceive things as a whole. For example, our ability to draw sketches (especially of three-dimensional objects), read maps, and construct complex objects out of smaller elements depends heavily on circuits of neurons that are located in the right hemisphere. Damage to the right hemisphere disrupts these abilities.

We are not aware of the fact that each hemisphere perceives the world differently. Although the two cerebral hemispheres perform somewhat different functions, our perceptions and our memories are unified. This unity is accomplished by the **corpus callosum,** a large band of axons that connects corresponding parts of the association cortex of the left and right hemispheres: The left and right temporal lobes are connected, the left and right parietal lobes are connected, and so on. Because of the corpus callosum, each region of the association cortex knows what is happening in the corresponding region of the opposite side of the brain.

Figure 3.11 shows a *midsagittal* view of the brain. The brain (and part of the spinal cord) has been sliced down the middle, dividing it into its two symmetrical halves. The left half has been removed, so we see the inner surface of the right half. The cerebral cortex that covers most of the surface of the cerebral hemispheres (including the frontal, parietal, occipital, and temporal lobes) is called the **neocortex** ("new" cortex, because it is of relatively recent evolutionary origin). Another form of cerebral cortex, the **limbic cortex,** is located around the medial edge of the cerebral hemispheres (*limbus* means "border"). The **cingulate gyrus,** an important region of the limbic cortex, can be seen in this figure. (See ***Figure 3.11.***) In addition, if you look back at the top two drawings in Figure 3.10, you will see that the limbic cortex occupies the regions that have not been colored in. (Refer to ***Figure 3.10.***)

Figure 3.11 also shows the corpus callosum. To slice the brain into its two symmetrical halves, one must slice through the middle of the corpus callosum. (Recall that I described the split-brain operation, in which the corpus callosum is severed, in Chapter 1.) (See ***Figure 3.11.***)

As I mentioned earlier, one of the Chapter 3 animations on the CD-ROM will permit you to view the brain from various angles and see the locations of the specialized regions of the cerebral cortex. (See ***Animation 3.2, The Rotatable Brain.***)

Limbic System. A neuroanatomist, Papez (1937), suggested that a set of interconnected brain structures formed a circuit whose primary function was motivation and emotion. This system included several regions of the limbic cortex (already described) and a set of interconnected structures surrounding the core of the forebrain. A physiologist, MacLean (1949), expanded the system to include other structures and coined the term **limbic system.** Besides the limbic cortex, the most important parts of the limbic system are the **hippocampus** ("sea horse") and the **amygdala** ("almond"), located next to the lateral ventricle in the temporal lobe. The

prefrontal cortex The region of the frontal lobe rostral to the motor association cortex.

corpus callosum (*ka* ***loh*** *sum*) A large bundle of axons that interconnects corresponding regions of the association cortex on each side of the brain.

neocortex The phylogenetically newest cortex, including the primary sensory cortex, primary motor cortex, and association cortex.

limbic cortex Phylogenetically old cortex, located at the medial edge ("limbus") of the cerebral hemispheres; part of the limbic system.

cingulate gyrus (***sing*** *yew lett*) A strip of limbic cortex lying along the lateral walls of the groove separating the cerebral hemispheres, just above the corpus callosum.

See Animation 3.2, The Rotatable Brain, for an interactive examination of the human brain.

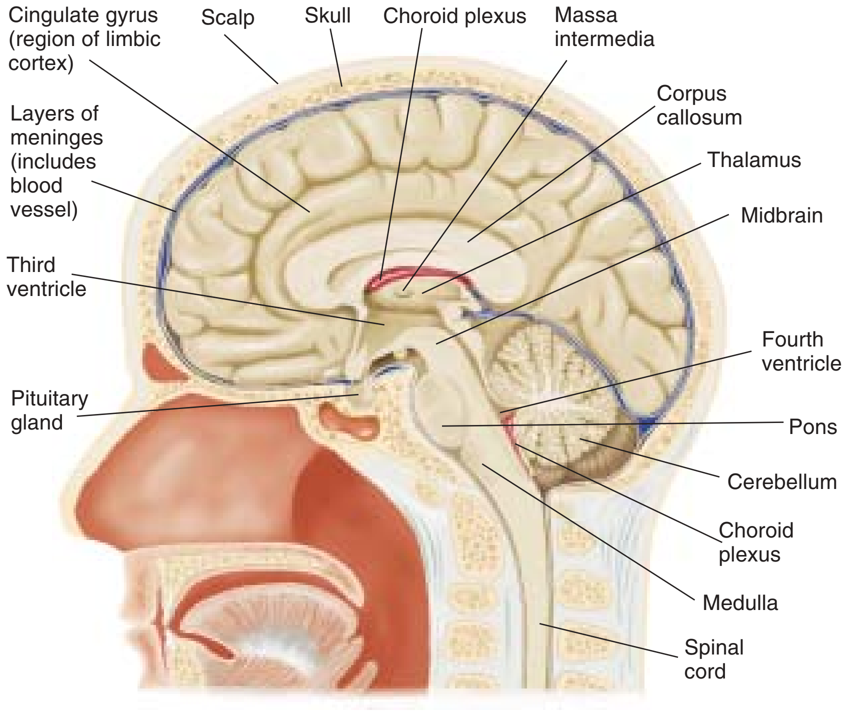
limbic system A group of brain regions including the anterior thalamic nuclei, amygdala, hippocampus, limbic cortex, and parts of the hypothalamus, as well as their interconnecting fiber bundles.

hippocampus A forebrain structure of the temporal lobe, constituting an important part of the limbic system; includes the hippocampus proper (Ammon's horn), dentate gyrus, and subiculum.

amygdala (*a* ***mig*** *da la*) A structure in the interior of the rostral temporal lobe, containing a set of nuclei; part of the limbic system.

Figure 3.11

A midsagittal view of the brain and part of the spinal cord.



fornix (“arch”) is a bundle of axons that connects the hippocampus with other regions of the brain, including the **mammillary** (“breast-shaped”) **bodies,** protrusions on the base of the brain that contain parts of the hypothalamus. (See ***Figure 3.12.***)

MacLean noted that the evolution of this system, which includes the first and simplest form of cerebral cortex, appears to have coincided with the development of emotional responses. As you will see in Chapter 14, we now know that parts of the limbic system (notably, the hippocampal formation and the region of limbic cortex that surrounds it) are involved in learning and memory. The amygdala and some regions of limbic cortex are specifically involved in emotions: feelings and expressions of emotions, emotional memories, and recognition of the signs of emotions in other people.

fornix A fiber bundle that connects the hippocampus with other parts of the brain, including the mammillary bodies of the hypothalamus; part of the limbic system.

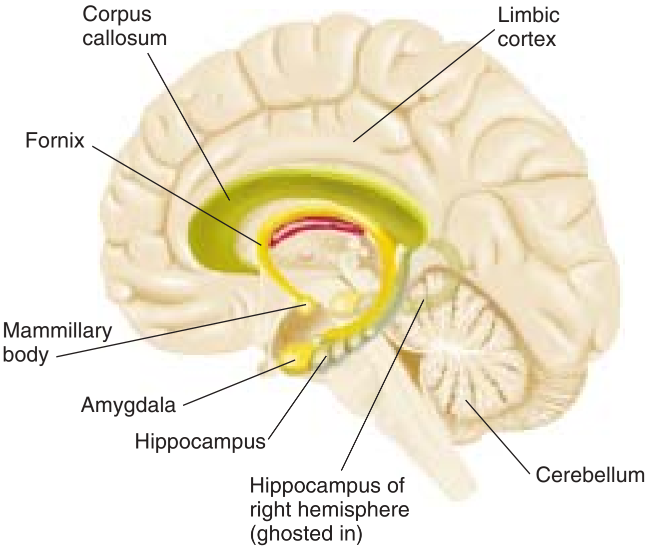
mammillary bodies (***mam*** *i lair ee*) A protrusion of the bottom of the brain at the posterior end of the hypothalamus, containing some hypothalamic nuclei; part of the limbic system.

basal ganglia A group of subcortical nuclei in the telencephalon, the caudate nucleus, the globus pallidus, and the putamen; important parts of the motor system.

nucleus (**plural: nuclei**) An identifiable group of neural cell bodies in the central nervous system.

