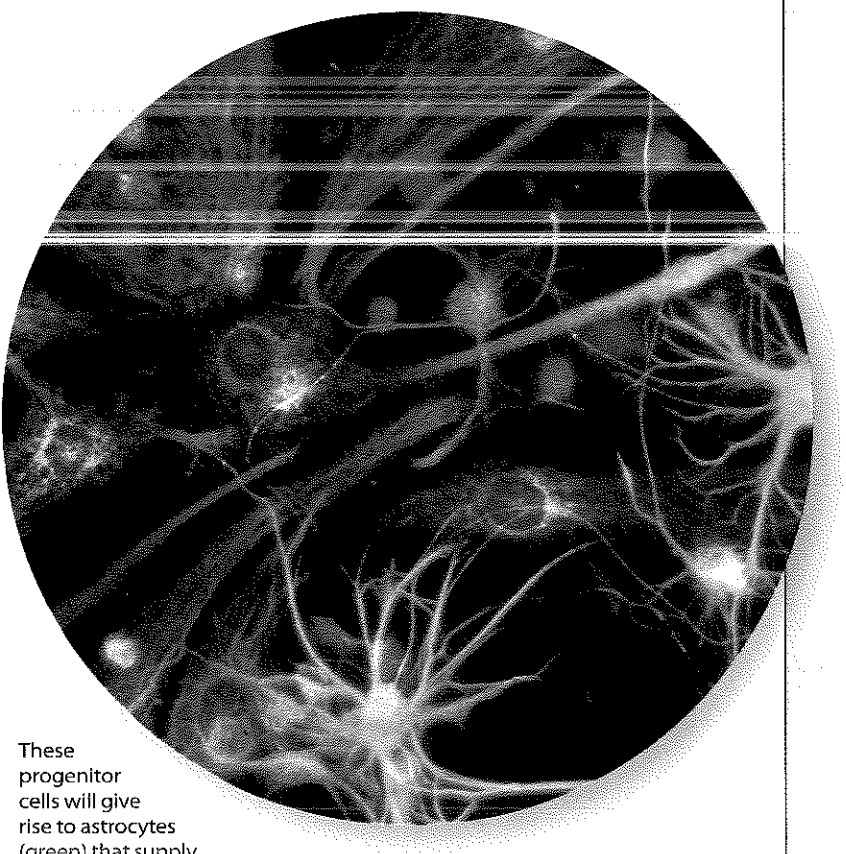
Unit III

10 Nervous System I

Basic Structure and Function



These progenitor cells will give rise to astrocytes (green) that supply neurons with nutrients. In this immunofluorescent light micrograph, cell nuclei are stained blue (1,150×).

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Module 7: Nervous System

Learning Outcomes

After you have studied this chapter, you should be able to:

10.1 Introduction

1 Describe the general functions of the nervous system. (p. 361)
2 Identify the two types of cells that comprise nervous tissue. (p. 361)
3 Identify the two major groups of nervous system organs. (p. 362)

10.2 General Functions of the Nervous System

4 List the functions of sensory receptors. (p. 362)
5 Describe how the nervous system responds to stimuli. (p. 362)

10.3 Description of Cells of the Nervous System

6 Describe the parts of a neuron. (p. 363)
7 Describe the relationships among myelin, the neurilemma, and nodes of Ranvier. (p. 365)
8 Distinguish between the sources of white matter and gray matter. (p. 366)

10.4 Classification of Cells of the Nervous System

9 Identify structural and functional differences among neurons. (p. 367)
10 Identify the types of neuroglia in the central nervous system and their functions. (p. 369)
11 Describe the role of Schwann cells in the peripheral nervous system. (p. 370)

10.5 The Synapse

12 Explain how information passes from a presynaptic neuron to a postsynaptic cell. (p. 372)

10.6 Cell Membrane Potential

13 Explain how a cell membrane becomes polarized. (p. 372)
14 Describe the events leading to the generation of an action potential. (p. 375)
15 Explain how action potentials move down an axon. (p. 376)
16 Compare impulse conduction in myelinated and unmyelinated neurons. (p. 378)

10.7 Synaptic Transmission

17 Identify the changes in membrane potential associated with excitatory and inhibitory neurotransmitters. (p. 379)
18 Explain what prevents a postsynaptic cell from being continuously stimulated. (p. 380)

10.8 Impulse Processing

19 Describe the basic ways in which the nervous system processes information. (p. 381)

LEARN PRACTICE ASSESS

Understanding Words

astr-, starlike: *astr*ocyte—star-shaped neuroglia.

ax-, axle: *ax*on—cylindrical nerve process that carries impulses away from a neuron cell body.

bi-, two: *bi*polar neuron—neuron with two processes extending from the cell body.

dendr-, tree: *dendr*ite—branched nerve process that serves as the receptor surface of a neuron.

ependym-, tunic: *ependyma*—neuroglia that line spaces in the brain and spinal cord.

-lemm, rind or peel: neuri*lemma*—sheath that surrounds the myelin of a nerve cell process.

moto-, moving: *motor* neuron—neuron that stimulates a muscle to contract or a gland to release a secretion.

multi-, many: *multi*polar neuron—neuron with many processes extending from the cell body.

oligo-, few: *oligo*dendrocyte—small type of neuroglia with few cellular processes.

peri-, all around: *peri*pheral nervous system—portion of the nervous system that consists of the nerves branching from the brain and spinal cord.

saltator-, a dancer: *saltatory* conduction—impulse conduction in which the impulse seems to jump from node to node along the nerve fiber.

sens-, feeling: *sens*ory neuron—neuron that can be stimulated by a sensory receptor and conducts impulses into the brain or spinal cord.

syn-, together: *syn*apse—junction between two neurons.

uni-, one: *uni*polar—neuron with only one process extending from the cell body.

Brain Banks

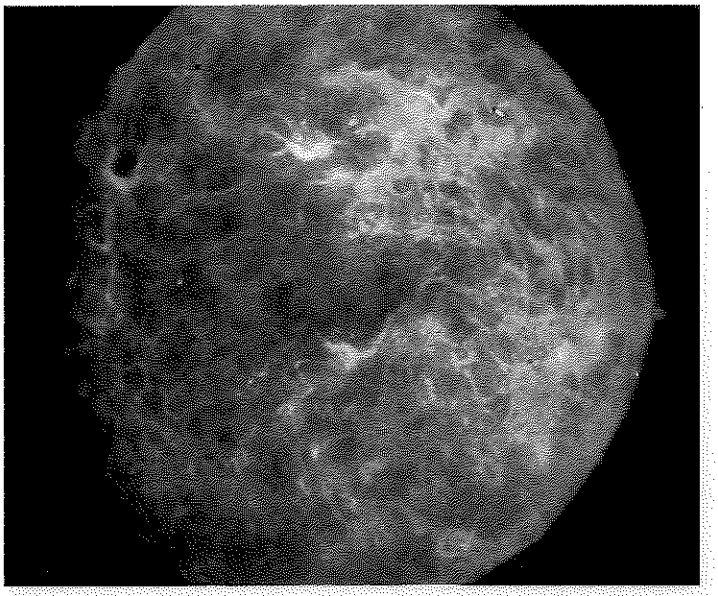
In a large room at the Croatian Institute for Brain Research, rows of shelves hold a variety of fluid-filled jars, a human brain suspended in each. Their sizes differ, reflecting their origins from embryos up to the elderly. Researchers can use the more than 1,000 brains and more than 130,000 histological slides at the bank to investigate brain-based diseases and injuries that affect many millions of people worldwide and also to better understand the functioning of the normal human brain.

In the United States, several brain banks offer tissue sections from thousands of people who willed their brains to science. Unlike donated hearts, lungs, or corneas, which directly help other people, donated brains go to research labs.

Many brain banks are specialized. The bank at Harvard University is devoted to neurodegenerative diseases, such as Alzheimer and Parkinson diseases, while the resource at the University of Maryland in Baltimore focuses on developmental disorders, including Down syndrome and autism. The brain bank at the University of Miami has brains from people who had schizophrenia, depression, amyotrophic lateral sclerosis, and several other disorders, as well as undiseased brains for comparison.

Brains must be removed from the skull within twelve hours of death. Then they are halved and cut into one-centimeter thick sections and frozen in plastic bags. The specimens are provided free to researchers.

Study of brain function and malfunction is also possible at the cellular level. The National Human Neural Stem Cell Resource provides neural stem cells, which function after death longer than neurons because their energy and oxygen requirements are not as high as those of the more specialized cells. Hospitals collect brain material upon autopsy and send it to the facility, where a special protocol is used to obtain and preserve the cells from several brain areas. Investigators use the human neural stem cells to study neurodegenerative disorders, stroke, traumatic brain injury, rare inborn errors of metabolism, as well as the development of the incredibly complex human brain from initial stem and progenitor cells. The material in brain and stem cell banks is also being used in drug discovery and in developing new treatments based on cell implants. The chapter opening image shows neural progenitor cells and the photo accompanying this vignette shows neural stem cells. ■



Neurospheres cultured in the laboratory consist of neural stem cells. These cells can divide and differentiate to give rise to neural progenitor cells, which in turn divide and differentiate, yielding neurons and neuroglia. In the brain, neural stem cells occupy certain areas but are exceedingly rare. Researchers are attempting to harness the natural ability of neural stem and progenitor cells to divide and replace damaged or diseased neural tissue.

10.1 INTRODUCTION

The nervous system oversees all that we do and largely determines who we are. Through a vast communicating network of cells and the information that they send and receive, the nervous system can detect changes in the body, make decisions, and stimulate muscles or glands to respond. Typically, these responses counteract the effects of the changes, and in this way, the nervous system helps maintain homeostasis. Clinical Application 10.1 discusses how environmental changes may trigger migraine headaches, a common medical problem attributed to the nervous system that may involve its blood supply as well as neurons.

The nervous system is composed predominantly of neural tissue, but also includes blood vessels and connective tissue. Neural tissue consists of two cell types: nerve cells, or **neurons** (nu'ronz), and **neuroglia** (nu-ro'gle-ah) (or neuroglial cells).

Neurons are specialized to react to physical and chemical changes in their surroundings. Small cellular processes called **dendrites** (den'drīts) receive the input. A longer process called an **axon** (ak'son), or nerve fiber, carries the information away from the cell in the form of bioelectric signals, often called **impulses,** which allow the neuron to communicate with other neurons and with cells outside the nervous system (fig. 10.1). Nerves are bundles of axons.

Neuroglia are found throughout the nervous system, and in the brain they greatly outnumber neurons. It was once thought that neuroglia only fill spaces and surround or support neurons. Today we know that they have many other functions, including nourishing neurons and sending and receiving messages.

An important part of the nervous system at the cellular level is not a cell at all, but the small space between a neuron and the cell(s) with which it communicates, called a **synapse** (sin'aps). Much of the work of the nervous system is to send and receive electrochemical messages across synapses. Biological messenger molecules called **neurotransmitters** (nu"ro-trans-mit'erz) convey this neural information.

The organs of the nervous system can be divided into two groups. One group, consisting of the brain and spinal cord, forms the **central nervous system (CNS).** The other, composed of the nerves (cranial and spinal nerves) that

10.1 CLINICAL APPLICATION

Migraine

The signs of a migraine are unmistakable—a pounding head, waves of nausea, shimmering images in the peripheral visual field, and extreme sensitivity to light or sound. Inherited susceptibilities and environmental factors probably cause migraines. Environmental triggers include sudden exposure to bright light, eating a particular food (chocolate, red wine, nuts, and processed meats top the list), lack of sleep, stress, high altitude, stormy weather, and excessive caffeine or alcohol intake. Hormonal influences may also be involved, because two-thirds of the 300 million people who suffer from migraines worldwide are women between the ages of 15 and 55.

A migraine attack may last only a few hours, or days. It is due to a phenomenon called "cortical spreading depression," in which an intense wave of excitation followed by a brief period of unresponsiveness in certain neurons stimulates the trigeminal nuclei at the base of the brain to produce pain sensations. The excitation and dampening of the activity level of these neurons also triggers changes in blood flow in the brain that were once thought to be the direct cause of migraine.

Drugs called triptans can very effectively halt a migraine attack, but must be taken as soon as symptoms begin. Triptans block the release of neurotransmitter from the neurons in the trigeminal nerves. Because triptans constrict blood vessels throughout the body, making them dangerous for some people, newer migraine drugs have been developed that block the specific neurotransmitter that the trigeminal nerves release (calcitonin gene-related peptide), better targeting the therapeutic effect.

Several drugs developed to treat other conditions are used on a long-term, daily basis to lessen the frequency of migraines. These drugs include certain antidepressants, anticonvulsants, and drugs used to treat high blood pressure (calcium channel blockers and beta blockers). A physician must consider an individual's family and health history before prescribing these drugs to prevent migraine. ■

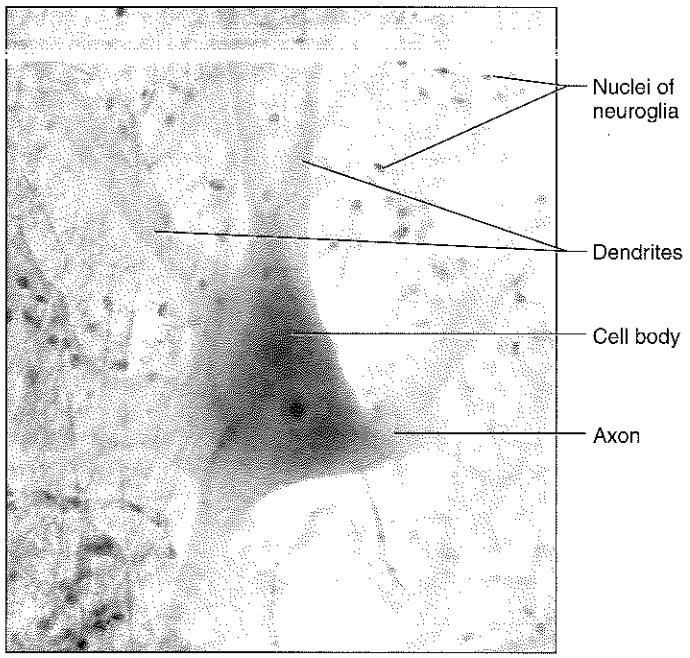


FIGURE 10.1 AP|R Neurons are the structural and functional units of the nervous system (600×). Neuroglia are cells that surround and support a neuron, appearing as dark dots. Note the locations of the neuron processes (dendrites and a single axon).

Q: *What structure forms the outer portion of the axon and dendrites of a neuron?*

Answer can be found in Appendix G on page 938.

connect the central nervous system to other body parts, is the **peripheral nervous system (PNS)** (fig. 10.2).

PRACTICE

1 Name two cell types in neural tissue.

2 Name two groups of nervous system organs.

10.2 GENERAL FUNCTIONS OF THE NERVOUS SYSTEM

The three general functions of the nervous system—receiving information, deciding what to do, and acting on those decisions—are termed sensory, integrative, and motor. Structures called **sensory receptors** at the ends of neurons in the peripheral nervous system (peripheral neurons) provide the sensory function of the nervous system (see chapter 11, p. 396). These receptors gather information by detecting changes inside and outside the body. They monitor external environmental factors such as light and sound intensities as well as the temperature, oxygen concentration, and other conditions of the body's internal environment.

Sensory receptors convert (or transduce) their information into impulses, which are then conducted along peripheral nerves to the CNS. There the signals are integrated. That is, they are brought together, creating sensations, adding to memory, or helping produce thoughts. Following integration, conscious or subconscious decisions are made and then acted upon by means of motor functions.

Neurons that conduct impulses from the CNS to responsive structures called *effectors* carry out the motor functions of the nervous system. These effectors are outside the nervous system and include muscles and glands whose actions are either controlled or modified by nerve activity. The motor portion of the PNS can be subdivided into the somatic and the autonomic nervous systems. The **somatic nervous system** communicates voluntary (conscious) instructions originating in the CNS to skeletal muscles, causing contraction. The **autonomic nervous system** communicates instructions from the CNS that control viscera, such as the heart and various glands, and thus causes involuntary subconscious actions.

PRACTICE

3 List the general functions of the nervous system.

11 Nervous System II
Divisions of the Nervous System

Falsely colored scanning electron micrograph (SEM) of the cell body of a single neuron of the human cerebral cortex—the outer gray matter of the brain (7,200×).

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Module 7: Nervous System

Learning Outcomes

After you have studied this chapter, you should be able to:

11.1 Introduction
1 Describe the relationship among the brain, brainstem, and spinal cord. (p. 390)

11.2 Meninges
2 Describe the coverings of the brain and spinal cord. (p. 391)

11.3 Ventricles and Cerebrospinal Fluid
3 Discuss the formation and function of cerebrospinal fluid. (p. 392)

11.4 Spinal Cord
4 Describe the structure of the spinal cord and its major functions. (p. 394)
5 Describe a reflex arc and reflex behavior. (p. 396)

11.5 Brain
6 Describe the development of the major parts of the brain and explain the functions of each part. (p. 403)
7 Distinguish among sensory, association, and motor areas of the cerebral cortex. (p. 407)
8 Discuss hemisphere dominance. (p. 410)
9 Explain the stages in memory storage. (p. 411)
10 Explain the functions of the limbic system and the reticular formation. (pp. 413 and 415)

11.6 Peripheral Nervous System
11 Distinguish between the major parts of the peripheral nervous system. (p. 417)
12 Describe the structure of a peripheral nerve and how its fibers are classified. (p. 418)
13 Identify the cranial nerves and list their major functions. (p. 420)
14 Explain how spinal nerves are named and their functions. (p. 423)

11.7 Autonomic Nervous System
15 Characterize the autonomic nervous system. (p. 430)
16 Distinguish between the sympathetic and the parasympathetic divisions of the autonomic nervous system. (p. 430)
17 Compare sympathetic and parasympathetic nerve pathways. (p. 430)
18 Explain how the autonomic neurotransmitters differently affect visceral effectors. (p. 435)

11.8 Life-Span Changes
19 Describe aging-associated changes in the nervous system. (p. 437)

LEARN PRACTICE ASSESS

Understanding Words

cephal-, head: enc*ephal*itis—inflammation of the brain.
chiasm-, cross: optic *chiasma*—X-shaped structure produced by the crossing over of optic nerve fibers.
flacc-, flabby: *flacc*id paralysis—paralysis characterized by loss of tone in muscles innervated by damaged axons.
funi-, small cord or fiber: *funi*culus—major nerve tract or bundle of myelinated axons within the spinal cord.
gangli-, swelling: *gangli*on—mass of neuron cell bodies.
mening-, membrane: *mening*es—membranous coverings of the brain and spinal cord.
plex-, interweaving: choroid *plex*us—mass of specialized capillaries associated with spaces in the brain.

Traumatic Brain Injury

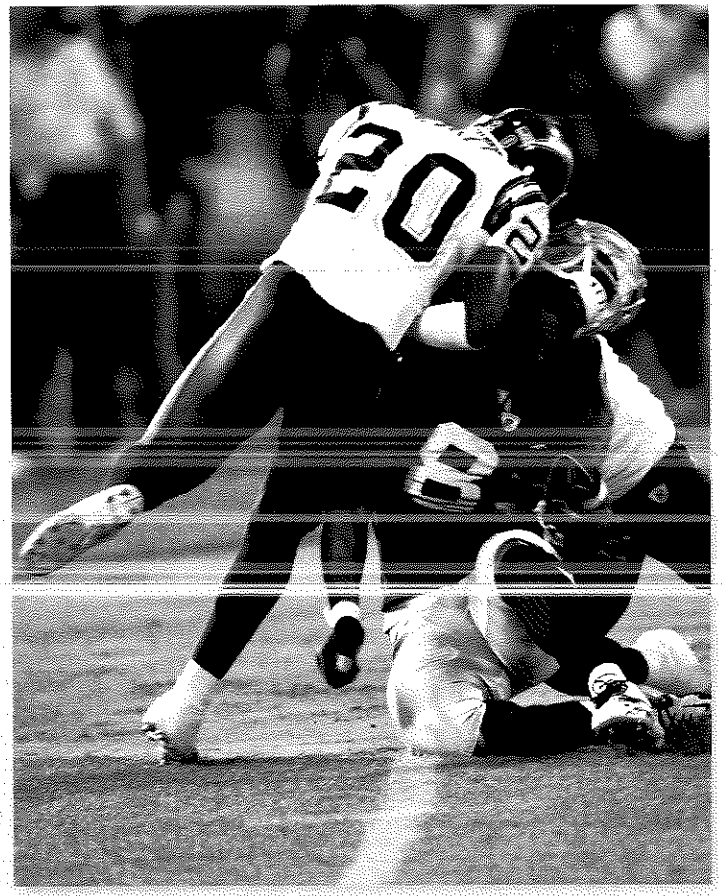
A traumatic brain injury (TBI) is partly defined by what it is not: it is not a birth defect or degenerative condition, but instead results from mechanical force such as from a fall, accident, attack, or sports-related injury. In the United States, more than 5 million people have such injuries, which are classified as mild, mild repetitive, or severe.