Figure 3.12

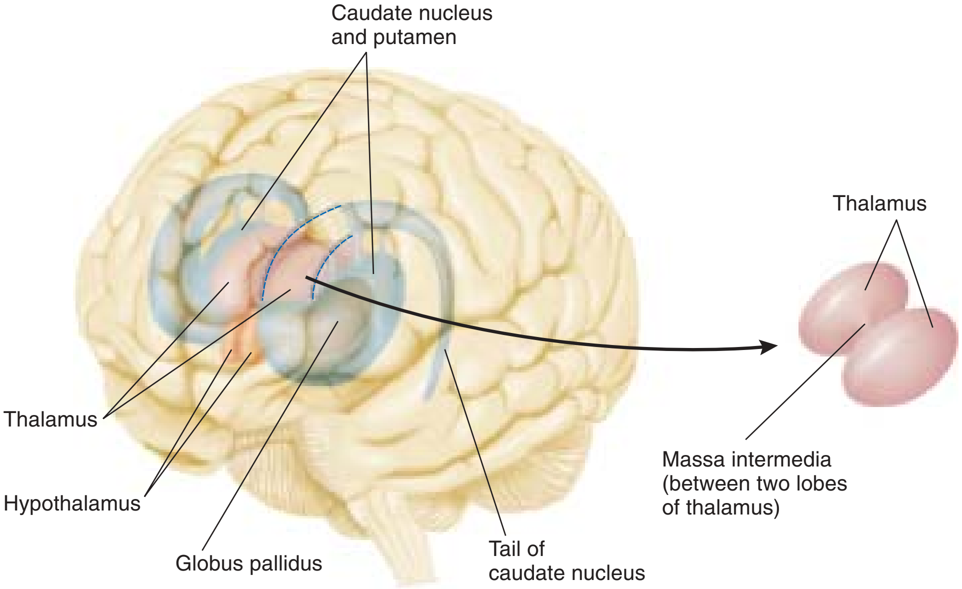
The major components of the limbic system. All of the left hemisphere except for the limbic system has been removed.



Basal Ganglia. The **basal ganglia** are a collection of subcortical nuclei in the forebrain that lie beneath the anterior portion of the lateral ventricles. **Nuclei** are groups of neurons of similar shape. (The word *nucleus,* from the Greek word for “nut,” can refer to the inner portion of an atom, to the structure of a cell that contains the chromosomes, and—as in this case—to a collection of neurons located within the brain.) The major parts of the basal ganglia are the *caudate nucleus,* the *putamen,* and the *globus pallidus* (the “nucleus with a tail,” the “shell,” and the “pale globe”). (See ***Figure 3.13***). The basal ganglia are involved in the control of movement. For example, Parkinson’s disease is caused by degeneration of certain neurons located in the midbrain that

Figure 3.13

The location of the basal ganglia and diencephalon, ghosted in to a semitransparent brain.



send axons to the caudate nucleus and the putamen. The symptoms of this disease are of weakness, tremors, rigidity of the limbs, poor balance, and difficulty in initiating movements.

Diencephalon

The second major division of the forebrain, the **diencephalon,** is situated between the telencephalon and the mesencephalon; it surrounds the third ventricle. Its two most important structures are the thalamus and the hypothalamus. (See ***Figure 3.13.***)

Thalamus. The **thalamus** (from the Greek *thalamos*, "inner chamber") makes up the dorsal part of the diencephalon. It is situated near the middle of the cerebral hemispheres, immediately medial and caudal to the basal ganglia. The thalamus has two lobes, connected by a bridge of gray matter called the *massa intermedia,* which pierces the middle of the third ventricle. (See ***Figure 3.13.***) The massa intermedia is probably not an important structure, because it is absent in the brains of many people. However, it serves as a useful reference point in looking at diagrams of the brain; it appears in Figures 3.4, 3.12, 3.13, 3.14, and 3.15.

Most neural input to the cerebral cortex is received from the thalamus; indeed, much of the cortical surface can be divided into regions that receive projections from specific parts of the thalamus. **Projection fibers** are sets of axons that arise from cell bodies located in one region of the brain and synapse on neurons located within another region (that is, they *project to* these regions).

The thalamus is divided into several nuclei. Some thalamic nuclei receive sensory information from the sensory systems. The neurons in these nuclei then relay the sensory information to specific sensory projection areas of the cerebral cortex. For example, the **lateral geniculate nucleus** receives information from the eye and sends axons to the primary visual cortex, and the **medial geniculate nucleus** receives information from the inner ear and sends axons to the primary auditory cortex. Other thalamic nuclei project to specific regions of the cerebral cortex, but they do not relay sensory information. For example, the **ventrolateral nucleus** receives

diencephalon (*dy en **seff** a lahn*) A region of the forebrain surrounding the third ventricle; includes the thalamus and the hypothalamus.

thalamus The largest portion of the diencephalon, located above the hypothalamus; contains nuclei that project information to specific regions of the cerebral cortex and receive information from it.

projection fiber An axon of a neuron in one region of the brain whose terminals form synapses with neurons in another region.

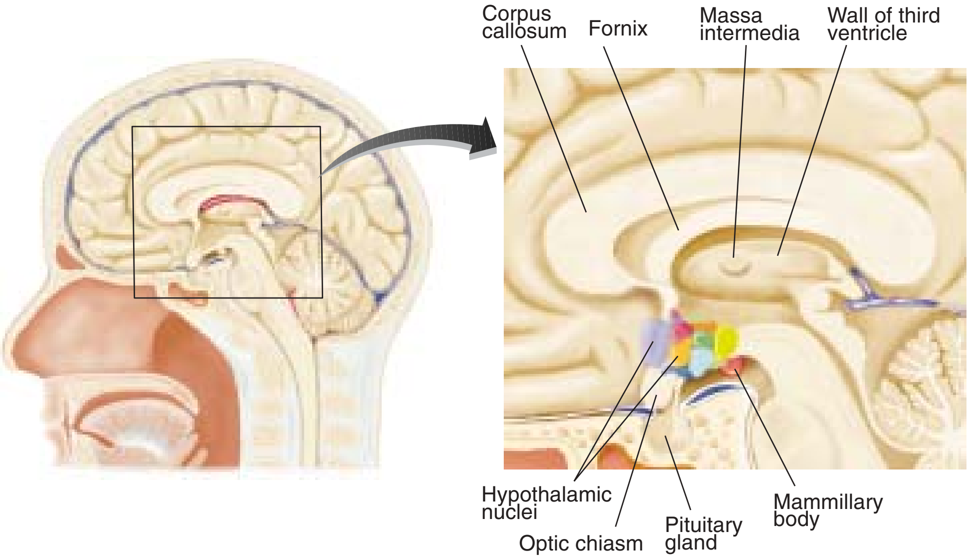
lateral geniculate nucleus A group of cell bodies within the lateral geniculate body of the thalamus that receives fibers from the retina and projects fibers to the primary visual cortex.

medial geniculate nucleus A group of cell bodies within the medial geniculate body of the thalamus; receives fibers from the auditory system and projects fibers to the primary auditory cortex.

ventrolateral nucleus A nucleus of the thalamus that receives inputs from the cerebellum and sends axons to the primary motor cortex.

Figure 3.14

A midsagittal view of part of the brain, showing some of the nuclei of the hypothalamus. The nuclei are situated on the far side of the wall of the third ventricle, inside the right hemisphere.



information from the cerebellum and projects it to the primary motor cortex. And as we will see in Chapter 9, several nuclei are involved in controlling the general excitability of the cerebral cortex. To accomplish this task, these nuclei have widespread projections to all cortical regions.

hypothalamus The group of nuclei of the diencephalon situated beneath the thalamus; involved in regulation of the autonomic nervous system, control of the anterior and posterior pituitary glands, and integration of species-typical behaviors.

optic chiasm (***kye*** *az'm*) An X-shaped connection between the optic nerves, located below the base of the brain, just anterior to the pituitary gland.

anterior pituitary gland The anterior part of the pituitary gland; an endocrine gland whose secretions are controlled by the hypothalamic hormones.

neurosecretory cell A neuron that secretes a hormone or hormonelike substance.

Hypothalamus. As its name implies, the **hypothalamus** lies at the base of the brain, under the thalamus. Although the hypothalamus is a relatively small structure, it is an important one. It controls the autonomic nervous system and the endocrine system and organizes behaviors related to survival of the species—the so-called four F's: fighting, feeding, fleeing, and mating.

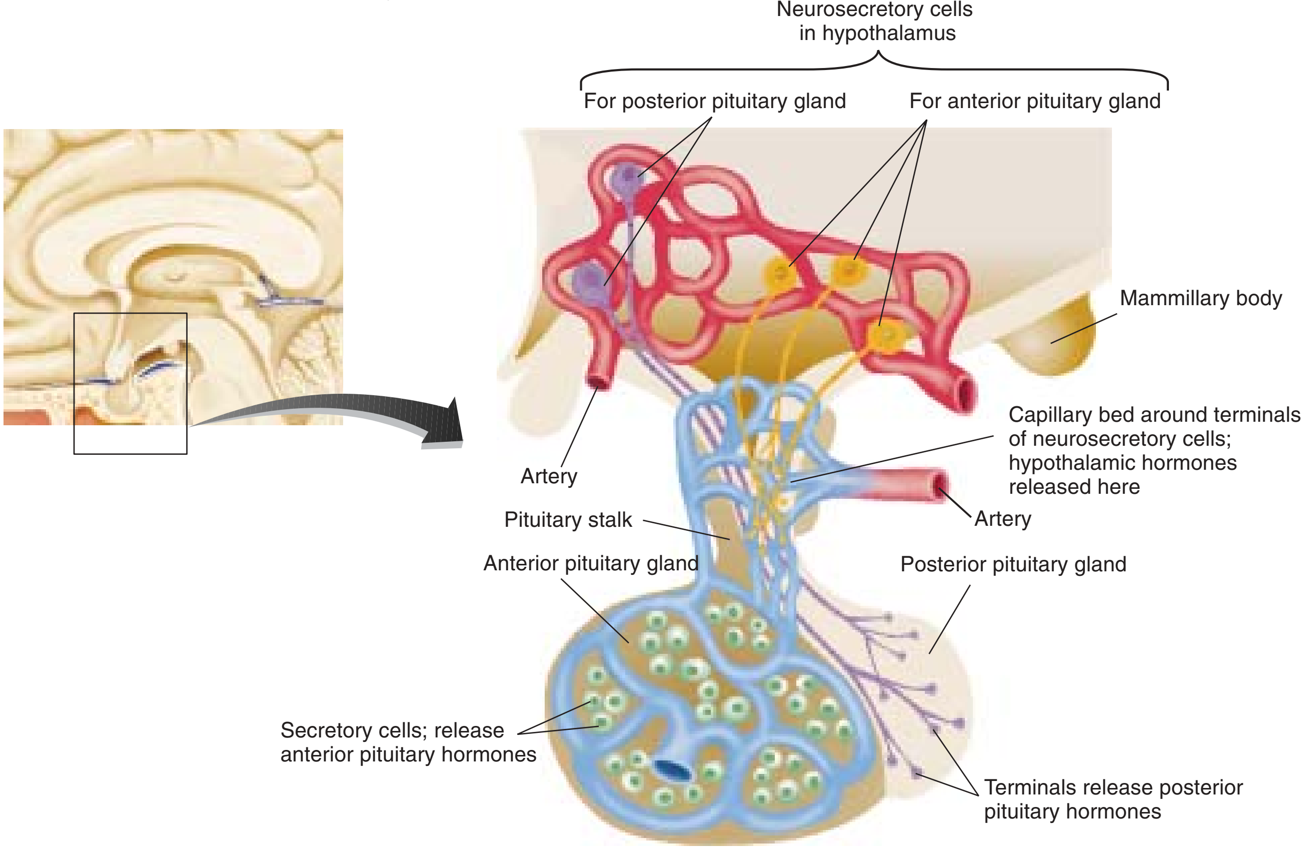
The hypothalamus is situated on both sides of the ventral portion of the third ventricle. The hypothalamus is a complex structure, containing many nuclei and fiber tracts. Figure 3.14 indicates its location and size. Note that the pituitary gland is attached to the base of the hypothalamus via the pituitary stalk. Just in front of the pituitary stalk is the **optic chiasm,** where half of the axons in the optic nerves (from the eyes) cross from one side of the brain to the other. (See ***Figure 3.14.***) The role of the hypothalamus in the control of the four F's (and other behaviors, such as drinking and sleeping) will be considered in several chapters later in this book.

Much of the endocrine system is controlled by hormones produced by cells in the hypothalamus. A special system of blood vessels directly connects the hypothalamus with the **anterior pituitary gland.** (See ***Figure 3.15.***) The hypothalamic hormones are secreted by specialized neurons called **neurosecretory cells,** located near the base of the pituitary stalk.

Prolactin, a hormone produced by the anterior pituitary gland, stimulates milk production in a nursing mother. Oxytocin, a hormone released by the posterior pituitary gland, stimulates the ejection of milk when the baby sucks on a nipple.

Figure 3.15

The pituitary gland. Hormones released by the neurosecretory cells in the hypothalamus enter capillaries and are conveyed to the anterior pituitary gland, where they control its secretion of hormones. The hormones of the posterior pituitary gland are produced in the hypothalamus and carried there in vesicles by means of axoplasmic transport.



These hormones stimulate the anterior pituitary gland to secrete its hormones. For example, *gonadotropin-releasing hormone* causes the anterior pituitary gland to secrete the *gonadotropic hormones,* which play a role in reproductive physiology and behavior.

Most of the hormones secreted by the anterior pituitary gland control other endocrine glands. Because of this function, the anterior pituitary gland has been called the body's "master gland." For example, the gonadotropic hormones stimulate the gonads (ovaries and testes) to release male or female sex hormones. These hormones affect cells throughout the body, including some in the brain. Two other anterior pituitary hormones—prolactin and somatotropic hormone (growth hormone)—do not control other glands but act as the final messenger. The behavioral effects of many of the anterior pituitary hormones are discussed in later chapters.

The **posterior pituitary gland** is in many ways an extension of the hypothalamus. The hypothalamus produces the posterior pituitary hormones and directly controls their secretion. These hormones include oxytocin, which stimulates ejection of milk and uterine contractions at the time of childbirth, and vasopressin, which regulates urine output by the kidneys. They are produced by two different sets of neurons in the hypothalamus whose axons travel down the pituitary stalk and terminate in the posterior pituitary gland. The hormones are carried in vesicles through the axoplasm of these neurons and collect in the terminal buttons in the posterior pituitary gland. When these axons fire, the hormone contained within their terminal buttons is liberated and enters the circulatory system.

posterior pituitary gland The posterior part of the pituitary gland; an endocrine gland that contains hormone-secreting terminal buttons of axons whose cell bodies lie within the hypothalamus.

midbrain The mesencephalon; the central of the three major divisions of the brain.

mesencephalon (*mezz en **seff** a lahn*) The midbrain; a region of the brain that surrounds the cerebral aqueduct; includes the tectum and the tegmentum.

tectum The dorsal part of the midbrain; includes the superior and inferior colliculi.

The Midbrain

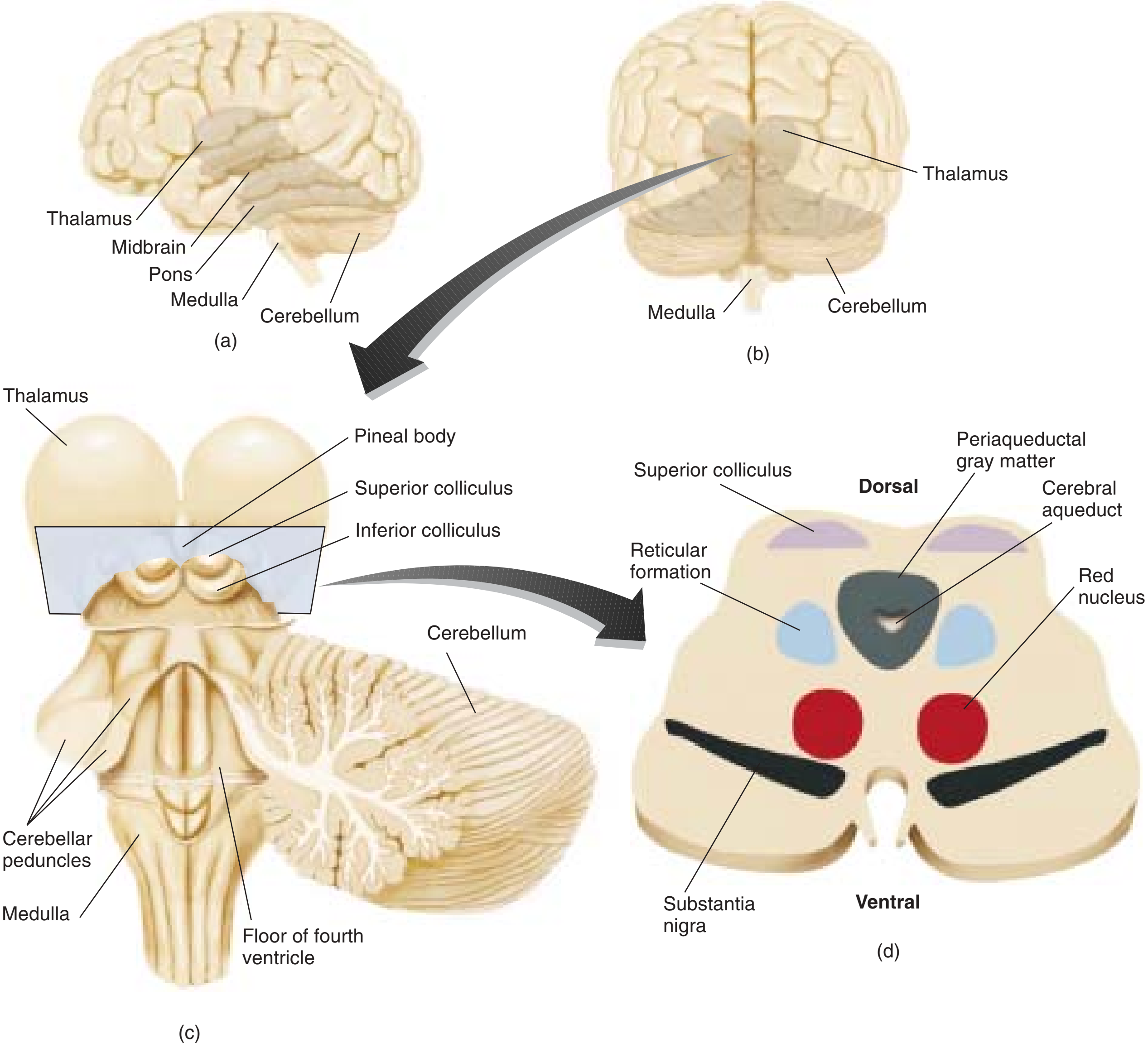
The **midbrain** (also called the **mesencephalon**) surrounds the cerebral aqueduct and consists of two major parts: the tectum and the tegmentum.