Mild TBI, also known as a concussion, produces loss of consciousness or altered mental status. Its effects are more psychological than neurological, and it does not appear to cause lasting damage. Symptoms include disturbed sleep, ringing in the ears, memory lapse, balance problems, irritability, and sensitivity to light and sounds. These physical symptoms are heightened if the person also suffers from depression or post-traumatic stress disorder (PTSD). Mild TBI may cause PTSD if, as the brain hits the skull, the injury generates a shearing force that impairs the prefrontal cortex's control of a region called the amygdala so that it becomes overactive. As a result, the person cannot let go of psychological trauma, which is the definition of PTSD.

A sports-related form of mild repetitive TBI is chronic traumatic encephalopathy (CTE). It results from many small injuries over time, rather than a single violent blow. The first report of the condition in a medical journal appeared in 2005, regarding a player for the National Football League, but in the 1980s CTE was recognized in boxers and wrestlers, in whom it was called "punch-drunk syndrome" and "dementia pugilistica." Symptoms typically begin years after the first of the repetitive head injuries associated with the sport. They include depression, impulsive and erratic behavior, headaches, dizziness, memory loss, dementia, and loss of executive function (ability to process information and make decisions). These difficulties stem from mechanical trauma to the cortex, hematomas (bleeding) in the subcortex, vasospasm, ischemia, and sudden movement of the skull, which tears axons. The brains of people who have died with CTE show changes characteristic of Alzheimer disease. At the University of North Carolina, researchers are studying CTE in football players who wear helmets with sensors to record the forces applied to their brains. The study so far shows that a college football player receives on average 950 hits to the head in a season.

Severe TBI is seen in combat situations, where the cause and pattern of damage is so distinct that it is called "blast-related brain injury." The damage results from a change in atmospheric pressure, a violent release of energy (sound, heat, pressure, or electromagnetic waves), and sometimes exposure to a neurotoxin released from the blast. Rocket-propelled grenades, improvised incendiary devices, and land mines are the primary causes of this most dangerous type of traumatic brain injury. The brain is initially jolted forward at a force exceeding 1,600 feet per second, and then is hit again as air in the cranium rushes forward.

A problem in treating blast-related brain injury is recognizing it swiftly, because symptoms may not appear until hours after the violent event. Whereas one soldier immediately after the blast might be blind or deaf or unable to move or speak, another soldier who has suffered similar injuries to the soft tissue of the brain might not show such effects until later. The effects of blast-related brain injury are lasting. Studies on veterans of the Vietnam War indicate injury-related cognitive decline years after the injury. ■



Chronic traumatic encephalopathy is a form of mild repetitive traumatic brain injury seen in football players. Studies in football players who wear helmets containing sensors indicate that a college athlete may receive a thousand or more damaging brain blows a year.

11.1 INTRODUCTION

The central nervous system (CNS) consists of the brain and the spinal cord. The **brain** is the largest and most complex part of the nervous system. It oversees many aspects of physiology, such as sensation and perception, movement, and thinking. The brain includes the two cerebral hemispheres, the diencephalon, the brainstem, and the cerebellum, all described in detail in section 11.5. The brain includes about one hundred billion (10^{11}) multipolar neurons and countless branches of the axons by which these neurons communicate with each other and with neurons elsewhere in the nervous system.

The brain connects to the spinal cord through the brainstem which allows two-way communication between them. The spinal cord, in turn, provides two-way communication between the CNS and the peripheral nervous system (PNS).

Bones, membranes, and fluid surround the organs of the CNS. More specifically, the brain lies in the cranial cavity of the skull, whereas the spinal cord occupies the vertebral canal in the vertebral column. Beneath these bony coverings, membranes called meninges, located between the bone and

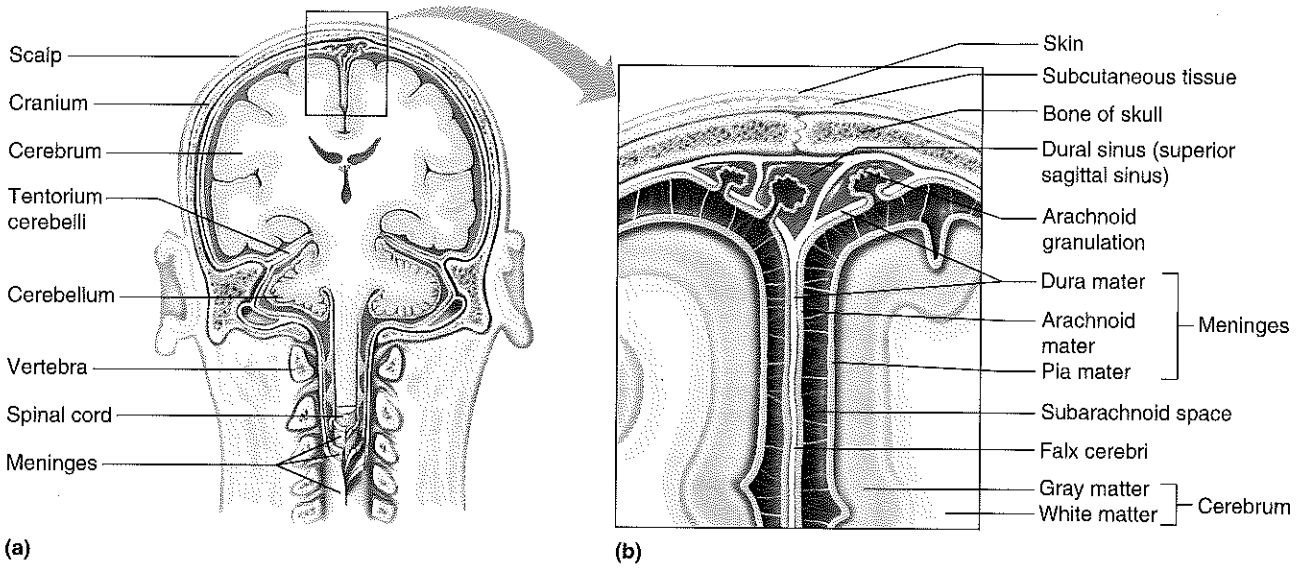


FIGURE 11.1 AP|R Meninges. (*a*) Membranes called meninges enclose the brain and spinal cord. (*b*) The meninges include three layers: dura mater, arachnoid mater, and pia mater.

the soft tissues of the nervous system, protect the brain and spinal cord (fig. 11.1*a*).

11.2 MENINGES

The meninges (sing., *meninx*) have three layers—dura mater, arachnoid mater, and pia mater (fig. 11.1*b*). The **dura mater** is the outermost layer. It is primarily composed of tough, white, dense connective tissue and contains many blood vessels and nerves. It attaches to the inside of the cranial cavity and forms the internal periosteum of the surrounding skull bones (see reference plate 13, p. 50).

In some regions, the dura mater extends inward between lobes of the brain and forms supportive and protective partitions (table 11.1). In other areas, the dura mater splits into two layers, forming channels called *dural sinuses,* shown in figure 11.1*b*. Venous blood flows through these channels as it returns from the brain to vessels leading to the heart.

The dura mater continues into the vertebral canal as a strong, tubular sheath that surrounds the spinal cord. It is attached to the cord at regular intervals by a band of pia mater (denticulate ligaments) that extends the length of the spinal cord on either side. The dural sheath terminates as a blind sac at the level of the second sacral vertebra, below the end of the spinal cord. The sheath around the spinal cord is not attached directly to the vertebrae but is separated by an *epidural space,* which lies between the dural sheath and the bony walls (fig. 11.2). This space contains blood vessels, loose connective tissue, and adipose tissue that pad the spinal cord.

TABLE **11.1** | Partitions of the Dura Mater

Partition	Location
Falx cerebelli	Separates the right and left cerebellar hemispheres
Falx cerebri	Extends downward into the longitudinal fissure, and separates the right and left cerebral hemispheres (fig. 11.1*b*)
Tentorium cerebelli	Separates the occipital lobes of the cerebrum from the cerebellum (fig. 11.1*a*)

A blow to the head may rupture some blood vessels associated with the brain, and the escaping blood may collect beneath the dura mater. This condition, called *subdural hematoma,* can increase pressure between the rigid bones of the skull and the soft tissues of the brain. Unless the accumulating blood is promptly evacuated, compression of the brain may lead to functional losses or even death.

The **arachnoid mater** is a thin, weblike membrane that does not have blood vessels and is located between the dura and pia maters. It spreads over the brain and spinal cord but generally does not dip into the grooves and depressions on their surfaces. Many thin strands extend from its undersurface and attach to the pia mater. A *subarachnoid space* between the arachnoid and pia maters contains the clear, watery **cerebrospinal fluid** (ser″ĕ-bro-spi′nal floo′id), or **CSF.**

The **pia mater** is thin and contains many nerves, as well as blood vessels that nourish the underlying cells of the brain and spinal cord. The pia mater is attached to the surfaces of these organs and follows their irregular contours, passing over the high areas and dipping into the depressions.

Meningitis, an inflammation of the meninges usually caused by bacterial or viral infection of the CSF, affects the arachnoid and pia maters and sometimes the dura mater, mostly in children. Complications include visual loss, hearing loss, paralysis, and intellectual disability. It may be fatal. Children are vaccinated against *Haemophilus influenza* type b, which was once the most common bacterial cause.

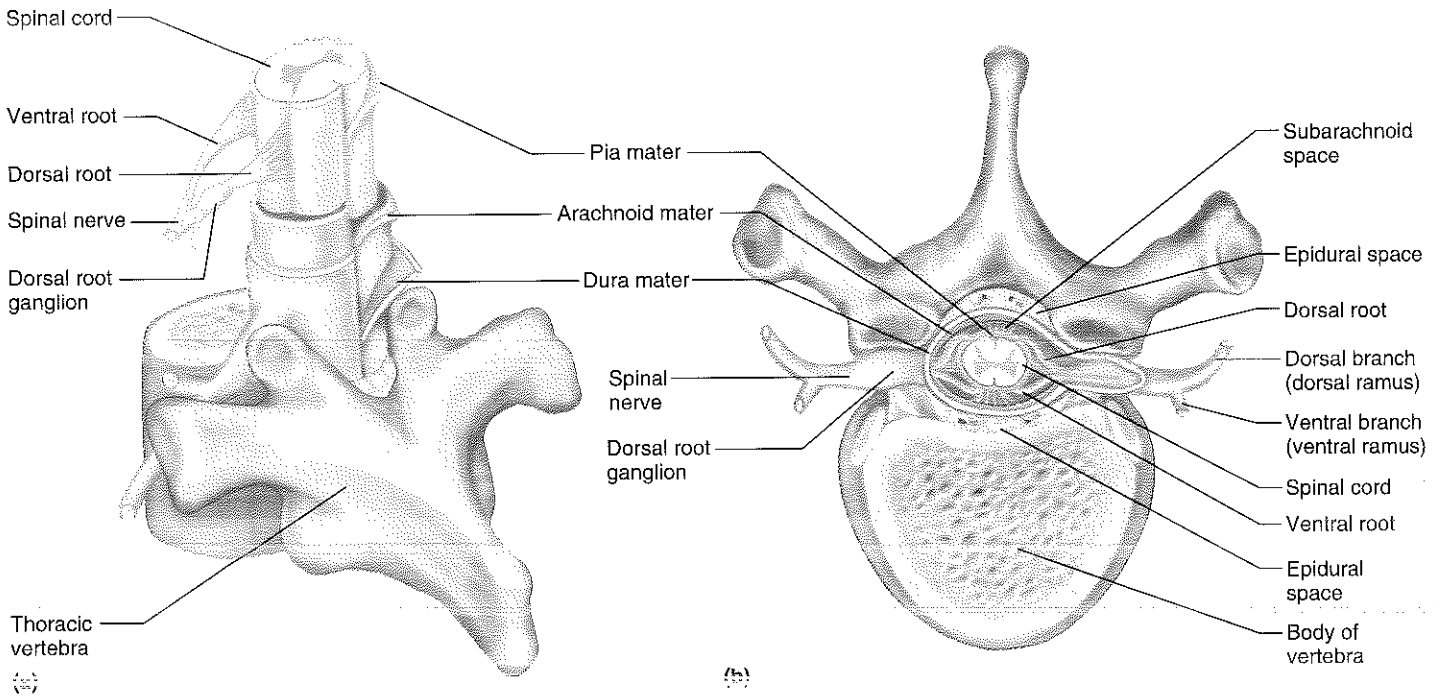


FIGURE 11.2 Meninges of the spinal cord. (*a*) The dura mater ensheathes the spinal cord. (*b*) Tissues forming a protective pad around the cord fill the epidural space between the dural sheath and the bone of the vertebra.

PRACTICE

1. Describe the meninges.
2. Name the layers of the meninges.
3. Explain the location of cerebrospinal fluid.

11.3 VENTRICLES AND CEREBROSPINAL FLUID

Four interconnected cavities called **ventricles** (ven'trĭ-klz) lie in the cerebral hemispheres and brainstem (fig. 11.3 and reference plates 13 and 14, p. 50). These spaces are continuous with the central canal of the spinal cord and are filled with CSF.

The two *lateral ventricles* are the largest. The first ventricle is in the left cerebral hemisphere and the second ventricle is in the right cerebral hemisphere. They extend anteriorly and posteriorly into the cerebral hemispheres.

A narrow space that constitutes the *third ventricle* is in the midline of the brain beneath the corpus callosum, which is a bridge of axons that links the two cerebral hemispheres. This ventricle communicates with the lateral ventricles through openings *(interventricular foramina)* in its anterior end.

The *fourth ventricle* is in the brainstem, just anterior to the cerebellum. A narrow canal, the *cerebral aqueduct* (aqueduct of Sylvius), connects it to the third ventricle and passes lengthwise through the brainstem. This ventricle is continuous with the central canal of the spinal cord and has openings in its roof that lead into the subarachnoid space of the meninges.

Tiny, reddish cauliflower-like masses of specialized capillaries from the pia mater, called **choroid plexuses** (ko'roid plek'sus-ez), secrete CSF. These structures project into the cavities of the ventricles (fig. 11.4). A single layer of specialized ependymal cells (see chapter 10, p. 370) joined closely by tight junctions covers the choroid plexuses. In much the same way that astrocytes provide a barrier between the blood and the brain interstitial fluid (blood-brain barrier), ependymal cells in the choroid plexuses block passage of water-soluble substances between the blood and the CSF (blood-CSF barrier). At the same time, the cells selectively transfer certain substances from the blood into the CSF by facilitated diffusion and transfer other substances by active transport (see chapter 3, pp. 101 and 103), regulating CSF composition.

Most CSF forms in the lateral ventricles, from where it slowly circulates into the third and fourth ventricles and into the central canal of the spinal cord. It also enters the subarachnoid space of the meninges by passing through the wall of the fourth ventricle near the cerebellum.

Humans secrete nearly 500 milliliters of CSF daily. However, only about 140 milliliters are in the nervous system at any time, because CSF is continuously reabsorbed into the blood through tiny, fingerlike structures called *arachnoid granulations* that project from the subarachnoid space into the blood-filled dural sinuses (see fig. 11.4).

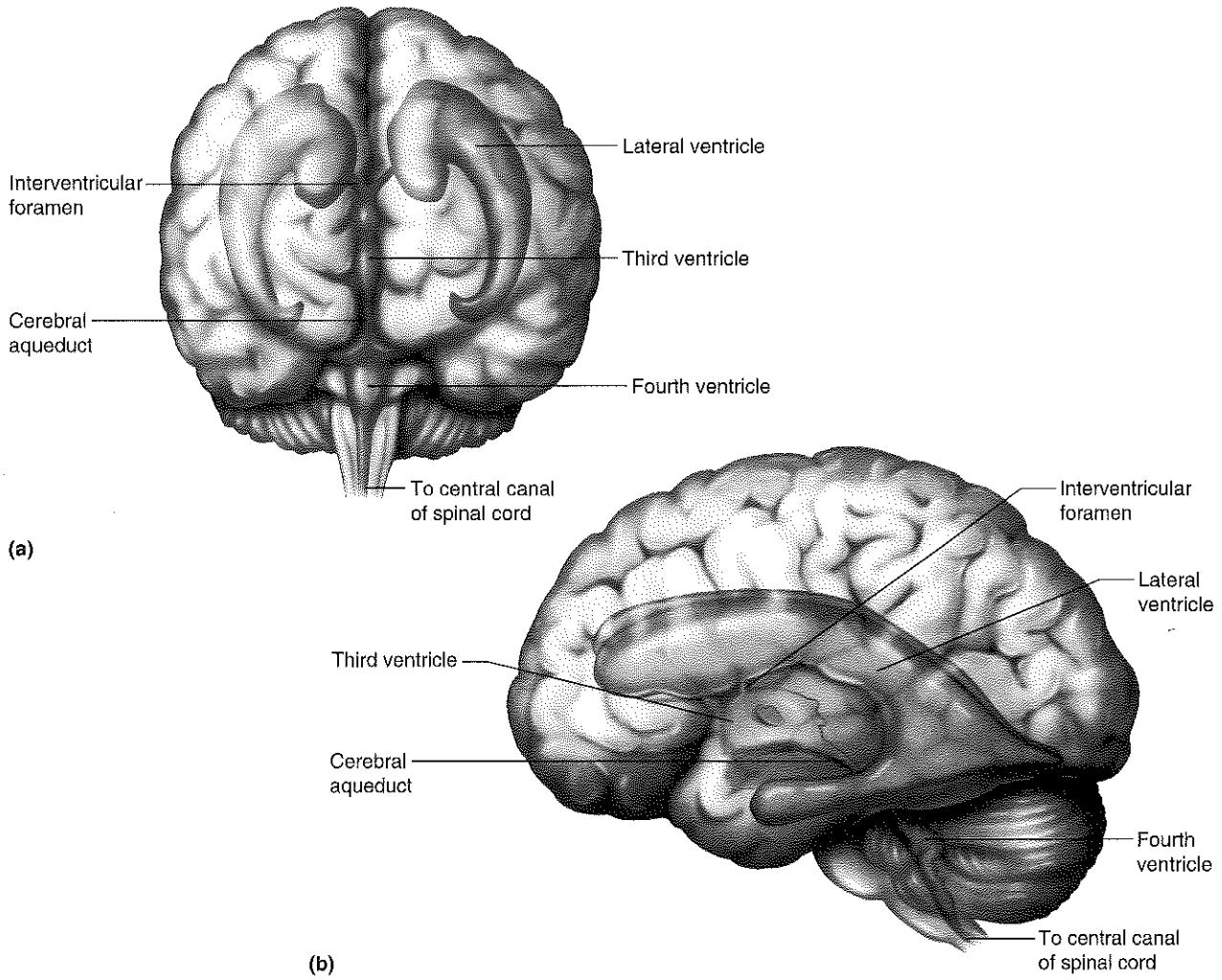


FIGURE 11.3 AP|R Ventricles in the brain. (*a*) Anterior view of the ventricles in the cerebral hemispheres and brainstem. (*b*) Lateral view.

CSF is a clear, somewhat viscid liquid that differs in composition from the fluid that leaves the capillaries in other parts of the body. Specifically, it contains a greater concentration of sodium and lesser concentrations of glucose and potassium than do other extracellular fluids. Its function is nutritive as well as protective. CSF helps maintain a stable ionic concentration in the CNS and provides a pathway to the blood for waste. The CSF may also supply information about the internal environment to autonomic centers in the hypothalamus and brainstem, because the fluid forms from blood plasma and therefore its composition reflects changes in body fluids. Clinical Application 11.1 discusses the pressure that CSF generates.

CSF occupies the subarachnoid space of the meninges, so it completely surrounds the brain and spinal cord. In effect, these organs float in the fluid. The CSF protects the brain and spinal cord by absorbing forces that might otherwise jar and damage their delicate tissues.

PRACTICE

4 Where are the ventricles of the brain located?

5 How does CSF form?

6 Describe the pattern of CSF circulation.

The term "muscle fiber" refers to an entire muscle cell, as discussed in chapter 9 (p. 295). The term "fiber" is also used in discussing the nervous system, but here it does not refer to an entire cell. A "nerve fiber" is another term for the axon of a neuron.

11.4 SPINAL CORD

The **spinal cord** is a slender column of nervous tissue that is continuous with the brain and extends downward through the vertebral canal. The spinal cord originates where

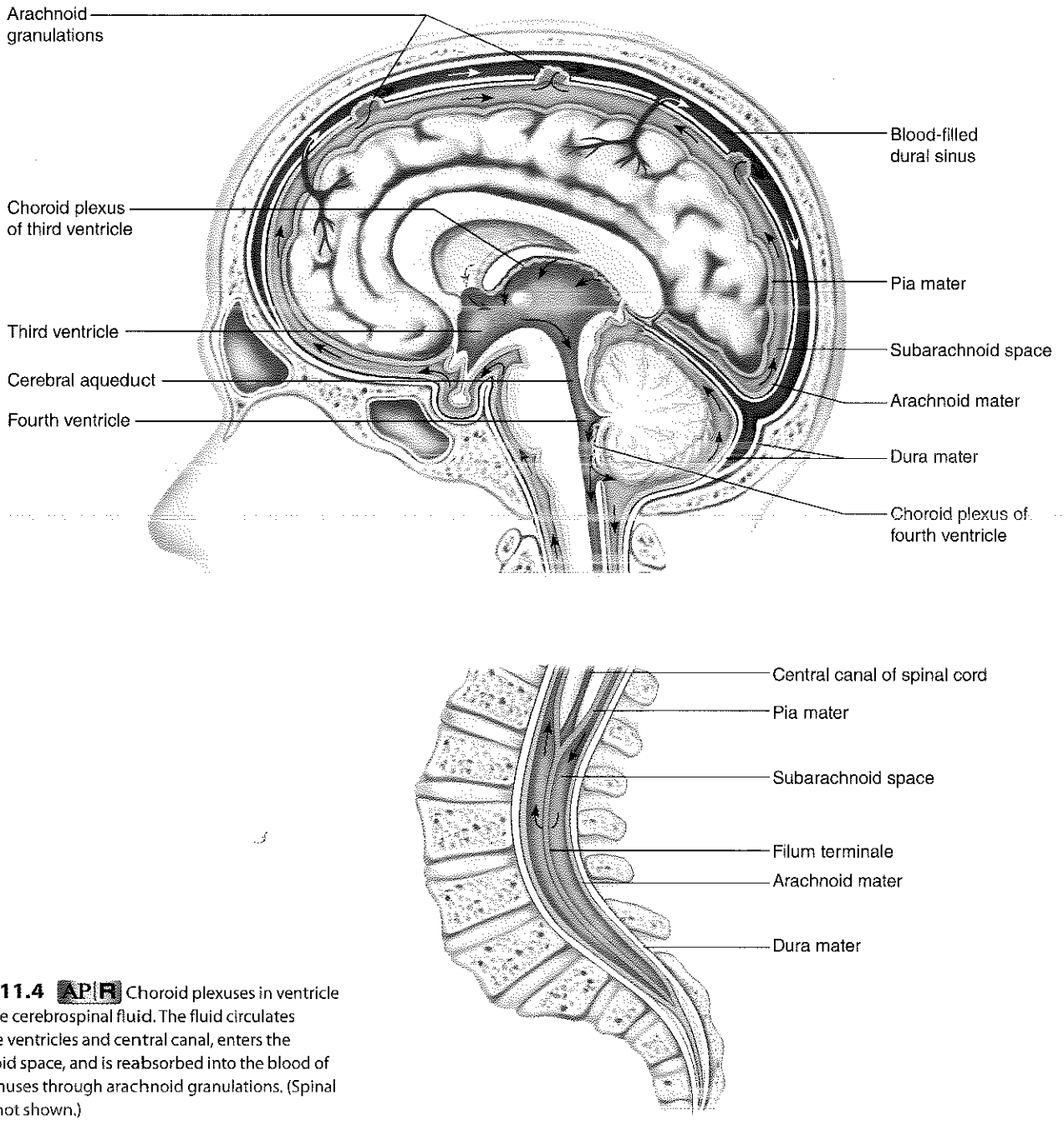


FIGURE 11.4 AP|R Choroid plexuses in ventricle walls secrete cerebrospinal fluid. The fluid circulates through the ventricles and central canal, enters the subarachnoid space, and is reabsorbed into the blood of the dural sinuses through arachnoid granulations. (Spinal nerves are not shown.)

nervous tissue leaves the cranial cavity at the level of the foramen magnum (see reference plate 15, p. 51). The cord tapers to a point and terminates near the intervertebral disc that separates the first and second lumbar vertebrae (fig. 11.5*a*).

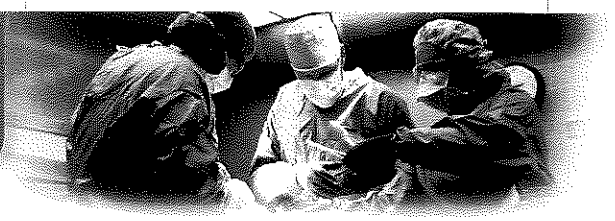
Structure of the Spinal Cord

The spinal cord consists of thirty-one segments, each of which gives rise to a pair of **spinal nerves.** These nerves branch to various body parts and connect them with the CNS.

In the neck region, a thickening in the spinal cord, called the *cervical enlargement,* supplies nerves to the upper limbs. A similar thickening in the lower back, the *lumbar enlargement,* gives off nerves to the lower limbs. Just inferior to the lumbar enlargement, the spinal cord tapers to a structure called the *conus medullaris.* From this tip, nervous tissue, including axons of both motor and sensory neurons, extends downward to become spinal nerves at the remaining lumbar and sacral levels. A thin cord of connective tissue originating from these spinal nerves descends to the upper surface of the coccyx. This cord, called the *filum terminale* (fig. 11.5*b*), and the spinal nerves below the conus medullaris form a structure that resembles a horse's tail, called the *cauda equina.*

Two grooves, a deep *anterior median fissure* and a shallow *posterior median sulcus,* extend the length of the spinal cord, dividing it into right and left halves. A cross section of the cord

11.1 CLINICAL APPLICATION



Cerebrospinal Fluid Pressure

Cerebrospinal fluid (CSF) is secreted and reabsorbed continuously, so the fluid pressure in the ventricles remains relatively constant. However, infection, a tumor, or a blood clot can interfere with the fluid's circulation, increasing pressure in the ventricles (intracranial pressure or ICP). The pressure can collapse cerebral blood vessels, slowing blood flow. Brain tissues forced against the skull may be injured.

A *lumbar puncture* (spinal tap) measures CSF pressure. A physician inserts a fine, hollow needle into the subarachnoid space between the third and fourth or between the fourth and fifth lumbar vertebrae—below the end of the spinal cord (fig. 11A). An instrument called a *manometer* measures the pressure of the fluid, which is usually about 130 millimeters of water (10 millimeters of mercury). At the same time, samples of CSF may be withdrawn and tested for abnormal constituents. Red blood cells in the CSF, for example, may indicate a hemorrhage in the central nervous system (CNS). A temporary drain inserted into the subarachnoid space between the fourth and fifth lumbar vertebrae can relieve pressure.

In a fetus or infant whose cranial sutures have not yet united, increasing ICP may enlarge the cranium, causing *hydrocephalus*, or "water on the brain" (fig. 11B). A shunt to relieve hydrocephalus drains fluid away from the cranial cavity and into the digestive tract, where it is either reabsorbed into the blood or excreted. ■

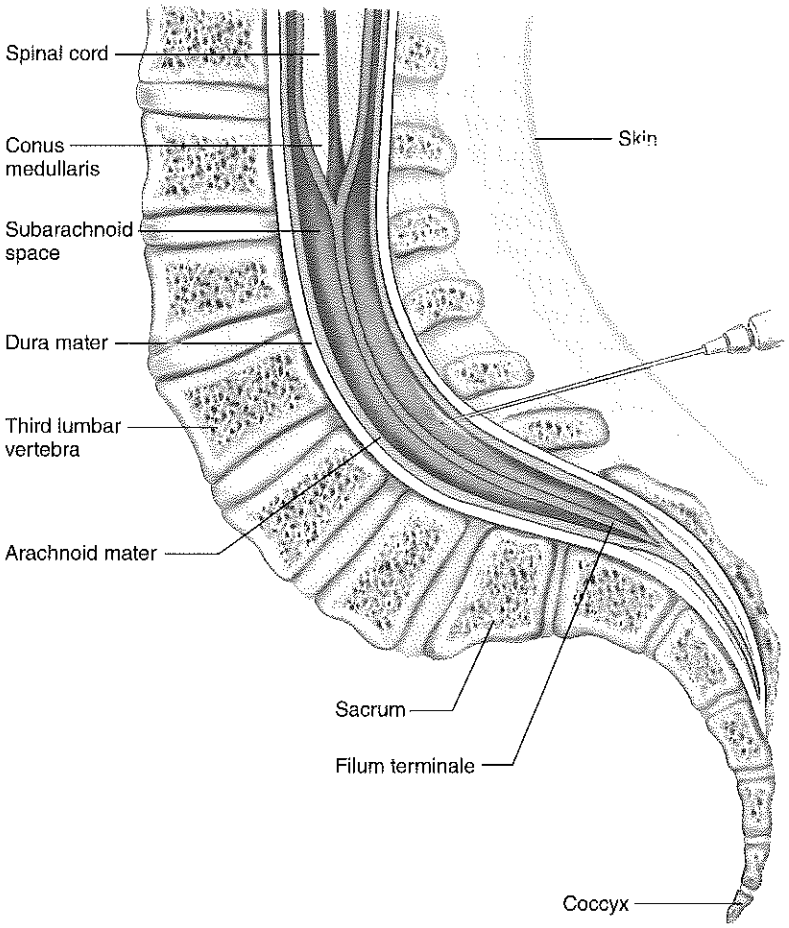


FIGURE 11A A lumbar puncture is performed by inserting a fine needle, usually below the fourth lumbar vertebra, and withdrawing a sample of CSF from the subarachnoid space. (For clarity, spinal nerves are not shown.)

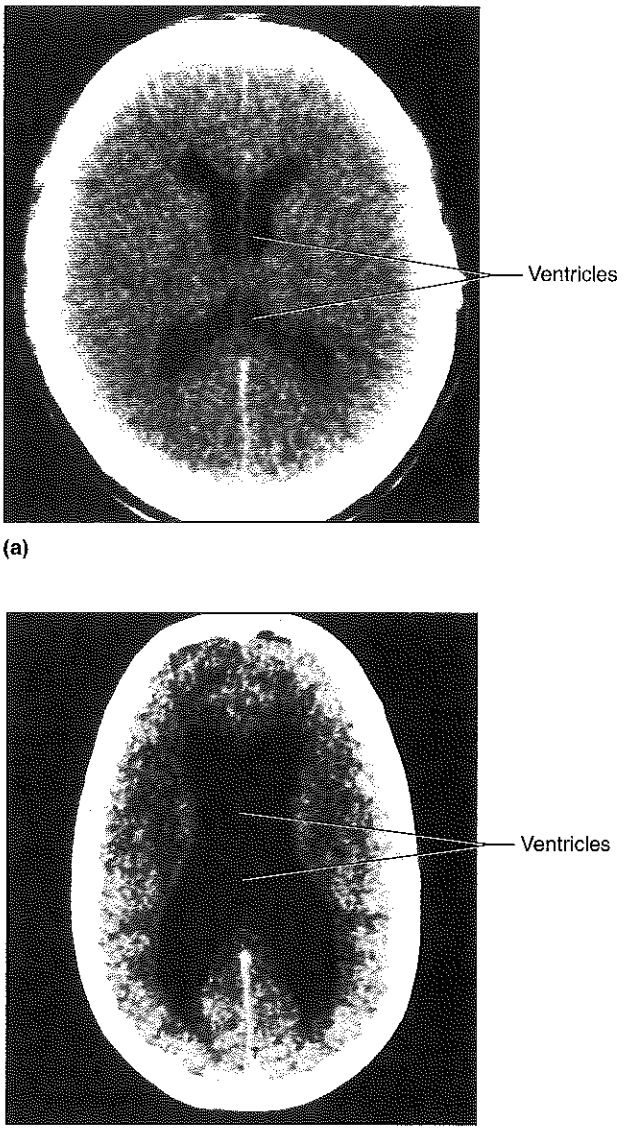


FIGURE 11B CT scans of the human brain. (*a*) Normal ventricles. (*b*) Ventricles enlarged by accumulated fluid.

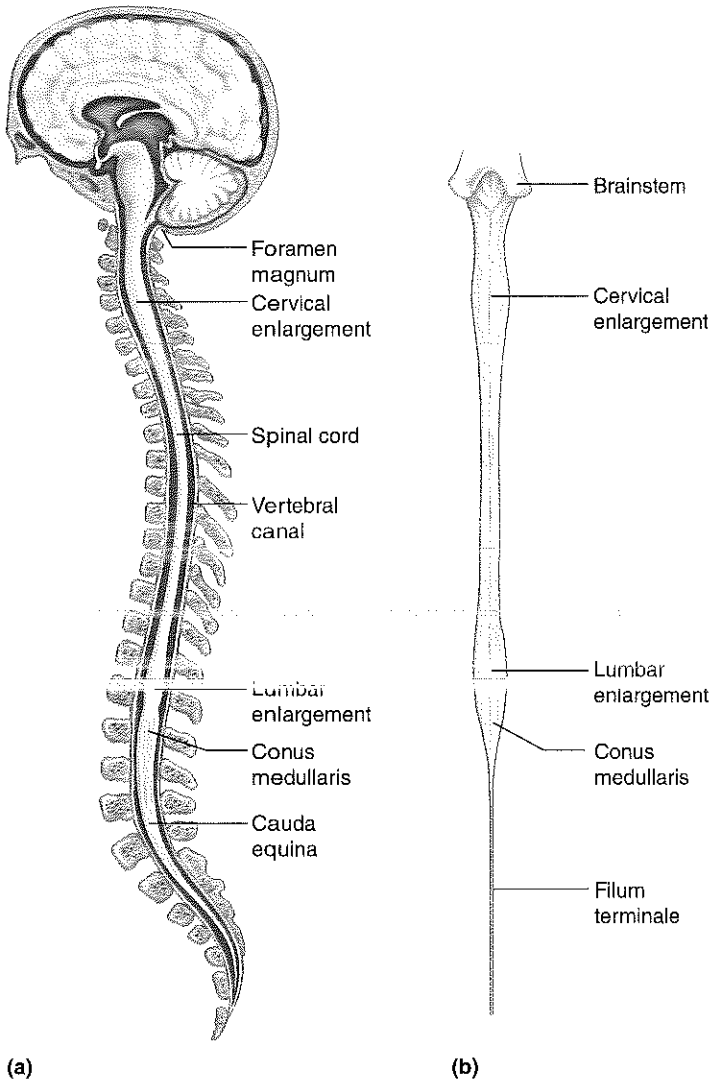


FIGURE 11.5 AP R Spinal cord. (*a*) The spinal cord begins at the level of the foramen magnum. (*b*) Posterior view of the spinal cord with the spinal nerves removed.

(fig. 11.6) reveals that it consists of white matter surrounding a core of gray matter. The pattern the gray matter produces roughly resembles a butterfly with its wings outspread. These posterior and anterior "wings" of gray matter are called the *posterior horns* and the *anterior horns*, respectively. Between them on either side in some regions is a protrusion of gray matter called the *lateral horn*. Motor neurons with relatively large cell bodies in the anterior horns (anterior horn cells) give rise to axons that pass out through spinal nerves to various skeletal muscles. However, the majority of neurons in the gray matter are interneurons (see chapter 10, p. 368).

A horizontal bar of gray matter in the middle of the spinal cord, the *gray commissure*, connects the wings of the gray matter on the right and left sides. This bar surrounds the **central canal**, which is continuous with the ventricles of the brain and contains CSF. The central canal is prominent during embryonic development, but it becomes almost microscopic in adulthood.

The gray matter divides the white matter of the spinal cord into three regions on each side—the *anterior, lateral,* and *posterior funiculi*. Each funiculus, or column, consists of longitudinal bundles of myelinated nerve fibers that compose major nerve pathways called **tracts.**

Functions of the Spinal Cord

The spinal cord has two main functions. It is a center for spinal reflexes, and it is a conduit for impulses to and from the brain.

Reflex Arcs

Communication in the nervous system combines a series of action potentials along the axon of a neuron and synaptic transmission between that neuron and a postsynaptic cell. Two or more neurons involved in such communication constitute a nerve pathway. The simplest of the nerve pathways begins with a sensory receptor and ends with an effector, and involves as few as two neurons. Such a nerve pathway is called a reflex (re'fleks).

All reflexes share the same basic components, which together are known as a reflex arc, as figure 11.7*a* shows. A reflex arc begins with a **sensory receptor** at the dendritic end of a sensory neuron. Impulses on these sensory neurons enter the CNS and constitute a sensory or afferent limb of the reflex. The CNS is a processing center. Afferent neurons may synapse with interneurons, which may in turn connect with other parts of the CNS. Afferent neurons or interneurons ultimately connect with motor neurons, whose fibers pass outward from the CNS to effectors. (It may help to remember that **eff**erent neurons control **eff**ector organs.)

Reflexes occur throughout the CNS. Those that involve the spinal cord are called spinal reflexes and reflect the simplest level of CNS function. Figure 11.7*b* shows the general components of a spinal reflex.

Reflex Behavior

Reflexes are automatic responses to changes (stimuli) inside or outside the body. They help maintain homeostasis by controlling many involuntary processes such as heart rate, breathing rate, blood pressure, and digestion. Reflexes also carry out the automatic actions involved in swallowing, sneezing, coughing, and vomiting.