Tectum

The **tectum** ("roof") is located in the dorsal portion of the mesencephalon. Its principal structures are the **superior colliculi** and the **inferior colliculi,** which appear as four bumps on the dorsal surface of the **brain stem.** The brain stem includes the diencephalon, midbrain, and hindbrain; it is so called because it looks just like

Figure 3.16

The cerebellum and brain stem. (a) Lateral view of a semitransparent brain, showing the cerebellum and brain stem ghosted in. (b) View from the back of the brain. (c) A dorsal view of the brain stem. The left hemisphere of the cerebellum and part of the right hemisphere have been removed to show the inside of the fourth ventricle and the cerebellar peduncles. (d) A cross section of the midbrain.



that—a stem. Figure 3.16 shows several views of the brain stem: lateral and posterior views of the brain stem inside a semitransparent brain, an enlarged view of the brain stem with part of the cerebellum cut away to reveal the inside of the fourth ventricle, and a cross section through the midbrain. (See ***Figure 3.16.***) The inferior colliculi are a part of the auditory system. The superior colliculi are part of the visual system. In mammals they are primarily involved in visual reflexes and reactions to moving stimuli.

Tegmentum

The **tegmentum** ("covering") consists of the portion of the mesencephalon beneath the tectum. It includes the rostral end of the reticular formation, several nuclei controlling eye movements, the periaqueductal gray matter, the red nucleus, the substantia nigra, and the ventral tegmental area. (See ***Figure 3.16d.***)

The **reticular formation** is a large structure consisting of many nuclei (over ninety in all). It is also characterized by a diffuse, interconnected network of neurons with complex dendritic and axonal processes. (Indeed, *reticulum* means "little net"; early anatomists were struck by the netlike appearance of the reticular formation.) The reticular formation occupies the core of the brain stem, from the lower border of the medulla to the upper border of the midbrain. (See ***Figure 3.16d.***) The reticular formation receives sensory information by means of various pathways and projects axons to the cerebral cortex, thalamus, and spinal cord. It plays a role in sleep and arousal, attention, muscle tonus, movement, and various vital reflexes. Its functions will be described more fully in later chapters.

The **periaqueductal gray matter** is so called because it consists mostly of cell bodies of neurons ("gray matter," as contrasted with the "white matter" of axon bundles) that surround the cerebral aqueduct as it travels from the third to the fourth ventricle. The periaqueductal gray matter contains neural circuits that control sequences of movements that constitute species-typical behaviors, such as fighting and mating. As we will see in Chapter 7, opiates such as morphine decrease an organism's sensitivity to pain by stimulating receptors on neurons located in this region.

The **red nucleus** and **substantia nigra** ("black substance") are important components of the motor system. A bundle of axons that arises from the red nucleus constitutes one of the two major fiber systems that bring motor information from the cerebral cortex and cerebellum to the spinal cord. The substantia nigra contains neurons whose axons project to the caudate nucleus and putamen, parts of the basal ganglia. As we will see in Chapter 4, degeneration of these neurons causes Parkinson's disease.

The Hindbrain

The **hindbrain,** which surrounds the fourth ventricle, consists of two major divisions: the metencephalon and the myelencephalon.

Metencephalon

The metencephalon consists of the pons and the cerebellum.

Cerebellum. The **cerebellum** ("little brain"), with its two hemispheres, resembles a miniature version of the cerebrum. It is covered by the **cerebellar cortex** and has a set of **deep cerebellar nuclei**. These nuclei receive projections from the cerebellar cortex and themselves send projections out of the cerebellum to

superior colliculi (*ka **lik** yew lee*) Protrusions on top of the midbrain; part of the visual system.

inferior colliculi Protrusions on top of the midbrain; part of the auditory system.

brain stem The "stem" of the brain, from the medulla to the diencephalon, excluding the cerebellum.

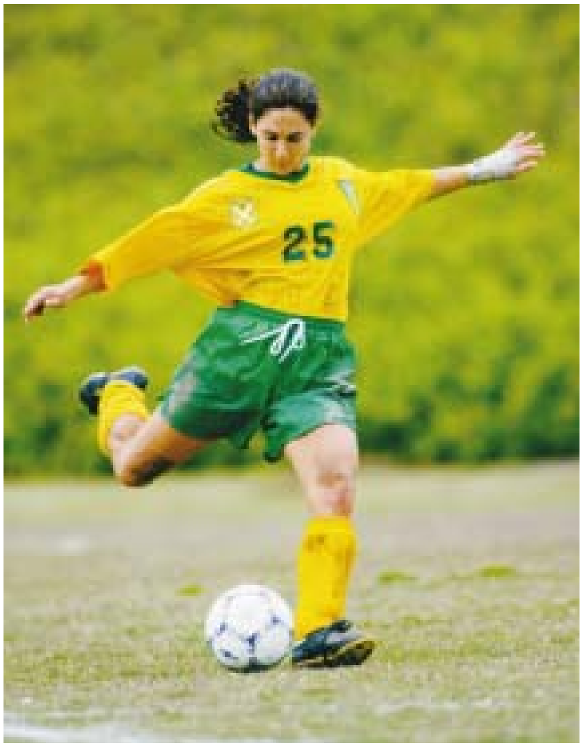
tegmentum The ventral part of the midbrain; includes the periaqueductal gray matter, reticular formation, red nucleus, and substantia nigra.

reticular formation A large network of neural tissue located in the central region of the brain stem, from the medulla to the diencephalon.

periaqueductal gray matter The region of the midbrain surrounding the cerebral aqueduct; contains neural circuits involved in species-typical behaviors.

red nucleus A large nucleus of the midbrain that receives inputs from the cerebellum and motor cortex and sends axons to motor neurons in the spinal cord.

substantia nigra A darkly stained region of the tegmentum that contains neurons that communicate with the caudate nucleus and putamen in the basal ganglia.



The cerebellum plays an important role in coordinating skilled movements.

hindbrain The most caudal of the three major divisions of the brain; includes the metencephalon and myelencephalon.

cerebellum (*sair a **bell** um*) A major part of the brain located dorsal to the pons, containing the two cerebellar hemispheres, covered with the cerebellar cortex; an important component of the motor system.

cerebellar cortex The cortex that covers the surface of the cerebellum.

deep cerebellar nuclei Nuclei located within the cerebellar hemispheres; receive projections from the cerebellar cortex and send projections out of the cerebellum to other parts of the brain.

cerebellar peduncle (***pee** dun kul*) One of three bundles of axons that attach each cerebellar hemisphere to the dorsal pons.

other parts of the brain. Each hemisphere of the cerebellum is attached to the dorsal surface of the pons by bundles of axons: the superior, middle, and inferior **cerebellar peduncles** ("little feet"). (See ***Figure 3.16c.***)

Damage to the cerebellum impairs standing, walking, or performance of coordinated movements. (A virtuoso pianist or other performing musician owes much to his or her cerebellum.) The cerebellum receives visual, auditory, vestibular, and somatosensory information, and it also receives information about individual muscle movements being directed by the brain. The cerebellum integrates this information and modifies the motor outflow, exerting a coordinating and smoothing effect on the movements. Cerebellar damage results in jerky, poorly coordinated, exaggerated movements; extensive cerebellar damage makes it impossible even to stand.

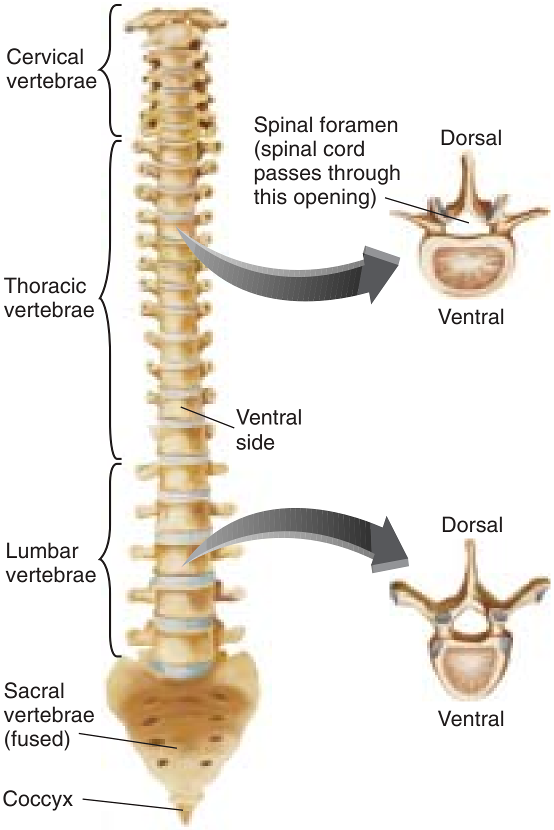
Pons. The **pons,** a large bulge in the brain stem, lies between the mesencephalon and medulla oblongata, immediately ventral to the cerebellum. *Pons* means "bridge," but it does not really look like one. (Refer to ***Figures 3.11*** and ***3.16a.***) The pons contains, in its core, a portion of the reticular formation, including some nuclei that appear to be important in sleep and arousal. It also contains a large nucleus that relays information from the cerebral cortex to the cerebellum.

Myelencephalon

The myelencephalon contains one major structure, the **medulla oblongata** (literally, "oblong marrow"), usually just called the *medulla.* This structure is the most caudal portion of the brain stem; its lower border is the rostral end of the spinal cord. (Refer to ***Figures 3.11*** and ***3.16a.***) The medulla contains part of the reticular formation, including nuclei that control vital functions such as regulation of the cardiovascular system, respiration, and skeletal muscle tonus.

Figure 3.17

A ventral view of the human spinal column, with details showing the anatomy of the vertebrae.



The Spinal Cord

The **spinal cord** is a long, conical structure, approximately as thick as an adult's little finger. The principal function of the spinal cord is to distribute motor fibers to the effector organs of the body (glands and muscles) and to collect somatosensory information to be passed on to the brain. The spinal cord also has a certain degree of autonomy from the brain; various reflexive control circuits (some of which are described in Chapter 8) are located there.

The spinal cord is protected by the vertebral column, which is composed of twenty-four individual vertebrae of the *cervical* (neck), *thoracic* (chest), and *lumbar* (lower back) regions and the fused vertebrae making up the *sacral* and *coccygeal* portions of the column (located in the pelvic region). The spinal cord passes through a hole in each of the vertebrae (the *spinal foramens*). Figure 3.17 illustrates the divisions and structures of the spinal cord and vertebral column. (See ***Figure 3.17.***) Note that the spinal cord is only about two-thirds as long as the vertebral column; the rest of the space is filled by a mass of **spinal roots** composing the **cauda equina** ("horse's tail"). (Refer to ***Figure 3.3c.***)

Early in embryological development the vertebral column and spinal cord are the same length. As development progresses, the vertebral column grows faster than the spinal cord.

This differential growth rate causes the spinal roots to be displaced downward; the most caudal roots travel the farthest before they emerge through openings between the vertebrae and thus compose the cauda equina. To produce the **caudal block** that is sometimes used in pelvic surgery or childbirth, a local anesthetic can be injected into the CSF contained within the sac of dura mater surrounding the cauda equina. The drug blocks conduction in the axons of the cauda equina.

Figure 3.18(a) shows a portion of the spinal cord, with the layers of the meninges that wrap it. Small bundles of fibers emerge from each side of the spinal cord in two straight lines along its dorsolateral and ventrolateral surfaces. Groups of these bundles fuse together and become the thirty-one paired sets of **dorsal roots** and **ventral roots.** The dorsal and ventral roots join together as they pass through the intervertebral foramens and become spinal nerves. (See ***Figure 3.18a.***)

Figure 3.18(b) shows a cross section of the spinal cord. Like the brain, the spinal cord consists of white matter and gray matter. Unlike the brain's, its white matter (consisting of ascending and descending bundles of myelinated axons) is on the outside; the gray matter (mostly neural cell bodies and short, unmyelinated axons) is on the inside. In Figure 3.18(b), ascending tracts are indicated in blue; descending tracts are indicated in red. (See ***Figure 3.18b.***)

pons The region of the metencephalon rostral to the medulla, caudal to the midbrain, and ventral to the cerebellum.

medulla oblongata (*me **doo** la*) The most caudal portion of the brain; located in the myelencephalon, immediately rostral to the spinal cord.

spinal cord The cord of nervous tissue that extends caudally from the medulla.

spinal root A bundle of axons surrounded by connective tissue that occurs in pairs, which fuse and form a spinal nerve.

cauda equina (*ee **kwye** na*) A bundle of spinal roots located caudal to the end of the spinal cord.

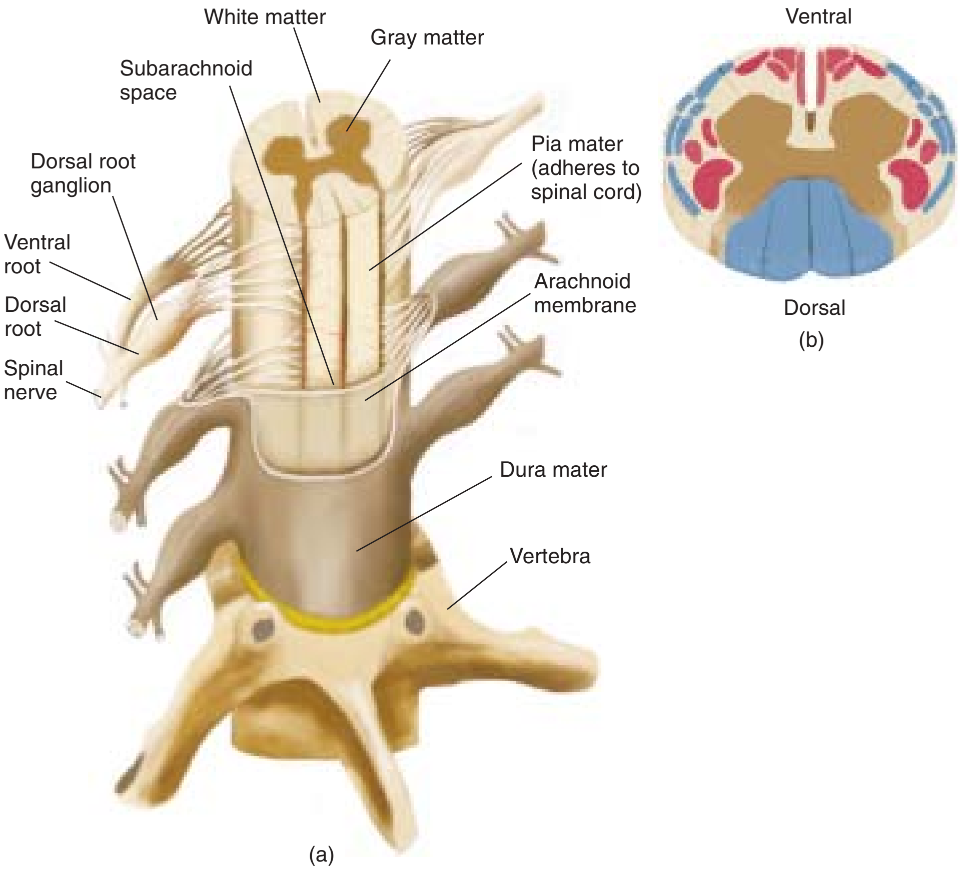
caudal block The anesthesia and paralysis of the lower part of the body produced by injection of a local anesthetic into the cerebrospinal fluid surrounding the cauda equina.

dorsal root The spinal root that contains incoming (afferent) sensory fibers.

ventral root The spinal root that contains outgoing (efferent) motor fibers.

Figure 3.18

The spinal cord. (a) A portion of the spinal cord, showing the layers of the meninges and the relation of the spinal cord to the vertebral column. (b) A cross section through the spinal cord. Ascending tracts are shown in blue; descending tracts are shown in red.



INTERIM SUMMARY

The Central Nervous System

The brain consists of three major divisions, organized around the three chambers of the tube that develops early in embryonic life: the forebrain, the midbrain, and the hindbrain. The development of the neural tube into the mature central nervous system is illustrated in Figure 3.6, and Table 3.2 outlines the major divisions and subdivisions of the brain.

During the first phase of brain development, symmetrical division of the founder cells of the ventricular zone, which lines the neural tube, increases its size. During the second phase, asymmetrical division of these cells gives rise to neurons, which migrate up the fibers of radial glial cells to their final resting places. There, neurons develop dendrites and axons and establish synaptic connections with other neurons. Later, neurons that fail to develop a sufficient number of synaptic connections are killed through apoptosis. The large size of the human brain, relative to the brains of other primates, appears to be accomplished primarily by lengthening the first and second periods of brain development.