The *patellar reflex* (knee-jerk reflex) is an example of a simple monosynaptic reflex, so-called because it uses only two neurons—a sensory neuron communicating directly to a motor neuron. Striking the patellar ligament just below the patella initiates this reflex. The quadriceps femoris muscle group, attached to the patella by a tendon, is pulled slightly, stimulating stretch receptors in the muscle group. These receptors, in turn, trigger impulses that pass along the peripheral process (see fig. 10.7, p. 368) of the axon of a unipolar sensory neuron, continuing along the central process of the axon into the lumbar region of the spinal cord. In the spinal cord, the sensory axon synapses with a motor neuron. An impulse is then triggered on the motor neuron and is conducted along its axon to

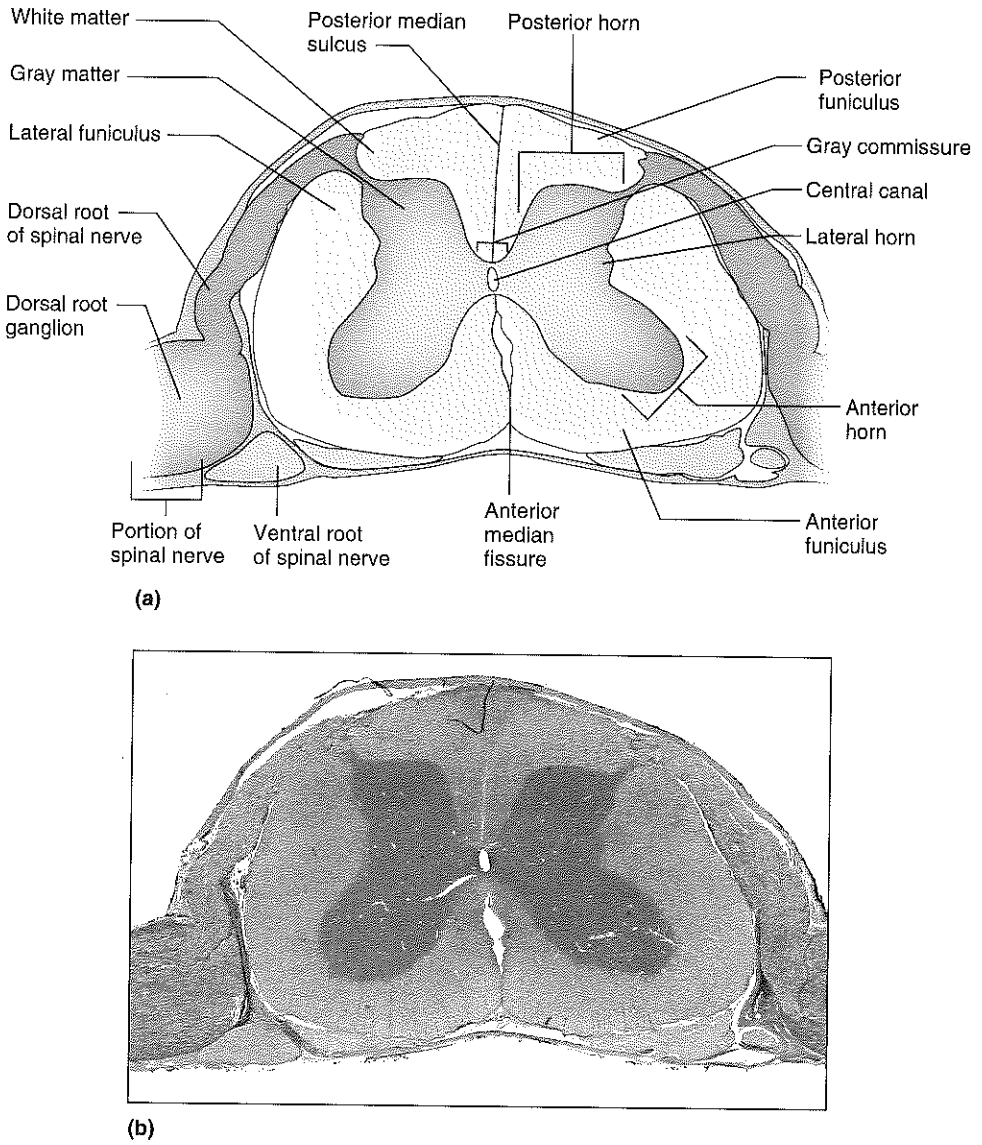


FIGURE 11.6 AP|R Spinal cord. (*a*) A cross section of the spinal cord. (*b*) Identify the parts of the spinal cord in this micrograph (7.5×).

Q: *Where would you expect to find the cell bodies of neurons in the above figure?*

Answer can be found in Appendix G on page 938.

the neuromuscular junctions in that motor unit of the quadriceps femoris. The muscle fibers involved respond by contracting, and the reflex is completed as the leg extends (fig. 11.8).

The patellar reflex helps maintain an upright posture. For example, if a person is standing still and the knee begins to bend in response to gravity, the quadriceps femoris is stretched, the reflex is triggered, and the leg straightens again. Adjustments within the stretch receptors keep the reflex responsive at different muscle lengths.

Another type of reflex, called a *withdrawal reflex* (fig. 11.9), happens when a person touches something painful (and potentially damaging), as in stepping on a tack. Activated skin receptors send impulses to the spinal cord along the axons of sensory neurons. There the sensory neurons synapse with interneurons of a reflex center, which in turn synapse with motor neurons. The motor neurons activate fibers in the flexor muscles of the leg and thigh, which contract in response, pulling the foot away from the painful stimulus. At the same time, some of the incoming sensory impulses stimulate interneurons that inhibit the action of the antagonistic extensor muscles (reciprocal innervation). This inhibition of antagonists allows the flexor muscles to effectively withdraw the affected part (fig. 11.10).

While flexor muscles on the affected side (ipsilateral side) contract, the flexor muscles of the limb on the other side (contralateral side) are inhibited. Furthermore, the extensor muscles on the contralateral side contract, helping to support the body weight shifted to that side. This phenomenon, called a *crossed extensor reflex*, is due to interneuron pathways in the spinal cord that allow sensory impulses

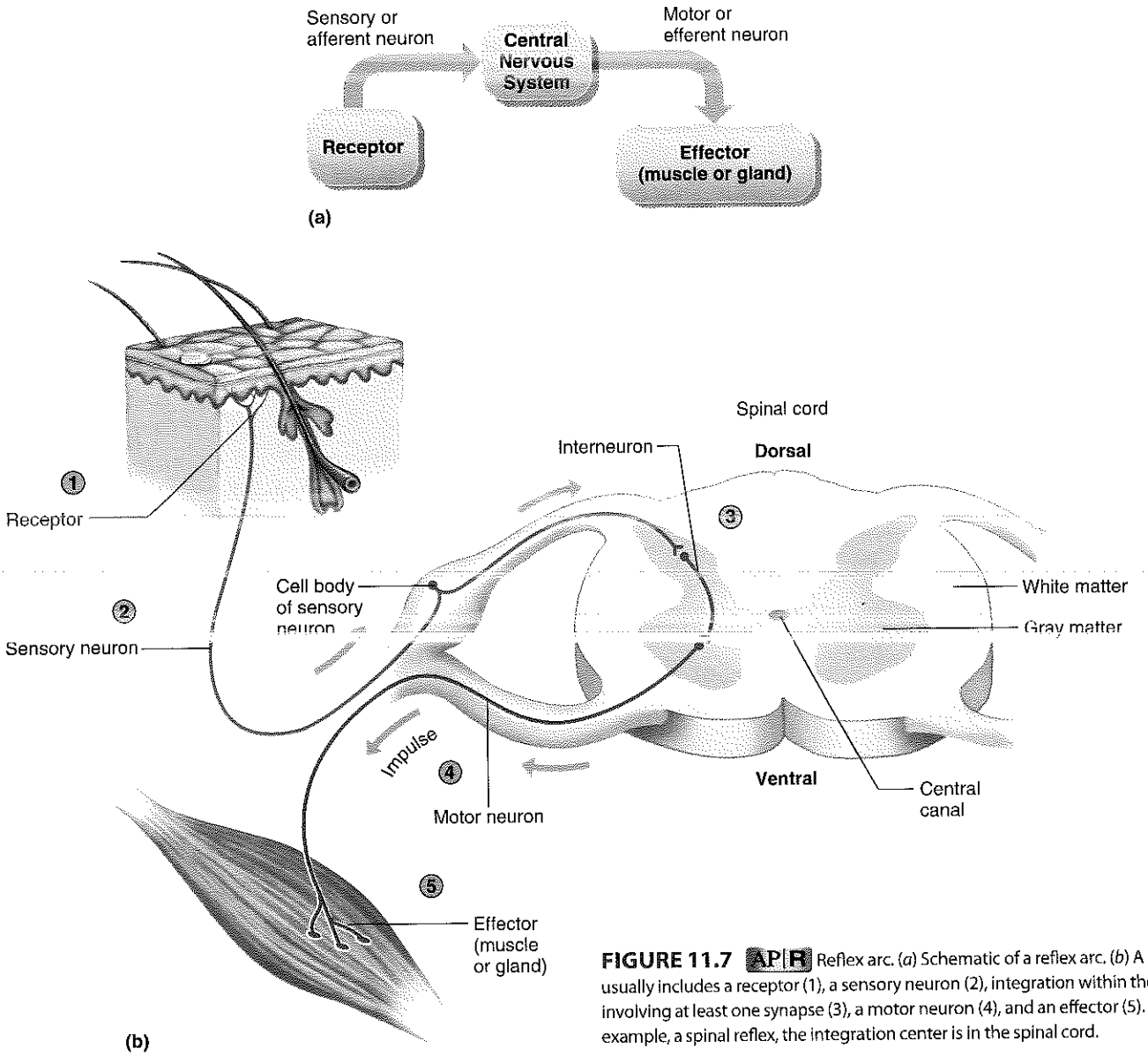


FIGURE 11.7 AP|R Reflex arc. (*a*) Schematic of a reflex arc. (*b*) A reflex arc usually includes a receptor (1), a sensory neuron (2), integration within the CNS involving at least one synapse (3), a motor neuron (4), and an effector (5). In this example, a spinal reflex, the integration center is in the spinal cord.

arriving on one side of the cord to pass across to the other side and produce an opposite effect (fig. 11.10). Reflexes like these can be found at different levels of the spinal cord and in the brain, depending on which body parts are involved.

Concurrent with the withdrawal reflex, other interneurons in the spinal cord carry sensory impulses upward to the brain. The person becomes aware of the experience and may feel pain.

A withdrawal reflex protects because it prevents or limits tissue damage when a body part touches something potentially harmful. Table 11.2 summarizes the components of a reflex arc. Clinical Application 11.2 discusses some familiar reflexes.

PRACTICE

7 What is a nerve pathway?

8 Describe a reflex arc.

9 Define *reflex*.

10 Describe the actions that are part of a withdrawal reflex.

TABLE **11.2** | Parts of a Reflex Arc

Part	Description	Function
Receptor	The receptor end of a dendrite or a specialized receptor cell in a sensory organ	Sensitive to a specific type of internal or external change
Sensory neuron	Dendrite, cell body, and axon of a sensory neuron	Conducts an impulse from the receptor into the brain or spinal cord
Interneuron	Dendrite, cell body, and axon of a neuron within the brain or spinal cord	Serves as processing center; conducts an impulse from the sensory neuron to its synapse with a motor neuron
Motor neuron	Dendrite, cell body, and axon of a motor neuron	Conducts an impulse from the brain or spinal cord out to the synapse with an effector
Effector	A muscle or gland	Responds to stimulation by the motor neuron and produces the reflex or behavioral action

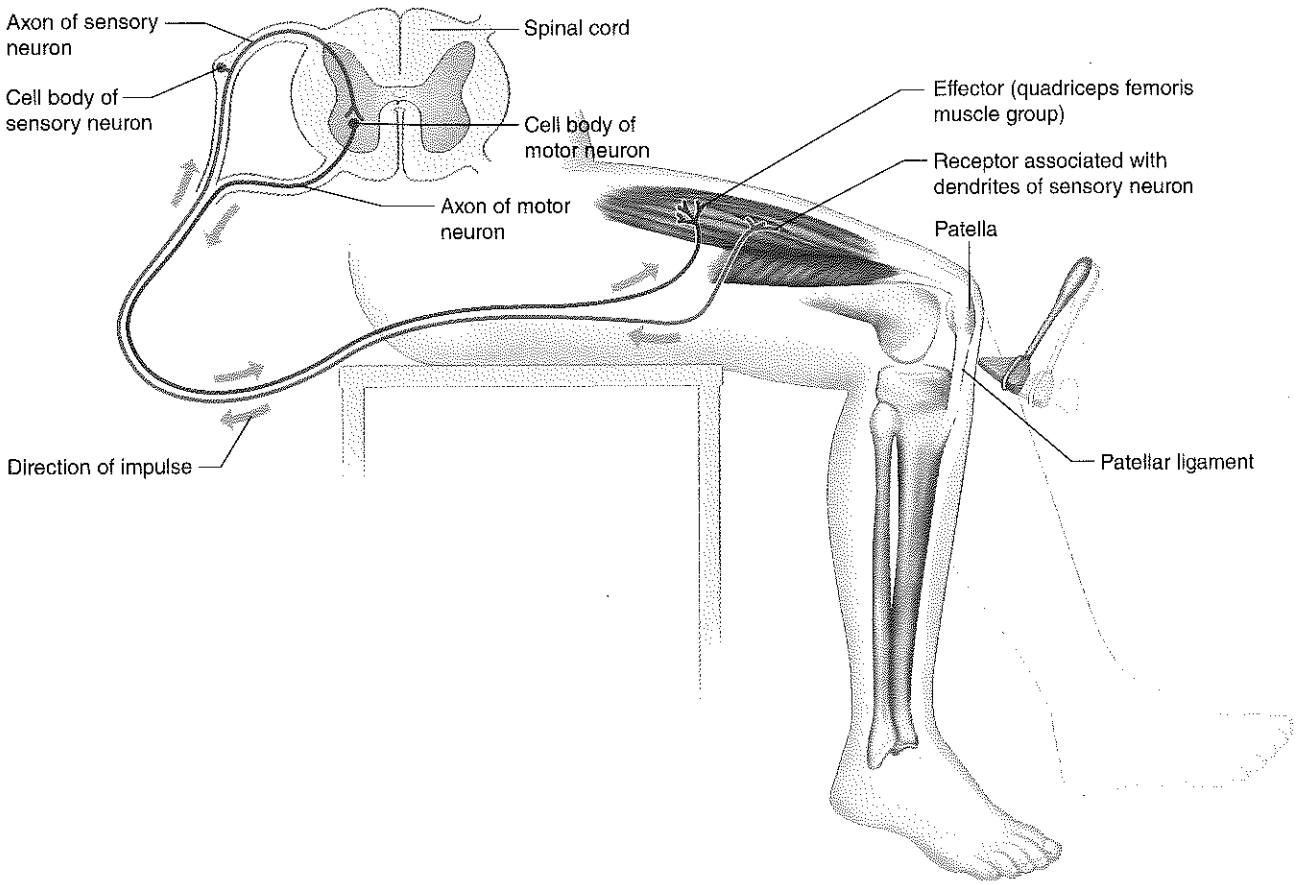


FIGURE 11.8 The patellar reflex involves two neurons—a sensory neuron and a motor neuron. Note the single synapse in the spinal cord.

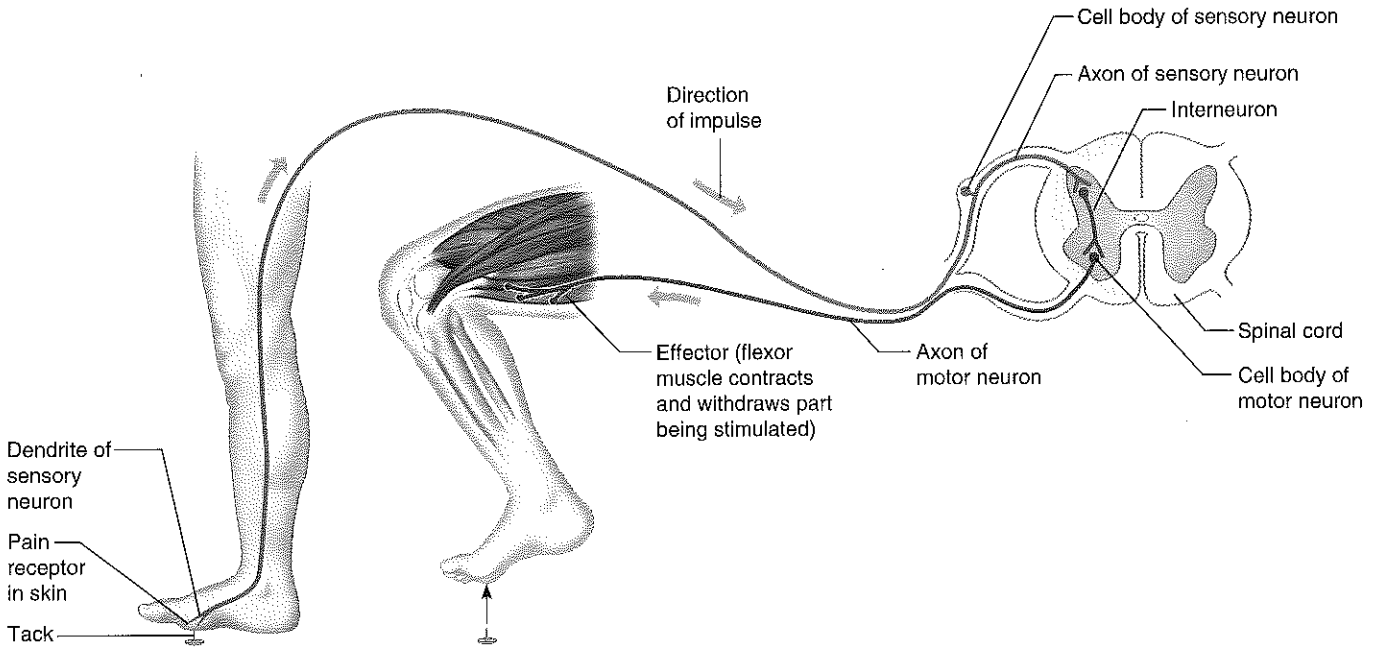


FIGURE 11.9 A withdrawal reflex involves a sensory neuron, an interneuron, and a motor neuron.

11.2 CLINICAL APPLICATION

Uses of Reflexes

Normal reflexes require and reflect normal neuron functions. Therefore, reflexes are commonly used to assess the condition of the nervous system. An anesthesiologist, for instance, initiates a reflex in a patient being anesthetized to determine how the anesthetic drug is affecting nerve functions. A physician assessing a patient with injury to the nervous system observes reflexes to judge the location and extent of damage.

Injury to any component of a reflex arc alters its function. For example, stroking the sole of the foot normally initiates a *plantar reflex,* which flexes the foot and toes. Damage to certain nerve pathways (corticospinal tract) may trigger an abnormal response called the *Babinski reflex,* which is a dorsiflexion that extends the great toe upward and fans apart the smaller toes. If the injury is minor, the response may consist of plantar flexion with failure of the great toe to flex, or plantar flexion followed by dorsiflexion. The Babinski reflex is normally present in infants up to the age of twelve months and may reflect immaturity in their corticospinal tracts.

Other reflexes that may be tested during a neurological examination include the following:

1. The *biceps-jerk reflex* is elicited by extending a person's forearm at the elbow. The examiner places a finger on the inside of the extended elbow over the tendon of the biceps muscle and taps the finger. The biceps contracts in response, flexing at the elbow.
2. The *triceps-jerk reflex* is elicited by flexing a person's forearm at the elbow and tapping the short tendon of the triceps muscle close to its insertion near the tip of the elbow. The muscle contracts in response, extending the elbow.
3. The *abdominal reflexes* are a response to stroking the skin of the abdomen. For example, a dull pin drawn from the sides of the abdomen upward toward the midline and above the umbilicus contracts the abdominal muscles underlying the skin, and the umbilicus moves toward the stimulated region.
4. The *ankle-jerk reflex* is elicited by tapping the calcaneal tendon just above its insertion on the calcaneus. Contraction of the gastrocnemius and soleus muscles causes plantar flexion.
5. The *cremasteric reflex* is elicited in males by stroking the upper inside of the thigh. In response, contracting muscles elevate the testis on the same side. ■

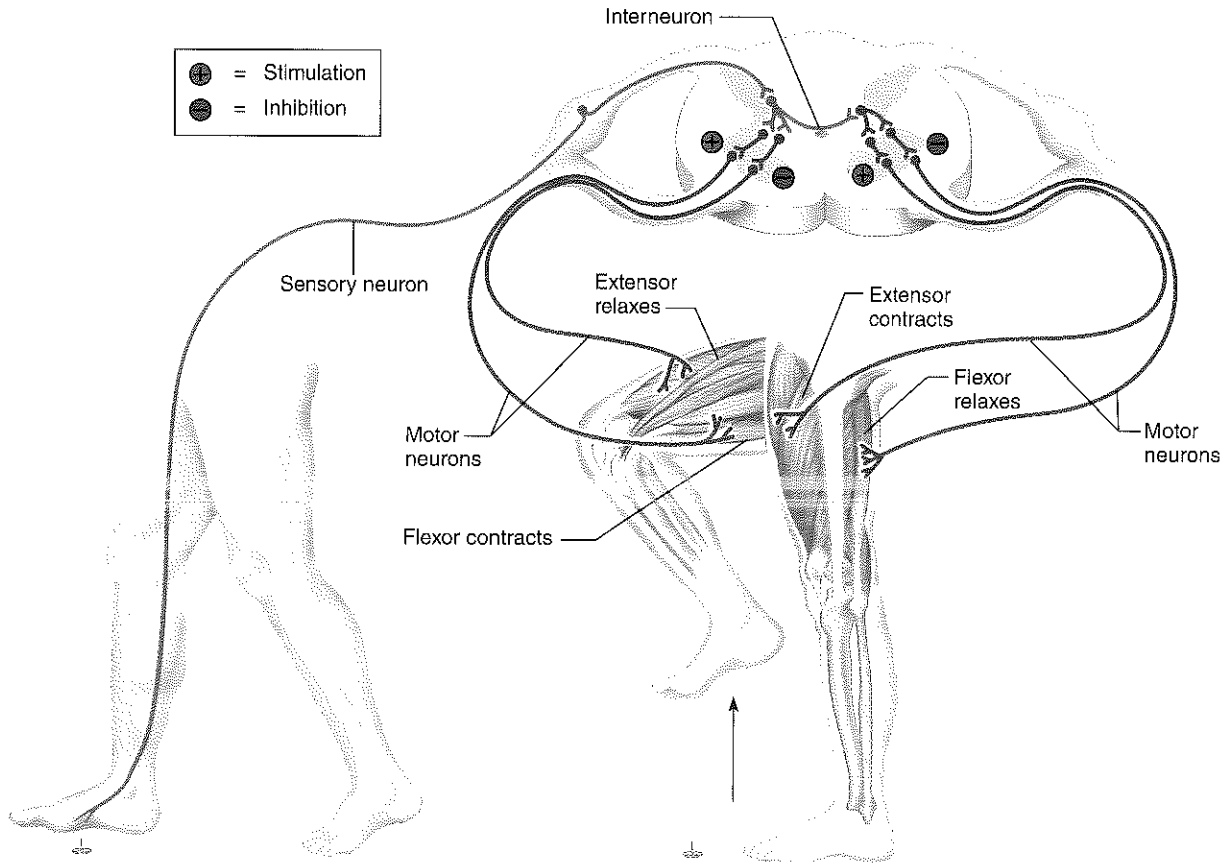


FIGURE 11.10 When the flexor muscle on one side is stimulated to contract in a withdrawal reflex, the extensor muscle on the opposite side also contracts. This helps to maintain balance.