The forebrain, which surrounds the lateral and third ventricles, consists of the telencephalon and diencephalon. The telencephalon contains the cerebral cortex, the limbic system, and the basal ganglia. The cerebral cortex is organized into the frontal, parietal, temporal, and occipital lobes. The central sulcus divides the frontal lobe, which deals specifically with movement and the planning of movement, from the other three lobes, which deal primarily with perceiving and learning. The limbic system, which includes the limbic cortex, the hippocampus, and the amygdala, is involved in emotion, motivation, and learning. The basal ganglia participate in the control of movement. The diencephalon consists of the thalamus, which directs information to and from the cerebral cortex, and the hypothalamus, which controls the endocrine system and modulates species-typical behaviors.

The midbrain, which surrounds the cerebral aqueduct, consists of the tectum and tegmentum. The tectum is involved in audition and the control of visual reflexes and reactions to moving stimuli. The tegmentum contains the reticular formation, which is important in sleep, arousal, and movement; the periaqueductal gray matter, which controls various species-typical behaviors; and the red nucleus and the substantia nigra, both of which are parts of the motor system. The hindbrain, which surrounds the fourth ventricle, contains the cerebellum, the pons, and the medulla. The cerebellum plays an important role in integrating and coordinating movements. The pons contains some nuclei that are important in sleep and arousal. The medulla oblongata, too, is involved in sleep and arousal, but it also plays a role in control of movement and in control of vital functions such as heart rate, breathing, and blood pressure.

The outer part of the spinal cord consists of white matter: axons conveying information up or down. The central gray matter contains cell bodies.

The Peripheral Nervous System

The brain and spinal cord communicate with the rest of the body via the cranial nerves and spinal nerves. These nerves are part of the peripheral nervous system, which conveys sensory information to the central nervous system and conveys messages from the central nervous system to the body's muscles and glands.

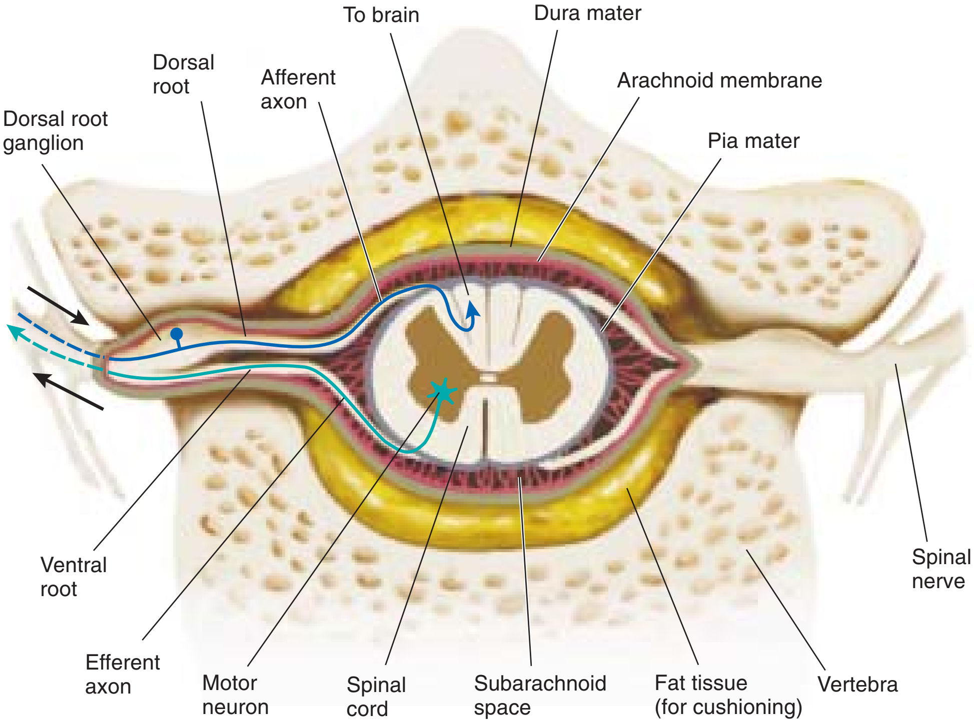
Spinal Nerves

The **spinal nerves** begin at the junction of the dorsal and ventral roots of the spinal cord. The nerves leave the vertebral column and travel to the muscles or sensory receptors they innervate, branching repeatedly as they go. Branches of spinal nerves

spinal nerve A peripheral nerve attached to the spinal cord.

Figure 3.19

A cross section of the spinal cord, showing the route taken by afferent and efferent axons through the dorsal and ventral roots.



often follow blood vessels, especially those branches that innervate skeletal muscles. (Refer to ***Figure 3.3.***)

Now let us consider the pathways by which sensory information enters the spinal cord and motor information leaves it. The cell bodies of all axons that bring sensory information into the brain and spinal cord are located outside the CNS. (The sole exception is the visual system; the retina of the eye is actually a part of the brain.) These incoming axons are referred to as **afferent axons** because they "bear toward" the CNS. The cell bodies that give rise to the axons that bring somatosensory information to the spinal cord reside in the **dorsal root ganglia,** rounded swellings of the dorsal root. (See ***Figure 3.19.***) These neurons are of the unipolar type (described in Chapter 2). The axonal stalk divides close to the cell body, sending one limb into the spinal cord and the other limb out to the sensory organ. Note that all of the axons in the dorsal root convey somatosensory information.

Cell bodies that give rise to the ventral root are located within the gray matter of the spinal cord. The axons of these multipolar neurons leave the spinal cord via a ventral root, which joins a dorsal root to make a spinal nerve. The axons that leave the spinal cord through the ventral roots control muscles and glands. They are referred to as **efferent axons** because they "bear away from" the CNS. (See ***Figure 3.19.***)

Cranial Nerves

Twelve pairs of **cranial nerves** are attached to the ventral surface of the brain. Most of these nerves serve sensory and motor functions of the head and neck region. One of them, the *tenth,* or **vagus nerve,** regulates the functions of organs in the thoracic

afferent axon An axon directed toward the central nervous system, conveying sensory information.

dorsal root ganglion A nodule on a dorsal root that contains cell bodies of afferent spinal nerve neurons.

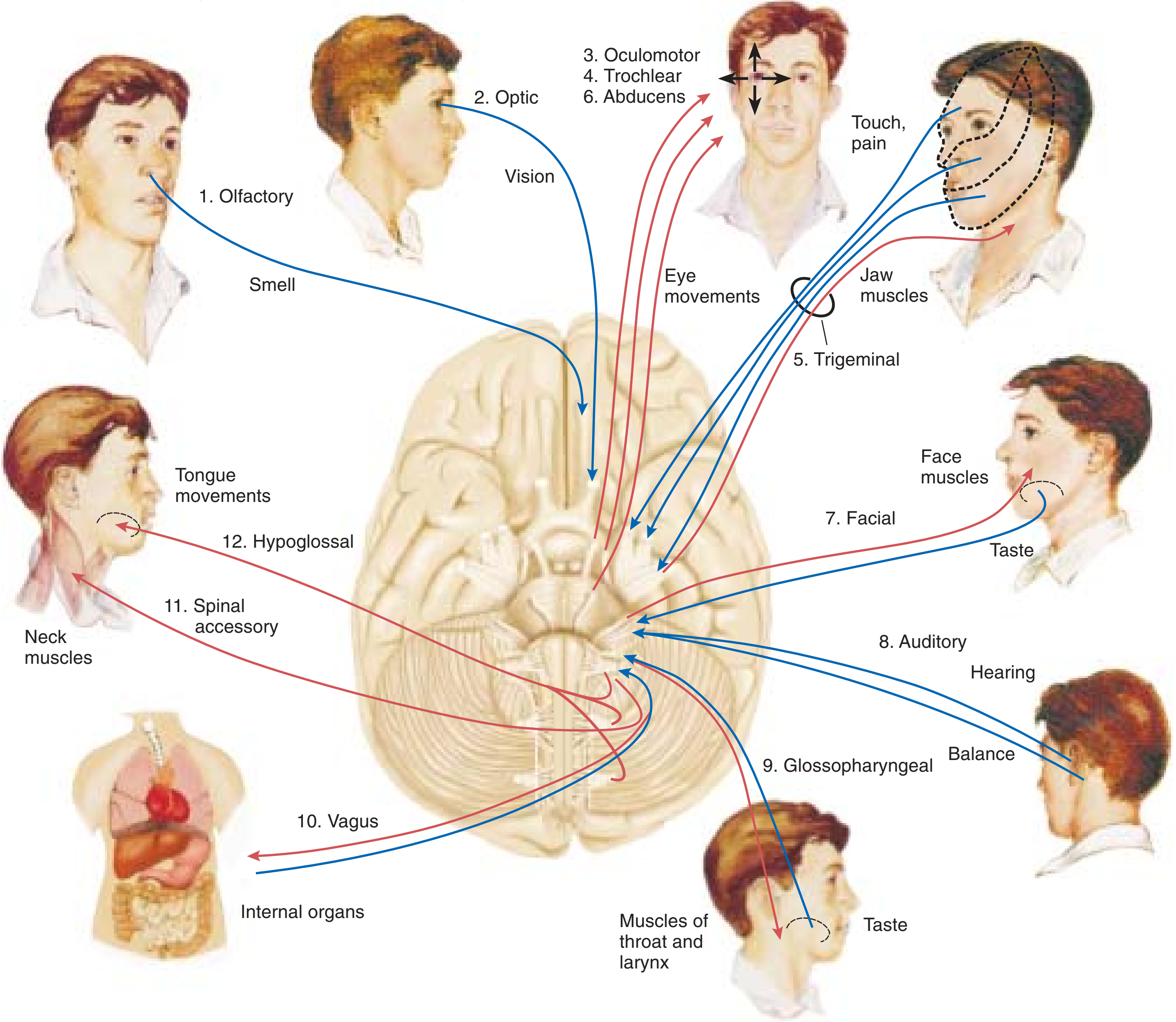
efferent axon (***eff*** *ur ent*) An axon directed away from the central nervous system, conveying motor commands to muscles and glands.

cranial nerve A peripheral nerve attached directly to the brain.

vagus nerve The largest of the cranial nerves, conveying efferent fibers of the parasympathetic division of the autonomic nervous system to organs of the thoracic and abdominal cavities.