Ascending and Descending Tracts

The tracts of the spinal cord together with the spinal nerves provide a two-way communication system between the brain and body parts outside the nervous system. The spinal tracts that conduct sensory impulses to the brain are called **ascending tracts;** those that conduct motor impulses from the brain to motor neurons reaching muscles and glands are **descending tracts.**

The ascending and descending tracts are comprised of axons. Typically, all the axons in a given tract originate from neuron cell bodies in the same part of the nervous system and end together in some other part. Many of the names that identify nerve tracts reflect these common origins and terminations. For example, a *spinothalamic tract* begins in the spinal cord and carries sensory impulses associated with the sensations of pain and touch to the thalamus of the brain (part of the diencephalon). A *corticospinal tract* originates in the cortex of the brain (the outer portion of the cerebrum) and carries motor impulses on so-called *upper motor neurons* downward through the spinal cord. These impulses control *lower motor neurons* whose cell bodies are in the anterior horn and whose axons lead to skeletal muscles.

Among the major ascending tracts of the spinal cord are the following:

1. **Fasciculus gracilis** (fah-sik'u-lus gras'il-is) and **fasciculus cuneatus** (ku'ne-at-us) are tracts in the posterior funiculi of the spinal cord (fig. 11.11). Their fibers conduct sensory impulses from the skin, muscles, tendons, and joints to the brain, where they are interpreted as sensations of touch, pressure, and body movement.

   At the base of the brain in an area called the medulla oblongata most of the fasciculus gracilis and fasciculus cuneatus fibers cross (decussate) from one side to the other—that is, those ascending on the left side of the spinal cord pass across to the right side, and vice versa. As a result, the impulses originating from sensory receptors on the left side of the body reach the right side of the brain, and those originating on the right side of the body reach the left side of the brain (fig. 11.12).
2. The lateral and anterior **spinothalamic** (spi"no-thah-lam'ik) **tracts** are in the lateral and anterior funiculi, respectively (see fig. 11.11). The lateral tracts conduct impulses from various body regions to the brain and give rise to sensations of pain and temperature. Impulses conducted on fibers of the anterior tracts are interpreted as touch and pressure. Impulses in these tracts cross over in the spinal cord (fig. 11.12).
3. The posterior and anterior **spinocerebellar** (spi"no-ser"ĕ-bel'ar) **tracts** lie near the surface in the lateral funiculi of the spinal cord (see fig. 11.11). Fibers in the posterior tracts remain uncrossed, whereas those in the anterior tracts cross over in the medulla. Impulses conducted on their fibers originate in the muscles of the lower limbs and trunk and then travel to the cerebellum. These impulses coordinate muscular movements.

The major descending tracts of the spinal cord include the following:

1. The lateral and anterior **corticospinal** (kor"tĭ-ko-spi'nal) **tracts** occupy the lateral and anterior funiculi, respectively (see fig. 11.11). Most of the fibers of the lateral tracts cross over in the lower medulla oblongata.

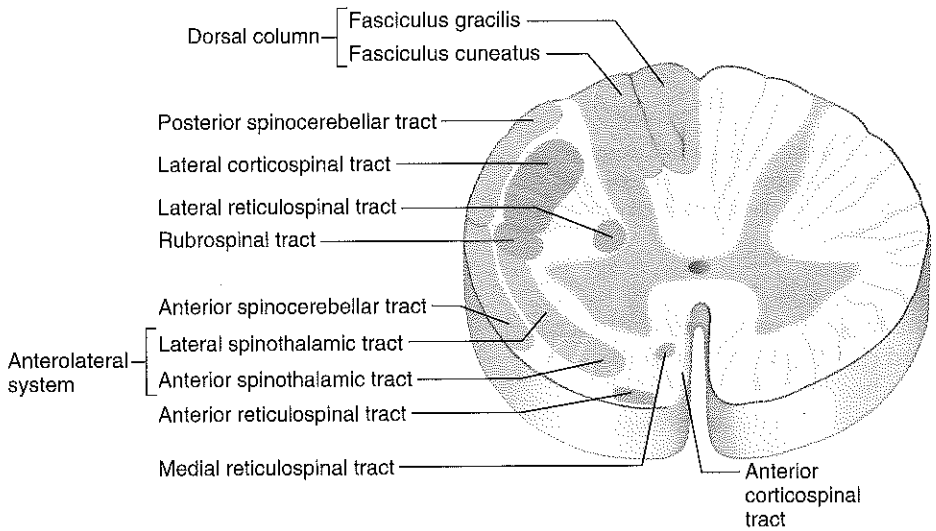


FIGURE 11.11 Major ascending and descending tracts in a cross section of the spinal cord. Ascending tracts are in pink, descending tracts in light brown. (Tracts are shown only on one side.) The pattern varies with the level of the spinal cord. This pattern is representative of the midcervical region.

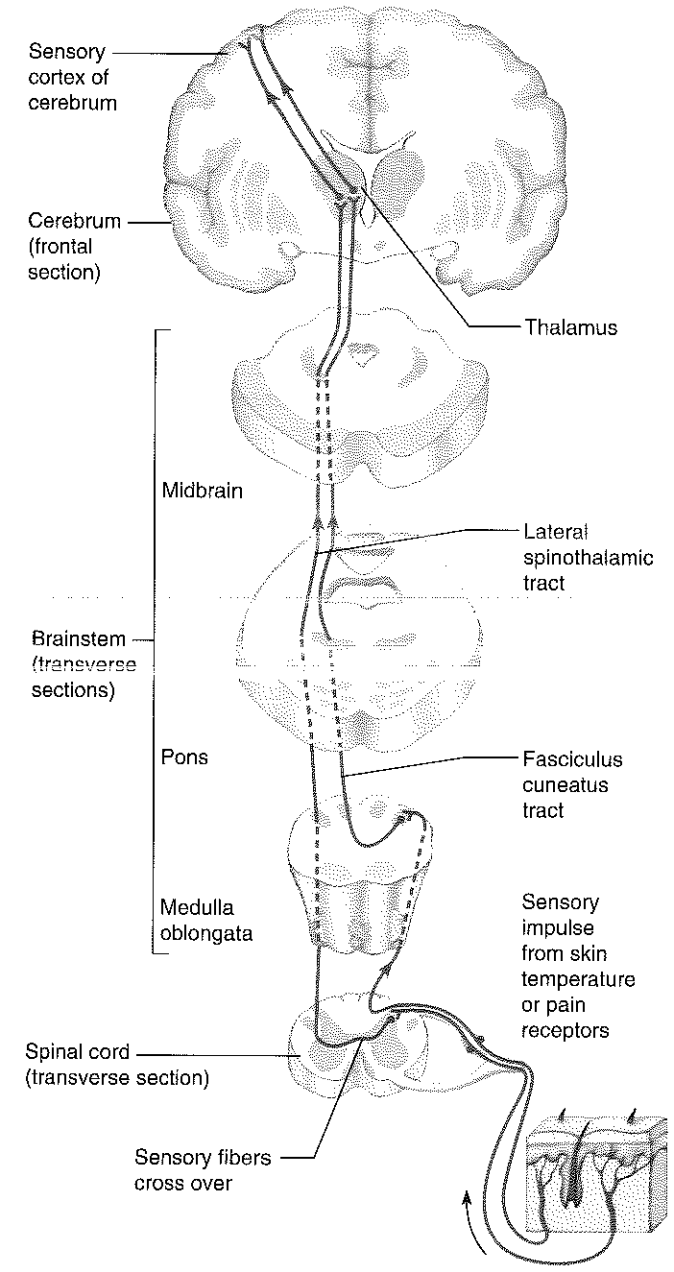


FIGURE 11.12 Sensory impulses originating in skin touch receptors ascend in the fasciculus cuneatus tract and cross over in the medulla of the brain. Pain and temperature information ascends in the lateral spinothalamic tract, which crosses over in the spinal cord.

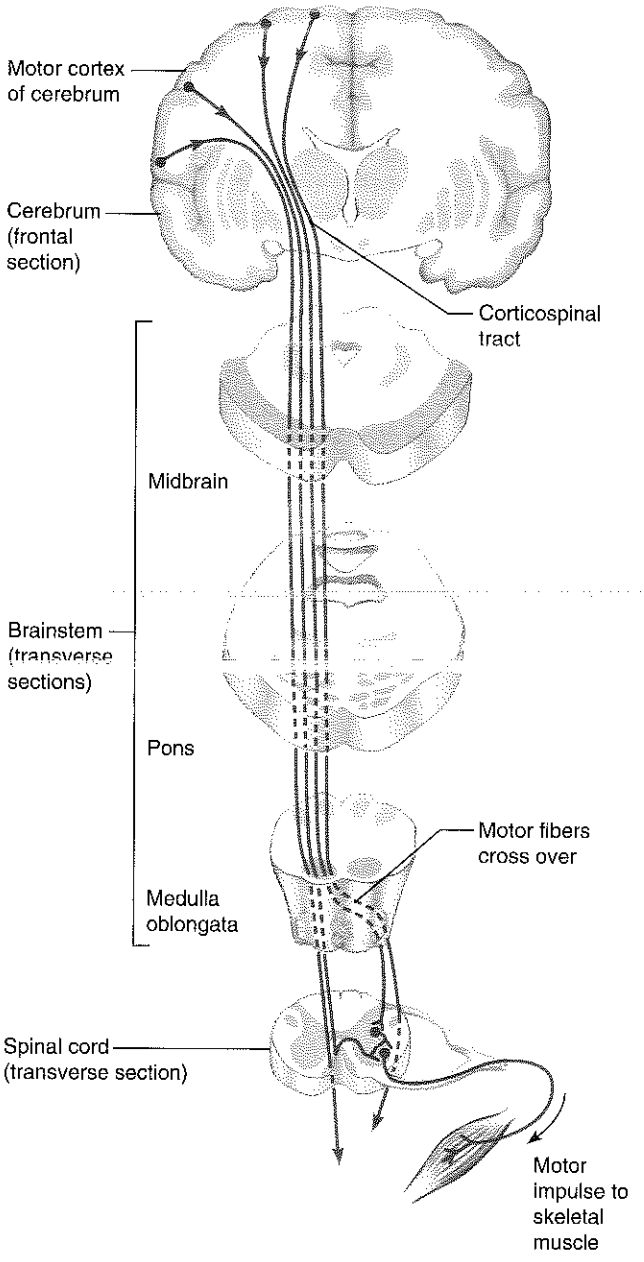


FIGURE 11.13 Most fibers of the corticospinal tract originate in the cerebral cortex, cross over in the medulla, and descend in the spinal cord, where they synapse with neurons whose fibers lead to spinal nerves supplying skeletal muscles. Some fibers cross over in the spinal cord.

Some fibers of the anterior tracts cross over at various levels of the spinal cord (fig. 11.13). Axons in the corticospinal tracts conduct motor impulses from the brain and synapse either directly or through interneurons with lower motor neurons, whose axons continue through spinal nerves to various skeletal muscles. Thus, they carry instructions that control voluntary movements.

The corticospinal tracts are sometimes called *pyramidal tracts* after the pyramid-shaped regions in the medulla oblongata through which they pass. Other descending tracts are called *extrapyramidal tracts*, and they include the reticulospinal and rubrospinal tracts.

2. The lateral **reticulospinal** (rĕ-tik″u-lo-spi′nal) **tracts** are in the lateral funiculi, whereas the anterior and medial reticulospinal tracts are in the anterior funiculi (see fig. 11.11). Some fibers in the lateral tracts cross over, whereas others remain uncrossed. Those of the anterior and medial tracts remain uncrossed. Motor impulses conducted on the reticulospinal tracts originate in the

brain and control muscular tone and activity of sweat glands.

3. The fibers of the **rubrospinal** (roo"bro-spi'nal) **tracts** cross over in the brain and pass through the lateral funiculi (see fig. 11.11). They conduct impulses from the brain to synapses with lower motor neurons, and help to coordinate muscle actions.

Table 11.3 summarizes the nerve tracts of the spinal cord. Clinical Application 11.3 describes injuries to the spinal cord.

A hemi-lesion of the spinal cord (severed on one side) affecting the corticospinal and spinothalamic tracts can cause Brown-Séquard syndrome. Ascending tracts cross over at different levels, so the injured side of the body becomes paralyzed and loses touch sensation. The other side of the body retains movement but loses sensations of pain and temperature.

PRACTICE

11 Describe the structure of the spinal cord.

12 What are ascending and descending tracts?

13 What is the consequence of fibers crossing over?

14 Name the major tracts of the spinal cord, and list the types of impulses each conducts.

TABLE 11.3 | Nerve Tracts of the Spinal Cord

Tract	Location	Function
Ascending Tracts		
1. Fasciculus gracilis and fasciculus cuneatus	Posterior funiculi	Conduct sensory impulses associated with the senses of touch, pressure, and body movement from skin, muscles, tendons, and joints to the brain
2. Spinothalamic tracts (lateral and anterior)	Lateral and anterior funiculi	Conduct sensory impulses associated with the senses of pain, temperature, touch, and pressure from various body regions to the brain
3. Spinocerebellar tracts (posterior and anterior)	Lateral funiculi	Conduct sensory impulses required for the coordination of muscle movements from muscles of the lower limbs and trunk to the cerebellum
Descending Tracts		
1. Corticospinal tracts (lateral and anterior)	Lateral and anterior funiculi	Conduct motor impulses associated with voluntary movements from the brain to skeletal muscles
2. Reticulospinal tracts (lateral, anterior, and medial)	Lateral and anterior funiculi	Conduct motor impulses associated with the maintenance of muscle tone and the activity of sweat glands from the brain
3. Rubrospinal tracts	Lateral funiculi	Conduct motor impulses associated with muscular coordination from the brain

Amyotrophic lateral sclerosis (ALS , Lou Gehrig's, or motor neuron disease) may begin with garbled speech, clumsiness, sudden fatigue, or limb weakness. Fasciculations (muscle twitches) that resemble moving ropes beneath the skin may prompt the person to seek medical attention. Because ALS is a diagnosis of exclusion, identifying it may take a year or more. About 10 percent of cases are inherited, due to mutations in any of several genes.

ALS affects the upper and lower parts of the body, and progresses faster if symptoms begin in the face or neck. Usually the battle is lost two to five years following diagnosis, typically from respiratory failure. Using assistive breathing devices and a drug, Riluzole, can extend life. The mind is often spared—one patient wrote a novel in his last months, and another remained a brilliant songwriter.

In ALS, motor neurons degenerate in the spinal cord, brainstem, and the cerebral cortex. ALS may be due to an inability of the motor neurons or associated astrocytes to counter buildup of oxygen free radicals. Using cellular reprogramming techniques (see the Chapter 3 opening vignette, p. 84), researchers are studying how ALS begins, which may lead to new treatments. A stem cell treatment is in clinical trials.

11.5 BRAIN

The brain contains nerve centers associated with sensory functions and is responsible for sensations and perceptions. It issues motor commands to skeletal muscles and carries on higher mental functions, such as memory and reasoning. It also contains centers that coordinate muscular movements, as well as centers and nerve pathways that regulate visceral activities. In addition to overseeing the function of the entire body, the brain provides characteristics such as personality.

Brain Development

The basic structure of the brain reflects the way it forms during early (embryonic) development. It begins as the neural tube that gives rise to the CNS. The portion that becomes the brain has three major cavities, or vesicles, at one end—the *forebrain* (prosencephalon), *midbrain* (mesencephalon), and *hindbrain* (rhombencephalon) (fig. 11.14). Later, the forebrain divides into anterior and posterior portions (telencephalon and diencephalon, respectively), and the hindbrain partially divides into two parts (metencephalon and myelencephalon). The resulting five cavities persist in the mature brain as the fluid-filled *ventricles* and the tubes that connect them. Cells of the tissue surrounding the spaces differentiate into the structural and functional regions of the brain.

The wall of the anterior portion of the forebrain gives rise to the *cerebrum* and *basal nuclei*, whereas the posterior portion forms a section of the brain called the *diencephalon*. The region the midbrain produces continues to be called the *midbrain* in the adult structure, and the hindbrain gives rise

11.3 CLINICAL APPLICATION

Spinal Cord Injuries

Thousands of people sustain spinal cord injuries each year. Treatment for spinal cord injury begins as soon as help arrives at the accident scene. Emergency health-care workers establish and maintain the person's ability to breathe, then use a rigid neck collar and carrying board to immobilize the person for transport. In the emergency department, a steroid drug, methylprednisolone, is given within the first 8 hours to minimize inflammation. Surgery may be done to remove bone fragments. Continuing immobilization is crucial because damage continues over days. During this time, the vertebrae are compressed and may break-killing many neurons. Dying neurons release calcium ions, which activate tissue-degrading enzymes. Then white blood cells arrive and produce inflammation that can destroy healthy as well as damaged neurons. Axons tear, myelin coatings are stripped off, and vital connections between neurons and muscle fibers are lost. The tissue cannot regenerate. By the third day, a complete neurological exam and MRIs are done.

The severity of a spinal cord injury depends on the extent and location of damage. Normal spinal reflexes require two-way communication between the spinal cord and the brain. A complete transection (damage through a cross section of the cord) injures nerve pathways, depressing the cord's reflex activities in sites below the injury. At the same time, sensations and muscle tone diminish in the parts that the affected fibers innervate. This condition, called spinal shock, may last for days or weeks, although normal reflex activity may eventually return. If axons are severed, some of the cord's functions may be permanently lost.

Less severe injuries to the spinal cord, such as from a blow to the head, whiplash, or rupture of an intervertebral disc, can compress or distort the cord (fig. 11C). Pain, weakness, and muscular atrophy may develop in the regions the damaged nerve fibers supply. A spinal cord injury increases risk of secondary problems. These include difficulty breathing (if the injury is above the fifth cervical vertebra), development of pneumonia, formation of blood clots, low blood pressure, an irregular heartbeat, pressure ulcers, spasticity, and impaired bowel, bladder, and sexual function.

The two most common causes of spinal cord injury are accidents in the workplace and motor vehicle accidents. Third most common are sports injuries. A spinal cord injury may result from a sudden and unexpected movement. For example, one man suffered a severe spinal cord injury after a powerful wave knocked him down while he was standing in just a foot of water at a shoreline. Regardless of the cause, if nerve fibers in ascending tracts are cut, sensations arising from receptors below the level of the injury are lost. Damage to descending tracts results in loss of motor functions below the level of the injury. For example, if the right lateral corticospinal tract is severed in the neck near the first cervical vertebra, control of the voluntary muscles in the left upper and lower limbs is lost, paralyzing them (hemiplegia). Problems of this type in fibers of the descending tracts produce *upper motor neuron syndrome,* characterized by *spastic paralysis* in which muscle tone increases, with little atrophy of the muscles.