Figure 3.20

The twelve pairs of cranial nerves and the regions and functions they serve. Red lines denote axons that control muscles or glands; blue lines denote sensory axons.



and abdominal cavities. It is called the *vagus* ("wandering") nerve because its branches wander throughout the thoracic and abdominal cavities. (The word *vagabond* has the same root.) Figure 3.20 presents a view of the base of the brain and illustrates the cranial nerves and the structures they serve. Note that efferent (motor) fibers are drawn in red and that afferent (sensory) fibers are drawn in blue. (See ***Figure 3.20***.)

As I mentioned in the previous section, cell bodies of sensory nerve fibers that enter the brain and spinal cord (except for the visual system) are located outside the central nervous system. Somatosensory information (and the sense of taste) is received, via the cranial nerves, from unipolar neurons. Auditory, vestibular, and visual information is received via fibers of bipolar neurons (described in Chapter 2). Olfactory information is received via the **olfactory bulbs,** which receive information

olfactory bulb The protrusion at the end of the olfactory nerve; receives input from the olfactory receptors.

from the olfactory receptors in the nose. The olfactory bulbs are complex structures containing a considerable amount of neural circuitry; actually, they are part of the brain. Sensory mechanisms are described in more detail in Chapters 6 and 7.

The Autonomic Nervous System

The part of the peripheral nervous system that I have discussed so far—which receives sensory information from the sensory organs and that controls movements of the skeletal muscles—is called the **somatic nervous system.** The other branch of the peripheral nervous system—the **autonomic nervous system (ANS)**—is concerned with regulation of smooth muscle, cardiac muscle, and glands. (*Autonomic* means "self-governing.") Smooth muscle is found in the skin (associated with hair follicles), in blood vessels, in the eyes (controlling pupil size and accommodation of the lens), and in the walls and sphincters of the gut, gallbladder, and urinary bladder. Merely describing the organs that are innervated by the autonomic nervous system suggests the function of this system: regulation of "vegetative processes" in the body.

The ANS consists of two anatomically separate systems: the *sympathetic division* and the *parasympathetic division.* With few exceptions organs of the body are innervated by both of these subdivisions, and each has a different effect. For example, the sympathetic division speeds the heart rate, whereas the parasympathetic division slows it.

Sympathetic Division of the ANS

The **sympathetic division** is most involved in activities associated with expenditure of energy from reserves that are stored in the body. For example, when an organism is excited, the sympathetic nervous system increases blood flow to skeletal muscles, stimulates the secretion of epinephrine (resulting in increased heart rate and a rise in blood sugar level), and causes piloerection (erection of fur in mammals that have it and production of "goose bumps" in humans).

The cell bodies of sympathetic motor neurons are located in the gray matter of the thoracic and lumbar regions of the spinal cord (hence the sympathetic nervous system is also known as the *thoracolumbar system*). The fibers of these neurons exit via the ventral roots. After joining the spinal nerves, the fibers branch off and pass into **sympathetic ganglia** (not to be confused with the dorsal root ganglia). Figure 3.21 shows the relation of these ganglia to the spinal cord. Note that individual sympathetic ganglia are connected to the neighboring ganglia above and below, thus forming the **sympathetic ganglion chain.** (See ***Figure 3.21.***)

The axons that leave the spinal cord through the ventral root belong to the **preganglionic neurons.** With one exception, all sympathetic preganglionic axons enter the ganglia of the sympathetic chain, but not all of them form synapses there. (The exception is the medulla of the adrenal gland, described in Chapter 10.) Some axons leave and travel to one of the other sympathetic ganglia, located among the internal organs. All sympathetic preganglionic axons form synapses with neurons located in one of the ganglia. The neurons with which they form synapses are called **postganglionic neurons.** In turn, the postganglionic neurons send axons to the target organs, such as the intestines, stomach, kidneys, or sweat glands. (See ***Figure 3.21.***)

Parasympathetic Division of the ANS

The **parasympathetic division** of the autonomic nervous system supports activities that are involved with increases in the body's supply of stored energy. These activities include salivation, gastric and intestinal motility, secretion of digestive juices, and increased blood flow to the gastrointestinal system.

Cell bodies that give rise to preganglionic axons in the parasympathetic nervous system are located in two regions: the nuclei of some of the cranial nerves (especially the vagus nerve) and the intermediate horn of the gray matter in the sacral region

somatic nervous system The part of the peripheral nervous system that controls the movement of skeletal muscles or transmits somatosensory information to the central nervous system.

autonomic nervous system (ANS) The portion of the peripheral nervous system that controls the body's vegetative functions.

sympathetic division The portion of the autonomic nervous system that controls functions that accompany arousal and expenditure of energy.

sympathetic ganglia Nodules that contain synapses between preganglionic and postganglionic neurons of the sympathetic nervous system.

sympathetic ganglion chain One of a pair of groups of sympathetic ganglia that lie ventrolateral to the vertebral column.

preganglionic neuron The efferent neuron of the autonomic nervous system whose cell body is located in a cranial nerve nucleus or in the intermediate horn of the spinal gray matter and whose terminal buttons synapse upon postganglionic neurons in the autonomic ganglia.

postganglionic neuron Neurons of the autonomic nervous system that form synapses directly with their target organ.

parasympathetic division The portion of the autonomic nervous system that controls functions that occur during a relaxed state.

Figure 3.21

The autonomic nervous system and the target organs and functions served by the sympathetic and parasympathetic branches.