Injury to motor neurons in the anterior horns of the spinal cord results in *lower motor neuron syndrome.* It produces *flaccid paralysis,* a total loss of muscle tone and reflex activity, and the muscles atrophy.

Basic research is exploring ways to limit damage after a spinal cord injury and stimulate regeneration. Studies are identifying molecules in the extracellular matrix (see Clinical Application 5.1, p. 162) and in myelin that inhibit axon regeneration in the CNS and might serve as drug targets, and finding growth factors and other neurotrophins that might promote regeneration. Several clinical trials are investigating the use of stem cells to treat spinal cord injury. These include stem cells taken from a patient's own bone marrow as well as oligodendrocyte progenitor cells derived from embryonic stem cells. The oligodendrocyte progenitors can produce myelin and release neurotrophic factors that may enhance survival of neurons. ■

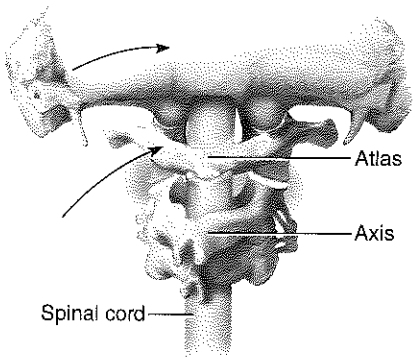


FIGURE 11C A dislocation of the atlas may cause a compression injury to the spinal cord.

to the *cerebellum, pons,* and *medulla oblongata* (fig. 11.15 and table 11.4). Together, the midbrain, pons, and medulla oblongata comprise the **brainstem** (brān'stem), by which the brain attaches to the spinal cord.

On a cellular level, the brain develops as specific neurons attract others by secreting growth factors. In the embryo and fetus, the brain overgrows, and then apoptosis (programmed cell death) destroys excess cells.

Structure of the Cerebrum

The **cerebrum** (ser'ē-brum), which develops from the anterior portion of the forebrain, is the largest part of the mature brain. It consists of two large masses, or **cerebral hemispheres** (ser'ē-bral hem'i-sfērz), which are essentially mirror images of each other (fig. 11.16 and reference plate 9, p. 47). A broad, flat bundle of axons called the **corpus callosum** connects the cerebral hemispheres. A layer of dura mater called the *falx cerebri* separates them (see fig. 11.1*b*).

Many ridges or convolutions, called **gyri** (ji'ri) (sing., *gyrus*), separated by grooves, mark the cerebrum's surface. Generally, a shallow to somewhat deep groove is called a **sulcus** (sul'kus; pl. *sulci,* sul'si), and a very deep groove is called a **fissure.** The pattern of these elevations and depressions is complex, but is similar in all normal brains. For example, a *longitudinal fissure* separates the right and left cerebral hemispheres; a *transverse fissure* separates the cerebrum from the cerebellum; and sulci divide each hemisphere into lobes (see figs. 11.15 and 11.16).

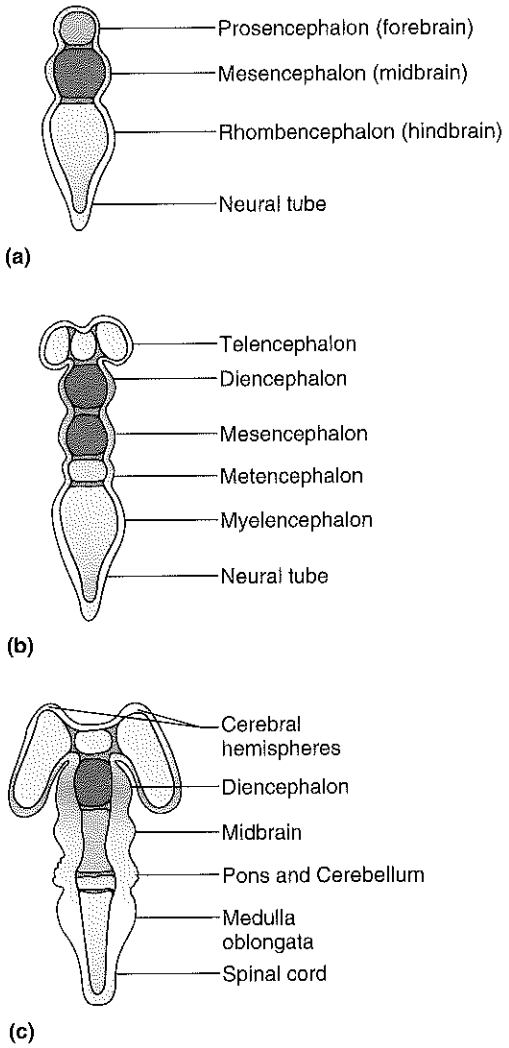


FIGURE 11.14 Brain development. (*a*) The brain develops from a tubular structure with three cavities. (*b*) The cavities persist as the ventricles and their interconnections. (*c*) The wall of the tube gives rise to various regions of the brain, brainstem, and spinal cord.

A fetus or newborn with *anencephaly* has a face and lower brain structures but lacks most higher brain structures. A newborn with this anomaly survives only a day or two.

Anencephaly is a type of neural tube defect (NTD). It occurs at about the twenty-eighth day of prenatal development, when a sheet of tissue that normally folds to form the neural tube, which develops into the CNS, remains open at the top. In *spina bifida*, an opening is farther down the neural tube, causing paralysis from that point downward. In some cases surgery, before or shortly after birth, can partially correct spina bifida. Taking folic acid supplements just before and during pregnancy can lower the risk of an NTD.

In a disorder called *lissencephaly* ("smooth brain"), a newborn has a smooth cerebral cortex, completely lacking convolutions. Absence of a protein early in prenatal development prevents certain neurons from migrating in the brain, which blocks formation of convolutions. The child is profoundly disabled intellectually, with frequent seizures and other neurological problems.

TABLE 11.4 | Structural Development of the Brain

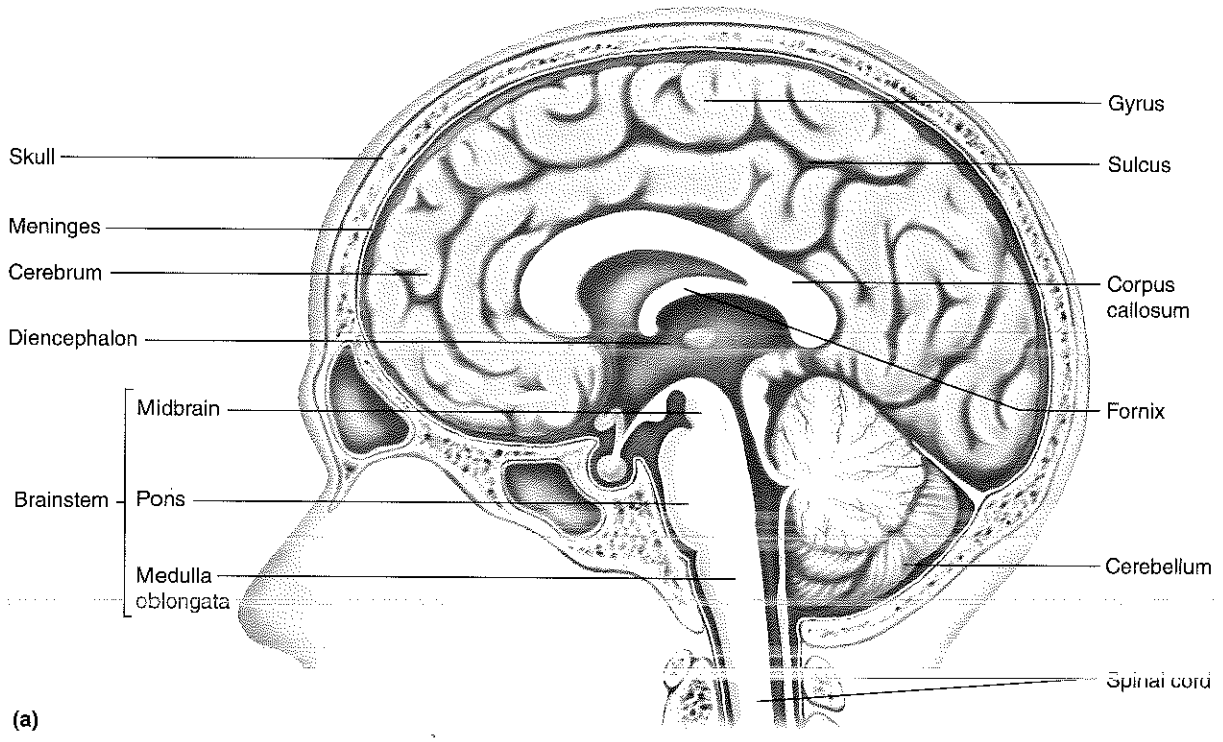
Embryonic Vesicle	Spaces Produced	Regions of the Brain Produced
Forebrain (prosencephalon)		
Anterior portion (telencephalon)	Lateral ventricles	Cerebrum Basal nuclei
Posterior portion (diencephalon)	Third ventricle	Thalamus Hypothalamus Posterior pituitary gland Pineal gland
Midbrain (mesencephalon)	Cerebral aqueduct	Midbrain
Hindbrain (rhombencephalon)		
Anterior portion (metencephalon)	Fourth ventricle	Cerebellum, pons
Posterior portion (myelencephalon)	Fourth ventricle	Medulla oblongata

The lobes of the cerebral hemispheres (fig. 11.16) are named after the skull bones that they underlie. The lobes include the following:

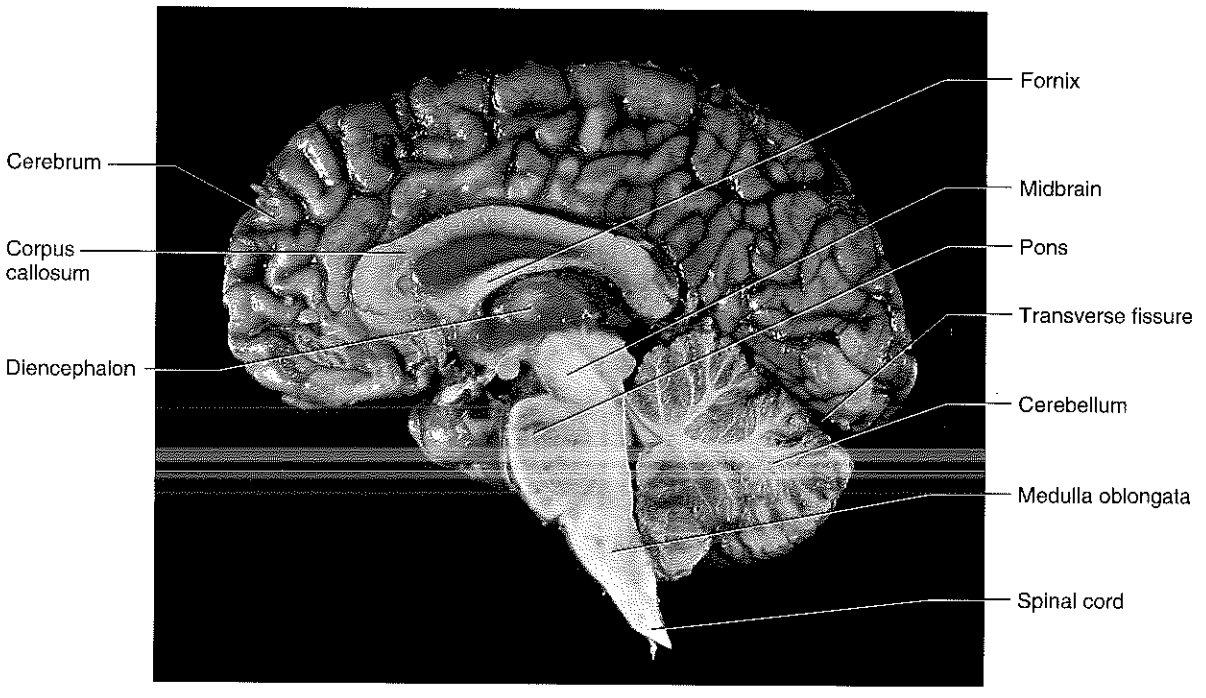
1. The **frontal lobe** forms the anterior portion of each cerebral hemisphere. It is bordered posteriorly by a *central sulcus* (fissure of Rolando), which passes out from the longitudinal fissure at a right angle, and inferiorly by a *lateral sulcus* (fissure of Sylvius), which exits the undersurface of the brain along its sides.
2. The **parietal lobe** is posterior to the frontal lobe and is separated from it by the central sulcus.
3. The **temporal lobe** lies inferior to the frontal and parietal lobes and is separated from them by the lateral sulcus.
4. The **occipital lobe** forms the posterior portion of each cerebral hemisphere and is separated from the cerebellum by a shelflike extension of dura mater called the *tentorium cerebelli*. The occipital lobe and the parietal and temporal lobes have no distinct boundary.
5. The **insula** (island of Reil) is a lobe deep within the lateral sulcus and is so named because it is covered by parts of the frontal, parietal, and temporal lobes. A *circular sulcus* separates the insula from the other lobes.

A thin layer of gray matter (2 to 5 millimeters thick) called the **cerebral cortex** (ser'ĕ-bral kor'teks) constitutes the outermost portion of the cerebrum. It covers the gyri, dipping into the sulci and fissures. The cerebral cortex contains nearly 75% of all the neuron cell bodies in the nervous system.

Just beneath the cerebral cortex is a mass of white matter that makes up the bulk of the cerebrum. This mass contains bundles of myelinated axons that connect neuron cell



(a)



(b)

FIGURE 11.15 AP|R Sagittal section of the brain and spinal cord, including the uncut medial surface of the right cerebral hemisphere. (*a*) The major portions of the brain include the cerebrum, the diencephalon, the cerebellum, and the brainstem. (*b*) Photo of human brain.

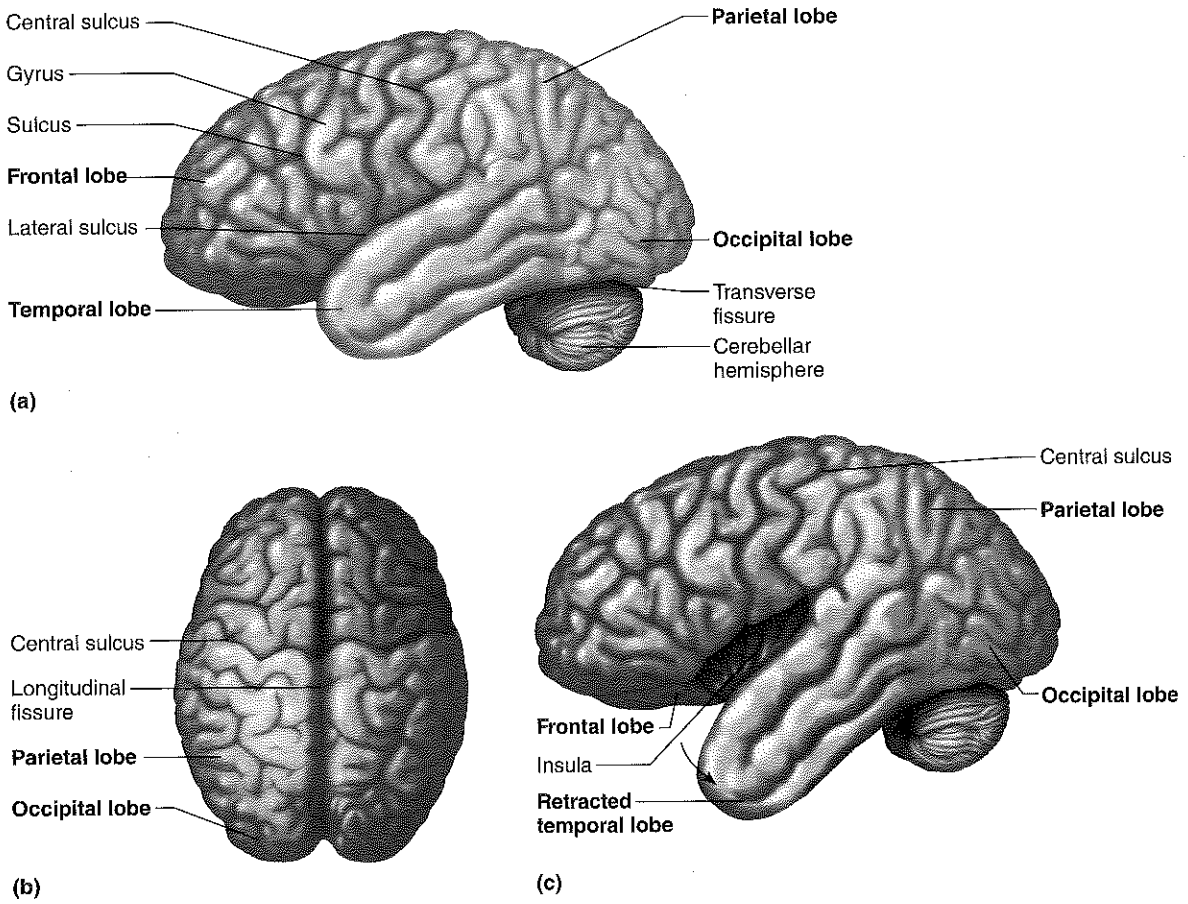


FIGURE 11.16 Colors in this figure distinguish the lobes of the cerebral hemispheres. (*a*) Lateral view of the left hemisphere. (*b*) Hemispheres viewed from above. (*c*) Lateral view of the left hemisphere with the insula exposed.

bodies of the cortex with other parts of the nervous system. Some of these fibers pass from one cerebral hemisphere to the other by way of the corpus callosum, and others carry sensory or motor impulses from the cortex to nerve centers in the brain or spinal cord.

In a "stroke," or *cerebrovascular accident* (CVA), a sudden interruption in blood flow in a vessel supplying brain tissues damages the cerebrum. The affected blood vessel may rupture, bleeding into the brain, or be blocked by a clot. In either case, brain tissues downstream from the vascular accident die and some loss of function may occur. Temporary interruption in cerebral blood flow, perhaps by a clot that quickly breaks apart, produces a much less serious *transient ischemic attack* (TIA), sometimes called a ministroke.

Functions of the Cerebrum

The cerebrum provides higher brain functions: interpreting impulses from sense organs, initiating voluntary muscular movements, storing information as memory, and retrieving this information in reasoning. The cerebrum is also the seat of intelligence and personality.

Functional Regions of the Cortex

A variety of techniques are used to study the specific functions of regions of the cerebral cortex. For example, From Science to Technology 2.3, figure 2E (p. 79) shows how PET scans provide images of the process of learning. Clues to cerebral functioning also come from investigating deficits in people who have suffered brain disease or injury.

In other studies, areas of cortices have been exposed surgically and stimulated mechanically or electrically. Researchers observe the responses in certain muscles or the specific sensations that result. Based on such investigations, researchers have divided the cerebral cortex into sensory, association, and motor areas that overlap somewhat.

Sensory Areas

Sensory areas in several lobes of the cerebrum interpret impulses from sensory receptors, producing feelings or sensations. For example, the sensations of temperature, touch, pressure, and pain in the skin arise in the postcentral gyri of

the anterior portions of the parietal lobes along the central sulcus and in the posterior wall of this sulcus (fig. 11.17). The posterior parts of the occipital lobes provide vision, whereas the superior posterior portions of the temporal lobes contain the centers for hearing. The sensory areas for taste are near the bases of the central sulci along the lateral sulci, and the sense of smell arises from centers deep in the cerebrum.

Like motor fibers, sensory fibers, such as those in the *fasciculus cuneatus tract,* cross over in the spinal cord or the brainstem (see fig. 11.12). Thus, the centers in the right central hemisphere interpret impulses originating from the left side of the body, and vice versa. However, the sensory areas concerned with vision receive impulses from both eyes, and those concerned with hearing receive impulses from both ears.

Not all sensory areas are bilateral. The *sensory speech area,* also called *Wernicke's area,* is in the temporal lobe near the parietal lobe, posterior to the lateral sulcus, usually in the left hemisphere (fig. 11.17). This area is important for understanding and formulating written and especially spoken language.

Association Areas

Association areas are neither primarily sensory nor motor. They connect with each other and with other brain structures. These areas occupy the anterior portions of the frontal lobes and are widespread in the lateral portions of the parietal, temporal, and occipital lobes. Association areas analyze and interpret sensory experiences and help provide memory, reasoning, verbalizing, judgment, and emotions (fig. 11.17).

The association areas of the frontal lobes provide higher intellectual processes, such as concentrating, planning, and complex problem solving. The anterior and inferior portions of these lobes (prefrontal areas) control emotional behavior and produce awareness of the possible consequences of behaviors. These abilities are also collectively called executive function.

The parietal lobes have association areas that help interpret sensory information and aid in understanding speech and choosing words to express thoughts and feelings. Awareness of the form of objects, including one's own body parts, stems from the posterior regions of these lobes.

The association areas of the temporal lobes and the regions at the posterior ends of the lateral sulci interpret complex sensory experiences, such as those needed to understand speech and to read. These regions also store memories of visual scenes, music, and other complex sensory patterns.

The occipital lobes have association areas adjacent to the visual centers. These are important in analyzing visual patterns and combining visual images with other sensory experiences, such as when one person recognizes another.

The functions of the insula are not as well known as those of the other lobes because the insula's location deep within the cerebrum makes it impossible to study with surface electrodes. However, studies that use functional MRI scanning suggest that the insula serves as a crossroads for translating sensory information into appropriate emotional responses, such as feeling disgust at the sight of something unpleasant, or a feeling of joy when hearing a symphony or when biting into a slice of pizza.

Wernicke's area borders closely on a brain region that has been referred to as a "general interpretive area," near where the occipital, parietal, and temporal lobes meet. The general interpretive area processes sensory information from

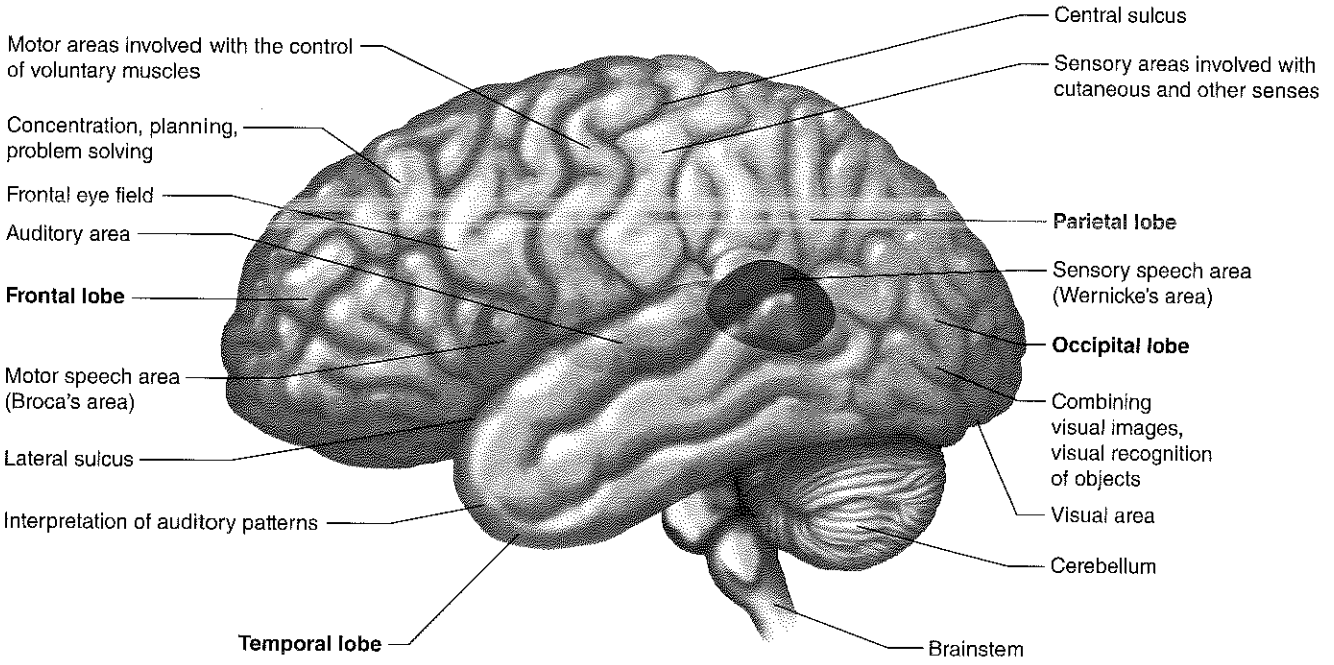


FIGURE 11.17 Some sensory association and motor areas of the left cerebral cortex.

all three of these association areas. It plays a role in integrating visual, auditory, and other sensory information and then interpreting a situation. For example, you hear a familiar voice, look up from your notes, see a friend from class, and realize that it is time for your study group.

A person with *dyslexia* sees letters separately and must learn to read differently than people whose nervous systems can group letters into words. Three to 10% of people have dyslexia. The condition probably has several causes, with inborn visual and perceptual skills interacting with the way the child learns to read. Dyslexia is not related to intelligence. Many brilliant thinkers with dyslexia were "slow" in school because educators did not know how to help them.

Motor Areas

The *primary motor areas* of the cerebral cortex lie in the precentral gyri of the frontal lobes just in front of the central sulcus and in the anterior wall of this sulcus (fig. 11.17). The nervous tissue in these regions contains many large *pyramidal cells,* named for their pyramid-shaped cell bodies.

Impulses from the pyramidal cells move downward through the brainstem and into the spinal cord on the *corticospinal tracts.* Most of the nerve fibers in these tracts cross over from one side of the brain to the other within the brainstem and descend as lateral corticospinal tracts. Other fibers, in the anterior corticospinal tracts, cross over at various levels of the spinal cord (see fig. 11.13).

In the spinal cord, the corticospinal fibers synapse with motor neurons in the gray matter of the anterior horns. Axons of the motor neurons lead outward through peripheral nerves to voluntary muscles. Nerve impulses transmitted on these pathways in special patterns and frequencies are responsible for fine movements in skeletal muscles. More specifically, as figure 11.18 shows, cells in the upper portions of the motor areas send impulses to muscles in the thighs and legs; those in the middle portions control muscles in the arms and forearms; and those in lower portions activate muscles of the head, face, and tongue.

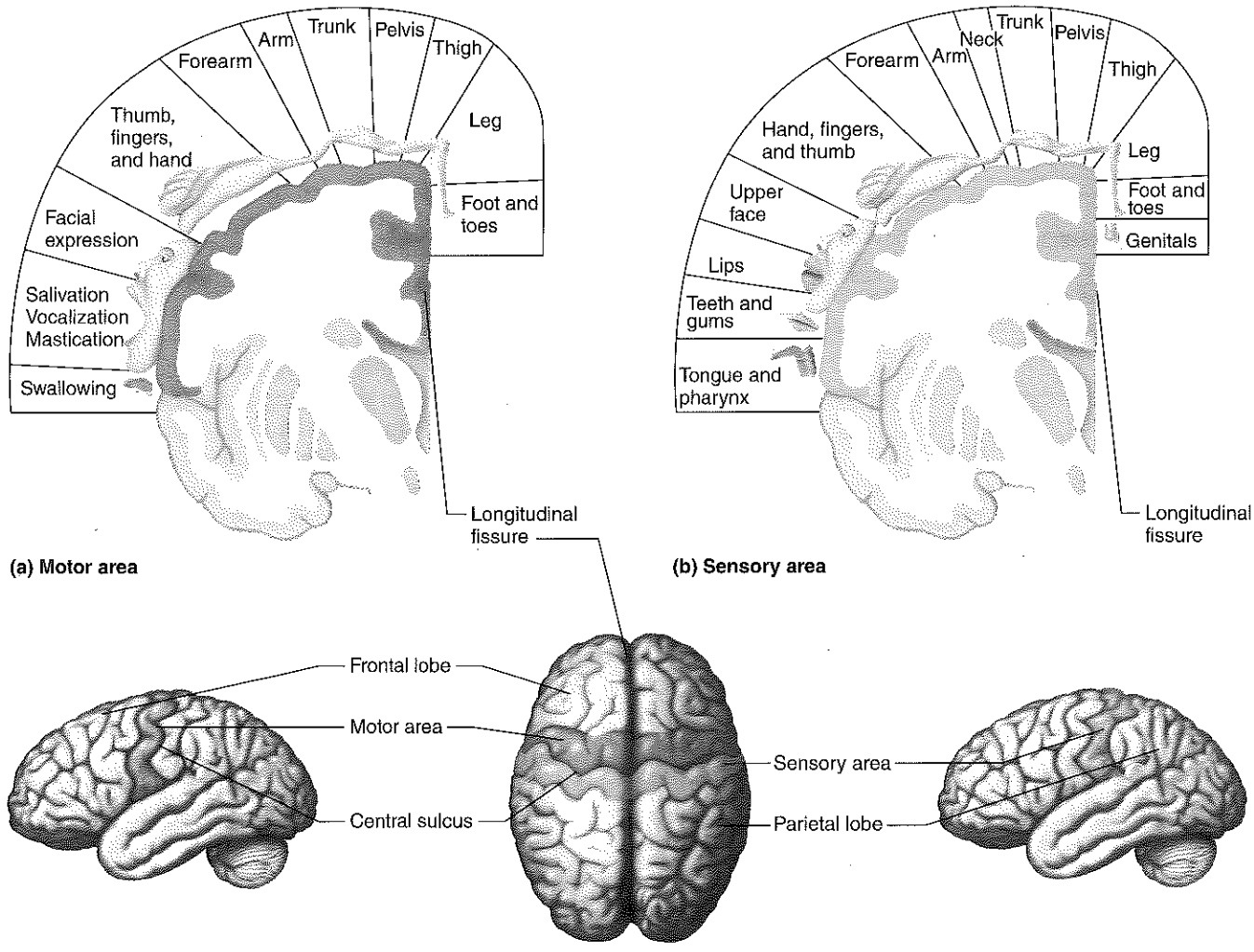


FIGURE 11.18 Functional regions of the cerebral cortex. (*a*) Motor areas that control voluntary muscles (only left hemisphere shown). (*b*) Sensory areas involved with cutaneous and other senses (only left hemisphere shown).

The *reticulospinal* and *rubrospinal tracts* coordinate and control motor functions that maintain balance and posture. Many of these fibers pass into the basal nuclei on the way to the spinal cord. Some of the impulses conducted on these pathways normally inhibit muscular actions.

In addition to the primary motor areas, certain other regions of the frontal lobe control motor functions. For example, a region called the *motor speech area,* also known as *Broca's area,* is in the frontal lobe, usually in the left hemisphere, just anterior to the primary motor cortex and superior to the lateral sulcus. The motor speech area is important in generating the complex muscular actions of the mouth, tongue, and larynx, which make speech possible (see fig. 11.17). Bundles of axons directly and indirectly connect the motor speech area to the sensory speech area. While the sensory speech area (Wernicke's area) functions when you decide what to say, the motor speech area initiates the muscle actions required to actually speak. A person with an injury to Broca's area may be able to understand spoken words but be unable to speak.

Above the motor speech area is a region called the *frontal eye field.* The motor cortex in this area controls voluntary movements of the eyes and eyelids. Nearby is the cortex responsible for movements of the head that direct the eyes. Another region just in front of the primary motor area controls the muscular movements of the hands and fingers that make such skills as writing possible (see fig. 11.17). Table 11.5 summarizes the functions of the cerebral lobes.

An injury to the motor system may impair the ability to produce purposeful muscular movements. Such a condition that affects use of the upper and lower limbs, head, or eyes is called *apraxia.* When apraxia affects the speech muscles, disrupting speaking ability, it is called *aphasia.*

TABLE **11.5** | Functions of the Cerebral Lobes

Lobe	Functions
Frontal lobes	Association areas carry on higher intellectual processes for concentrating, planning, complex problem solving, and judging the consequences of behavior.
	Motor areas control movements of voluntary skeletal muscles.
Parietal lobes	Sensory areas provide sensations of temperature, touch, pressure, and pain involving the skin.
	Association areas function in understanding speech and in using words to express thoughts and feelings.
Temporal lobes	Sensory areas are responsible for hearing.
	Association areas interpret sensory experiences and remember visual scenes, music, and other complex sensory patterns.
Occipital lobes	Sensory areas are responsible for vision.
	Association areas combine visual images with other sensory experiences.

PRACTICE

15 How does the brain form during early development?
16 Describe the cerebrum.
17 List the general functions of the cerebrum.
18 Where in the brain are the sensory areas located?
19 Explain the functions of association areas.
20 Where in the brain are the motor areas located?

Hemisphere Dominance

Both cerebral hemispheres participate in basic functions, such as receiving and analyzing sensory impulses, controlling skeletal muscles on opposite sides of the body, and storing memory. However, one side usually acts as a *dominant hemisphere* for certain other functions.

Tests indicate that the left hemisphere is dominant in 90% of right-handed adults and in 64% of left-handed ones. The right hemisphere is dominant in 10% of right-handed adults and in 20% of left-handed ones. The hemispheres are equally dominant in the remaining 16% of left-handed persons. As a consequence of hemisphere dominance, the motor speech area on one side almost completely controls the motor activities associated with speech. For this reason, over 90% of patients with language impairment stemming from problems in the cerebrum have disorders in the left hemisphere.

In most persons, the left hemisphere is dominant for the language-related activities of speech, writing, and reading. It is also dominant for complex intellectual functions requiring verbal, analytical, and computational skills. In other persons, the right hemisphere is dominant, and in some, the hemispheres are equally dominant.

The nondominant hemisphere specializes in nonverbal functions, in addition to carrying on basic functions. Nonverbal functions include motor tasks that require orientation of the body in space, understanding and interpreting musical patterns, and visual experiences. The nondominant hemisphere also provides emotional and intuitive thought processes. For example, the region in the nondominant hemisphere that corresponds to the motor speech area does not control speech, but it influences the emotional aspects of spoken language.

Nerve fibers of the *corpus callosum,* which connect the cerebral hemispheres, enable the dominant hemisphere to control the motor cortex of the nondominant hemisphere. These fibers also transfer sensory information reaching the nondominant hemisphere to the general interpretative area of the dominant one, where the information can be used in decision making.

Memory

Memory, one of the most astonishing capabilities of the brain, is the consequence of learning. Whereas learning is the acquisition of new knowledge, memory is the persistence of that learning, with the ability to access it at a later time.

Two types of memory, short term and long term, have been recognized for many years, and researchers are now beginning to realize that they differ in characteristics other than duration.

Short-term, or "working" memories are thought to be electrical. Neurons may be connected in a circuit so that the last in the series stimulates the first. As long as the pattern of stimulation continues, the thought is remembered. When the electrical events cease, so does the memory—unless it enters long-term memory.

Long-term memory probably changes the structure or function of neurons in ways that enhance synaptic transmission, perhaps by establishing certain patterns of synaptic connections. Synaptic patterns fulfill two requirements of long-term memory. First, there are enough synapses to encode an almost limitless number of memories. Each of the 10 billion neurons in the cortex can make tens of thousands of synaptic connections to other neurons, forming 60 trillion synapses. Second, a certain pattern of synapses can remain unchanged for years.

Understanding how neurons in different parts of the brain encode memories and how short-term memories are converted to long-term memories, a process called **memory consolidation,** is at the forefront of research into the functioning of the human brain. According to one theory, **long-term synaptic potentiation,** near simultaneous repeated stimulation of the same neurons strengthens their synaptic connections. In response, in an area of the temporal lobe called the **hippocampus,** more frequent action potentials are triggered in postsynaptic cells. Another area of the temporal lobe, the amygdala, assigns value to a memory, such as whether it was pleasant.

Unusual behaviors and skills of people who have damaged the hippocampus have taught researchers much about this intriguing part of the brain. In 1953, a surgeon removed parts of the hippocampus and the amygdala of a young man called H. M., to relieve his severe epilepsy. His seizures became less frequent, but H. M. suffered a profound loss in the ability to consolidate short-term memories into long-term ones. As a result, events in H. M.'s life faded quickly from his memory. He was unable to recall any events that took place since surgery, living always as if it was the 1950s. He would read the same magazine article repeatedly with renewed interest each time.

Basal Nuclei

The **basal nuclei,** often called the basal ganglia, are masses of gray matter deep within the cerebral hemispheres. They are called the *caudate nucleus,* the *putamen,* and the *globus pallidus,* and they develop from the anterior portion of the forebrain (fig. 11.19). The basal nuclei produce the inhibitory neurotransmitter *dopamine.* The neurons of the basal nuclei interact with other brain areas, including the motor cortex, thalamus, and cerebellum. These interactions, through a combination of stimulation and inhibition, facilitate voluntary movement. Clinical Application 11.4 discusses Parkinson disease, in which neurons in the basal nuclei degenerate.

PRACTICE

21 What is hemisphere dominance?

22 What are the functions of the nondominant hemisphere?

23 Distinguish between short-term and long-term memory.

24 What is the function of the basal nuclei?

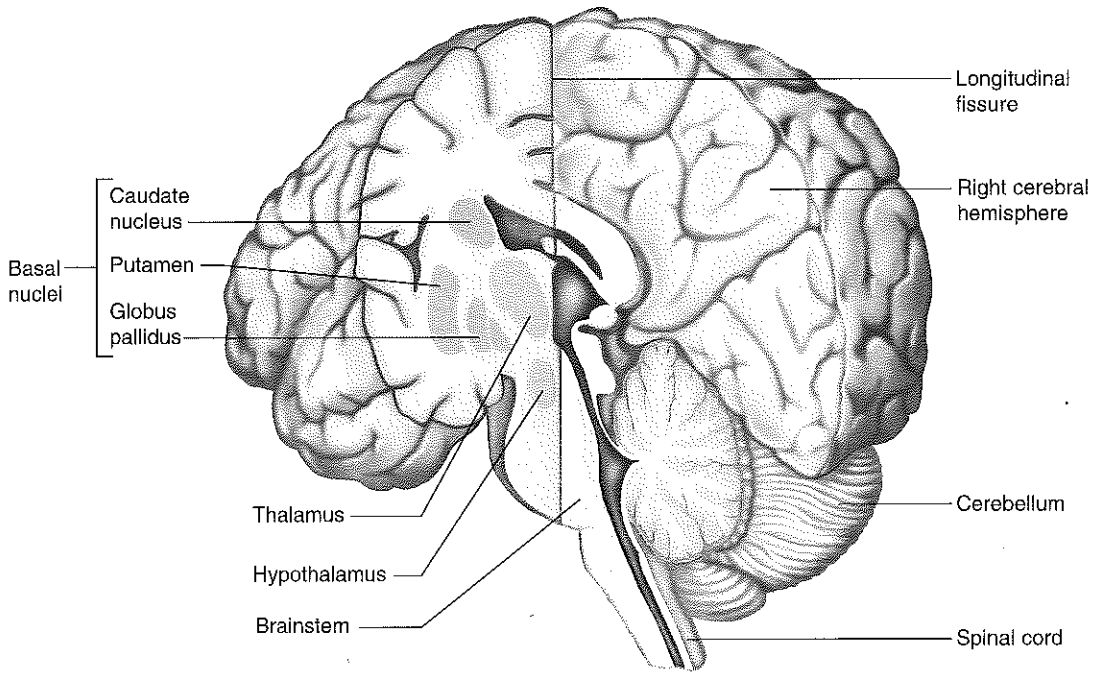
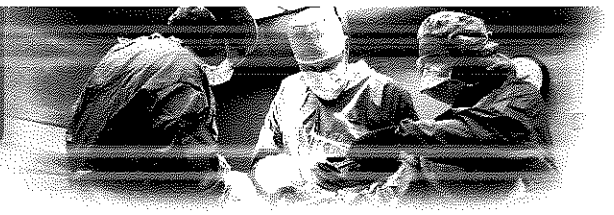


FIGURE 11.19 AP|R A frontal section of the left cerebral hemisphere reveals some of the basal nuclei.