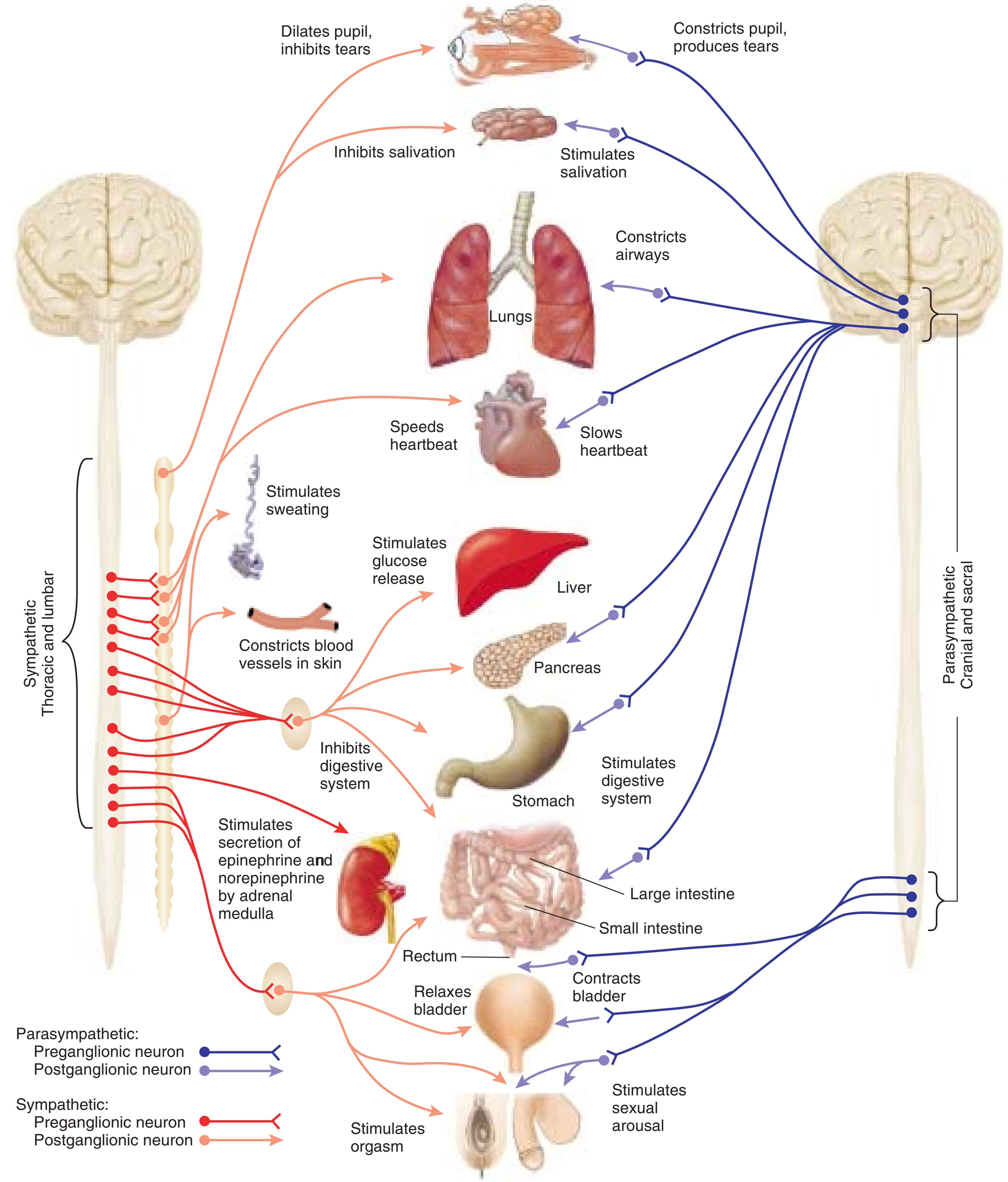


Table 3.3

The Major Divisions of the Peripheral Nervous System

Somatic Nervous System	Autonomic Nervous System (ANS)
SPINAL NERVES	SYMPATHETIC BRANCH
Afferents from sense organs	Spinal nerves (from thoracic and lumbar regions)
Efferents to muscles	Sympathetic ganglia
CRANIAL NERVES	PARASYMPATHETIC BRANCH
Afferents from sense organs	Cranial nerves (3rd, 7th, 9th, and 10th)
Efferents to muscles	Spinal nerves (from sacral region)
	Parasympathetic ganglia (adjacent to target organs)

of the spinal cord. Thus, the parasympathetic division of the ANS has often been referred to as the *craniosacral system*. Parasympathetic ganglia are located in the immediate vicinity of the target organs; the postganglionic fibers are therefore relatively short. The terminal buttons of both preganglionic and postganglionic neurons in the parasympathetic nervous system secrete acetylcholine.

Table 3.3 summarizes the major divisions of the peripheral nervous system.

INTERIM SUMMARY

The Peripheral Nervous System

The spinal nerves and the cranial nerves convey sensory axons into the central nervous system and motor axons out from it. Spinal nerves are formed by the junctions of the dorsal roots, which contain incoming (afferent) axons, and the ventral roots, which contain outgoing (efferent) axons. The autonomic nervous system consists of two divisions: the sympathetic division, which controls activities that occur during excitement or exertion, such as increased heart rate; and the parasympathetic division, which controls activities that occur during relaxation, such as decreased heart rate and increased activity of the digestive system. The pathways of the autonomic nervous system contain preganglionic axons, from the brain or spinal cord to the sympathetic or parasympathetic ganglia, and postganglionic axons, from the ganglia to the target organ.

EPILOGUE:

Unilateral Neglect

When we see people like Miss S., the woman with unilateral neglect, we realize that perception and attention are somewhat independent. The perceptual mechanisms of our brain provide the information, and the mechanisms involved in attention determine whether we become conscious of this information.

Unilateral neglect occurs when the right parietal lobe is damaged. The parietal lobe contains the primary somatosensory cortex. It receives information from the skin, the muscles, the joints, the internal organs, and the part of the inner ear that is concerned with balance. Thus, it is concerned with the body and its position. But that is not all; the association cortex of the parietal lobe also receives auditory and visual information from the association cortex of the occipital and temporal lobes. Its most important function seems to be to put together information about the movements and location of the parts of the body with the locations of objects in space around us. The right and left parietal lobes each handle somewhat different tasks; the left concerns itself with the position of the parts of the body, and the right concerns itself with the three-dimensional space around the body and the contents of that space. (The left parietal lobe is also involved in language abilities, but they will be discussed later, in Chapter 13.)

If unilateral neglect simply consisted of blindness in the left side of the visual field and anesthesia of the left side of the body, it would not be nearly as interesting. Individuals with pure unilateral neglect are neither half blind nor half numb. Under the proper circumstances they *can* see things located to their left, and they *can* tell when someone touches the left side of their bodies. But normally, they ignore such stimuli and act as if the left side of the world and of their bodies did not exist.

Volpe, LeDoux, and Gazzaniga (1979) presented pairs of visual stimuli to people with unilateral neglect—one stimulus in the left visual field and one stimulus in the right. Invariably, the people reported seeing only the right-hand stimulus. But when the investigators asked the people to say whether or not the two stimuli were identical, they answered correctly—*even though they said that they were unaware of the left-hand stimulus.*

If you think about the story that the chief of neurology told about the man who ate only the right half of a pancake, you will realize that people with unilateral neglect *must* be able to perceive more than the right visual field. Remember that people with unilateral neglect fail to notice not only things to their left but also the *left halves* of things. But to distinguish between the left and right halves of an object, you first have to perceive the entire object—otherwise, how would you know where the middle was?

People with unilateral neglect also demonstrate their unawareness of the left half of things when they draw pictures. For example, when asked to draw a clock, they almost always successfully draw a circle; but then when they fill in the numbers, they scrunch them all in on the right side. Sometimes they simply stop after reaching 6 or 7, and sometimes they write the rest of the numbers underneath the circle. When asked to draw a daisy, they begin with a stem and a leaf or two and then draw all the petals to the right. When asked to draw a bicycle, they draw wheels and then put in spokes, but only on the right halves of the wheels.

Bisiach and Luzzatti (1978) demonstrated a similar phenomenon, which suggests that unilateral neglect extends even to a person's own visual imagery. The investigators asked two patients with unilateral neglect to describe the Piazza del Duomo, a well-known landmark in Milan, the city in which they and the patients lived. They asked the patients to imagine that they were standing at the north end of the piazza and to tell them what they saw. The patients duly named the buildings, but only those on the west, to their right. Then the investigators asked the patients to imagine themselves at the south end of the piazza. This time, they named the buildings on the east—again, to their right. Obviously, they knew about *all* of the buildings and their locations, but they visualized them only when the buildings were located in the right side of their (imaginary) visual field.

You might wonder whether damage to the *left* parietal lobe causes unilateral *right* neglect. The answer is yes, but it is very slight, it is difficult to detect, and it seems to be temporary. For all practical purposes, then, there is no right neglect. But why not? The answer is still a mystery. To be sure, people have suggested some possible explanations, but they are still quite speculative. Not until we know a lot more about the brain mechanisms of attention we will be able to understand this discrepancy.

KEY CONCEPTS

BASIC FEATURES OF THE NERVOUS SYSTEM

1. The central nervous system consists of the brain and spinal cord; it is covered with the meninges and floats in cerebrospinal fluid.

THE CENTRAL NERVOUS SYSTEM

2. The nervous system develops first as a tube, which thickens and forms pockets and folds as cells are produced. The tube becomes the ventricular system.
3. The primary cause of the difference between the human brain and that of other primates is a slightly extended period of symmetrical and asymmetrical division of founder cells located in the ventricular zone.
4. The forebrain, surrounding the lateral and third ventricles, consists of the telencephalon (cerebral cortex, limbic system, and basal ganglia) and diencephalon (thalamus and hypothalamus).
5. The midbrain, which surrounds the cerebral aqueduct, consists of the tectum and tegmentum.
6. The hindbrain, which surrounds the fourth ventricle, contains the cerebellum, the pons, and the medulla.

THE PERIPHERAL NERVOUS SYSTEM

7. The spinal and cranial nerves connect the central nervous system with the rest of the body. The autonomic nervous system consists of two divisions, sympathetic and parasympathetic.

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SUGGESTED WEB SITES

Neuroscience Images

http://synergy.mcg.edu/pt/PT413/images/image.html

Color images of the external surface of the human brain are provided by this site.

The Global Spinal Cord

http://www.anatomy.wisc.edu/sc97/text/SC/contents.htm

The ascending and descending fibers of the spinal cord are the focus of this Web site.

Harvard Brain Atlas

http://www.med.harvard.edu/AANLIB/home.html

This link provides access to the Whole Brain Atlas page that provides images of normal as well as damaged human brains.

Insights from a Broken Brain

http://science-education.nih.gov/nihHTML/ose/snapshots/multimedia/ritn/Gage/Broken_brain1.html

Phineas Gage is the subject of this Web site. The site briefly describes the accident that resulted in damage to his frontal lobes and the personality changes that followed the accident. The site contains several graphics and a description of two recent imaging techniques (PET and MRI).

Medical Neuroscience

http://www.indiana.edu/~m555/

This Web site provides a large number of sections of human brain. Each section can be viewed in either a labeled or unlabeled mode. A unique feature of the site relates to a series of clinical cases relating brain damage to function.