11.4 CLINICAL APPLICATION



Parkinson Disease

Actor Michael J. Fox was in his late twenties when his wife noticed the first sign of Parkinson disease (PD)—he leaned when walking. When one of his fingers began twitching, Fox consulted a physician, and so began the journey toward his diagnosis. Of the approximately six million people worldwide who have PD, only 10% develop symptoms before the age of forty, like Michael J. Fox did.

Fox kept his diagnosis private, but by the late 1990s his co-workers began to notice symptoms that emerged when medication wore off—rigidity, a shuffling and off-balance gait, and poor small-motor control. Fox's face became maskiike, a characteristic called hypomimia. It took a huge effort to speak, a symptom called hypophia. Even though his brain could string thoughts into sentences, the muscles of his jaw, lips, and tongue would not utter them. He also developed micrographia, or small handwriting. Fox founded the Michael J. Fox Foundation for Parkinson's Research, and he continues to act.

In PD, neurons degenerate in the substantia nigra area of the brainstem. *Substantia nigra* means "large black area," named for the dark pigment that the neurons release as a by-product of synthesizing the neurotransmitter dopamine. When these neurons degenerate, less dopamine reaches synapses with neurons in the striatum of the basal nuclei. The decrease in dopamine causes the motor symptoms of PD. Some patients develop other symptoms, including depression, dementia, constipation, incontinence, sleep problems, and orthostatic hypotension (dizziness upon standing).

Until recently PD was diagnosed based on neurological symptoms alone, because MRI and CT scans appear normal. However, an imaging technology called SPECT (single photon emission computed tomography) uses a chemical compound similar to cocaine that binds specifically to dopamine transporter molecules in the striatum, marking them. This compound used with SPECT is called a DaTscan. It distinguishes tremors that are specifically due to PD, which is useful both for diagnosis and in research to ensure that people in clinical trials to evaluate PD treatments actually have PD.

So far, no treatments can cure or slow the course of PD, but replacing or enhancing use of dopamine can temporarily alleviate symptoms. The standard treatment for many years has been levodopa, a precursor to dopamine that crosses the blood-brain barrier. In the brain, levodopa is converted to dopamine. Levodopa provides temporary relief from twitching and rigidity.

Drug treatment for PD becomes less effective over time. By a feedback mechanism the brain senses the external supply of dopamine and decreases its own production, so that eventually higher doses of levodopa are needed to achieve the effect. Taking too much levodopa leads to another condition, tardive dyskinesia, that produces uncontrollable facial tics and spastic extensions of the limbs. Tardive dyskinesia may result from effects of excess dopamine in brain areas other than those affected in PD.

Surgery can alleviate Parkinson's symptoms. Fox underwent thalamotomy, in which an electrode caused a lesion in his thalamus that calmed violent shaking in his left arm. Another surgical procedure, pallidotomy, causes lesions in the globus pallidus internus, a part of the basal nuclei, and the approach is also used on an area posterior to the thalamus. Deep brain implants of electrodes may also control some symptoms.

Researchers are turning to cells in a patient's own body as sources of the dopamine needed in PD. For example, cells in the eye's retinal pigment epithelium (chapter 12, p. 474) can be cultured with biochemicals that stimulate them to produce dopamine or levodopa. Perhaps cells can be sampled from the patient without impairing vision and implanted in the substantia nigra. Neural stem and progenitor cells may also be useful. Implants of fetal dopamine-producing cells performed in the late 1990s alleviated symptoms in some patients for several years.

PD may have several causes. Symptoms have been attributed to use of certain designer drugs, exposure to pesticides, and frequent violent blows to the head (fig. 11D). Most cases are not inherited. One gene that causes PD when mutant encodes a protein called alpha-synuclein. The abnormal protein folds improperly, forming deposits in the brain called Lewy bodies (fig. 11E). People may inherit a susceptibility to PD that progresses to symptoms in response to environmental triggers. ■

FIGURE 11D Professional boxers are at higher risk of developing Parkinson disease (PD) from repeated blows to the head. Muhammad Ali has PD from many years of head injuries. Michael J. Fox, an actor, not a boxer, first experienced symptoms of PD at age 29, which is unusual.

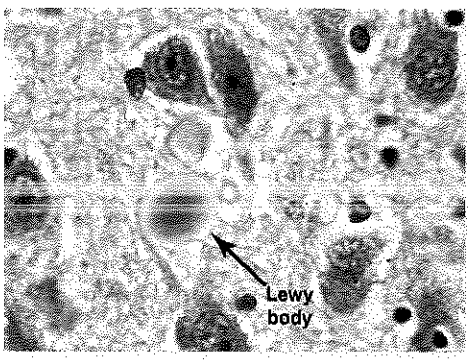


FIGURE 11E The chemical composition of Lewy bodies, characteristic of the brains of people with Parkinson disease, may provide clues to the cause of the condition. Lewy bodies include alpha-synuclein and other components.

Diencephalon

The **diencephalon** (di″en-sef′ah-lon) develops from the posterior forebrain and is located between the cerebral hemispheres and superior to the brainstem (see figs. 11.15 and 11.19). It surrounds the third ventricle and is largely composed of gray matter. In the diencephalon, a dense mass called the **thalamus** (thal′ah-mus) bulges into the third ventricle from each side. Another region of the diencephalon that includes many nuclei is the **hypothalamus** (hi″po-thal′ah-mus). It lies inferior to the thalamic nuclei and forms the lower walls and floor of the third ventricle (see reference plates 9 and 13, pp. 47 and 50).

Other parts of the diencephalon include (1) the **optic tracts** and the **optic chiasma,** formed by the optic nerve fibers crossing over; (2) the **infundibulum,** which is a conical process behind the optic chiasma to which the pituitary gland is attached; (3) the **posterior pituitary gland,** which hangs from the floor of the hypothalamus; (4) the **mammillary** (mam′ĭ-lar″e) **bodies,** which are two rounded structures behind the infundibulum; and (5) the **pineal gland,** which forms as a cone-shaped projection from the roof of the diencephalon (see chapter 13, p. 515).

The thalamus is a selective gateway for sensory impulses ascending from other parts of the nervous system to the cerebral cortex. It receives all sensory impulses (except those associated with the sense of smell) and channels them to appropriate regions of the cortex for interpretation. In addition, all regions of the cerebral cortex can communicate with the thalamus by means of descending fibers.

The thalamus transmits sensory information by synchronizing action potentials. Consider vision. An image on the retina stimulates the *lateral geniculate nucleus* (LGN) region of the thalamus, which then sends action potentials to a part of the visual cortex. Those action potentials are synchronized—fired simultaneously—by the LGN's neurons only if the stimuli come from a single object, such as a bar. If the stimulus is two black dots, the resulting thalamic action potentials are not synchronized. The synchronicity of action potentials, therefore, may be a way that the thalamus selects which stimuli to relay to higher brain structures. Therefore, the thalamus is not only a messenger but also an editor.

Nerve fibers connect the hypothalamus to the cerebral cortex, thalamus, and parts of the brainstem so that it can receive impulses from them and send impulses to them. The hypothalamus maintains homeostasis by regulating a variety of visceral activities and by linking the nervous and endocrine systems.

The hypothalamus regulates:

1. heart rate and arterial blood pressure
2. body temperature
3. water and electrolyte balance
4. control of hunger and body weight
5. control of movements and glandular secretions of the stomach and intestines
6. production of neurosecretory substances that stimulate the pituitary gland to release hormones that help regulate growth, control various glands, and influence reproductive physiology
7. sleep and wakefulness

Structures in the region of the diencephalon also are important in controlling emotional responses. Parts of the cerebral cortex in the medial parts of the frontal and temporal lobes connect with the hypothalamus, thalamus, basal nuclei, and other deep nuclei. These structures form a complex called the **limbic system.** It controls emotional experience and expression and can modify the way a person acts, producing such feelings as fear, anger, pleasure, and sorrow. The limbic system reacts to potentially life-threatening upsets in a person's physical or psychological condition. By causing pleasant or unpleasant feelings about experiences, the limbic system guides behavior that may increase the chance of survival. In addition, parts of the limbic system interpret sensory impulses from the receptors associated with the sense of smell (olfactory receptors).

Brainstem

The **brainstem** connects the brain to the spinal cord. It consists of the midbrain, pons, and medulla oblongata. These structures include many tracts of nerve fibers and masses of gray matter called *nuclei* (see figs. 11.15, 11.19, and 11.20).

Midbrain

The **midbrain** (mesencephalon) is a short section of the brainstem between the diencephalon and the pons. It contains bundles of myelinated nerve fibers that join lower parts of the brainstem and spinal cord with higher parts of the brain. The midbrain includes several masses of gray matter that serve as reflex centers. It also contains the *cerebral aqueduct* that connects the third and fourth ventricles (fig. 11.21).

Two prominent bundles of nerve fibers on the underside of the midbrain comprise the *cerebral peduncles.* These fibers include the corticospinal tracts and are the main motor pathways between the cerebrum and lower parts of the nervous system (see fig. 11.20). Beneath the cerebral peduncles are large bundles of sensory fibers that carry impulses upward to the thalamus.

Two pairs of rounded knobs on the superior surface of the midbrain mark the location of four nuclei, known collectively as *corpora quadrigemina.* The upper masses (superior colliculi) contain the centers for certain visual reflexes, such as those responsible for moving the eyes to view something as the head turns. The lower ones (inferior colliculi) contain the auditory reflex centers that operate when it is necessary to move the head to hear sounds more distinctly (see fig. 11.20).

Near the center of the midbrain is a mass of gray matter called the *red nucleus.* This nucleus communicates with the cerebellum and with centers of the spinal cord, and it plays a

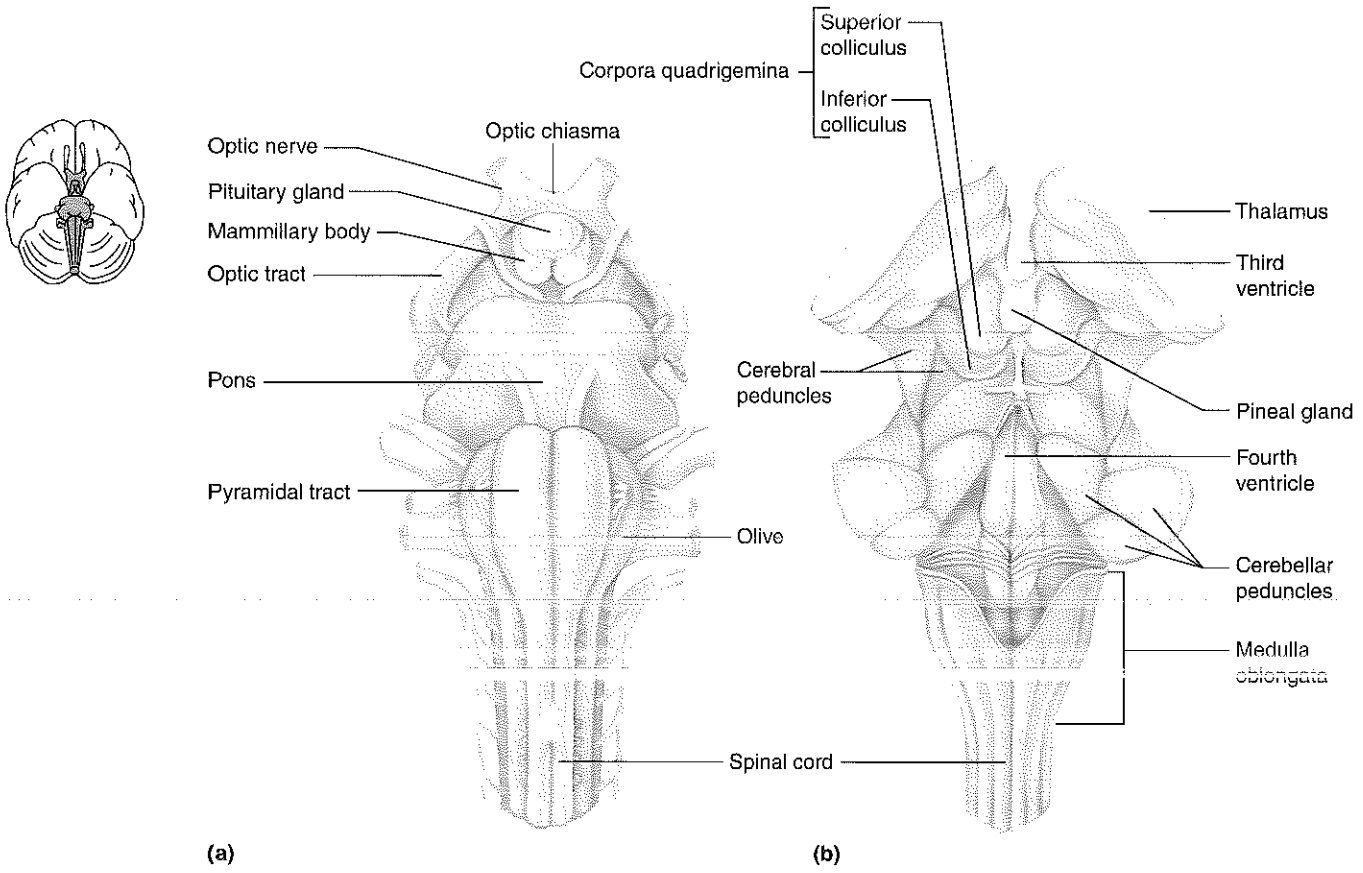


FIGURE 11.20 AP|R Brainstem. (*a*) Ventral view of the brainstem. (*b*) Dorsal view of the brainstem with the cerebellum removed, exposing the fourth ventricle.

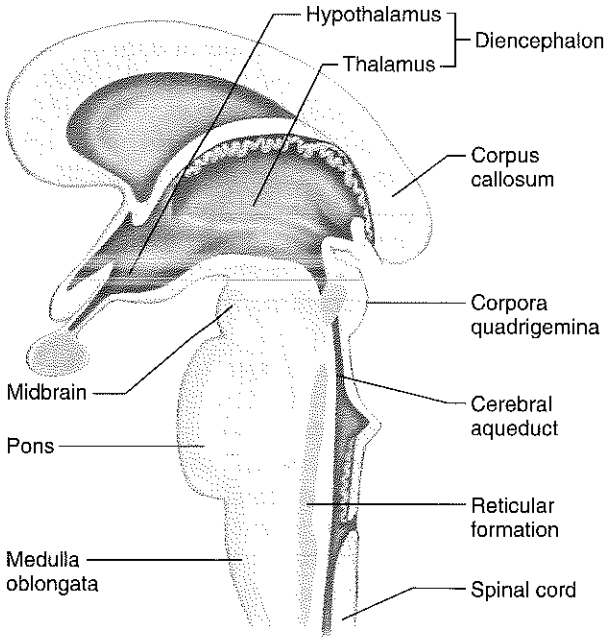


FIGURE 11.21 AP|R The reticular formation (shown in gold) extends from the superior portion of the spinal cord into the diencephalon.

role in reflexes that maintain posture. It appears red because it is richly supplied with blood vessels.

Pons

The **pons** appears as a rounded bulge on the underside of the brainstem where it separates the midbrain from the medulla oblongata (see fig. 11.20). The dorsal portion of the pons consists mostly of longitudinal nerve fibers, which relay impulses to and from the medulla oblongata and the cerebrum. Its ventral portion contains large bundles of transverse nerve fibers, which transmit impulses from the cerebrum to centers within the cerebellum.

Several nuclei of the pons relay sensory impulses from peripheral nerves to higher brain centers. Other nuclei may function with centers of the medulla oblongata to control the rhythm of breathing.

Medulla Oblongata

The **medulla oblongata** (mĕ-dul'ah ob"long-ga'tah) is an enlarged continuation of the spinal cord, extending from the level of the foramen magnum to the pons (see fig. 11.20). Its dorsal surface flattens to form the floor of the fourth ventricle, and its ventral surface is marked by the corticospinal

tracts, most of whose fibers cross over at this level. On each side of the medulla oblongata is an oval swelling called the *olive,* from which a large bundle of nerve fibers arises and passes to the cerebellum.

The ascending and descending nerve fibers connecting the brain and spinal cord must pass through the medulla oblongata because of its location. As in the spinal cord, the white matter of the medulla surrounds a central mass of gray matter. Here, however, the gray matter breaks up into nuclei separated by nerve fibers. Some of these nuclei relay ascending impulses to the other side of the brainstem and then on to higher brain centers. The *nucleus gracilis* and the *nucleus cuneatus,* for example, receive sensory impulses from fibers of the fasciculus gracilis and the fasciculus cuneatus and pass them on to the thalamus or the cerebellum.

Other nuclei in the medulla oblongata control vital visceral activities. These reflex centers include the following:

1. Peripheral nerves conduct impulses originating in the **cardiac center** to the heart, where they increase or decrease heart rate.
2. Certain cells of the **vasomotor center** initiate impulses that affect smooth muscles in the walls of blood vessels and stimulate them to contract, constricting the vessels (vasoconstriction) and thereby increasing blood pressure. A decrease in the activity of these cells can produce the opposite effect—dilation of the blood vessels (vasodilation) and a consequent drop in blood pressure.
3. The **respiratory center** maintains the basic rhythm of breathing and adjusts the rate and depth of breathing to meet changing needs.

Some nuclei in the medulla oblongata are centers for certain nonvital reflexes, such as those associated with coughing, sneezing, swallowing, and vomiting. However, because the medulla also contains vital reflex centers, injuries to this part of the brainstem are often fatal.

Reticular Formation

Scattered throughout the medulla oblongata, pons, and midbrain is a complex network of nerve fibers associated with tiny islands of gray matter. This network, the **reticular formation** (rĕ-tik'u-lar fōr-ma'shun), or reticular activating system, extends from the superior portion of the spinal cord into the diencephalon (fig. 11.21). Its intricate system of nerve fibers connects centers of the hypothalamus, basal nuclei, cerebellum, and cerebrum with fibers in all the major ascending and descending tracts.

When sensory impulses reach the reticular formation, it responds by activating the cerebral cortex into a state of wakefulness. Without this arousal, the cortex remains unaware of stimulation and cannot interpret sensory information or carry on thought processes. Decreased activity in the reticular formation results in sleep. If the reticular formation is injured and ceases to function, the person remains unconscious, even with strong stimulation. This is called a comatose state.

The reticular formation filters incoming sensory impulses. Impulses judged to be important, such as those originating in pain receptors, are passed on to the cerebral cortex, while others are disregarded. This selective action of the reticular formation frees the cortex from what would otherwise be a continual bombardment of sensory stimulation and allows it to concentrate on more significant information. Because the cerebral cortex can also activate the reticular system, intense cerebral activity keeps a person awake. In addition, the reticular formation regulates motor activities so that various skeletal muscles move together evenly, and it inhibits or enhances certain spinal reflexes.

A person in a persistent vegetative state may occasionally be awake and responsive to stimuli, but is not aware; a person in a coma does not appear awake and is not aware. In some cases following a severe injury, a person will become comatose and then gradually enter a persistent vegetative state. Coma and persistent vegetative state are also seen in the end stage of neurodegenerative disorders such as Alzheimer disease; when there is an untreatable mass in the brain, such as a blood clot or tumor; or in anencephaly, when a newborn lacks higher brain structures.

Types of Sleep

The two types of normal sleep are *slow-wave* and *rapid eye movement* (REM). Slow-wave sleep (also called non-REM sleep) occurs when a person is very tired, and it reflects decreasing activity of the reticular formation. It is restful, dreamless, and accompanied by reduced blood pressure and respiratory rate. Slow-wave sleep may range from light to heavy and is usually described in four stages. It may last from seventy to ninety minutes. Slow-wave and REM sleep alternate.

REM sleep is also called "paradoxical sleep" because some areas of the brain are active. As its name implies, the eyes can be seen rapidly moving beneath the eyelids. Cats and dogs in REM sleep sometimes twitch their limbs. In humans, REM sleep usually lasts from five to fifteen minutes. This "dream sleep" is apparently important. If a person lacks REM sleep for just one night, sleep on the next night makes up for it. During REM sleep, heart and respiratory rates are irregular. Certain drugs, such as marijuana and alcohol, interfere with REM sleep. Table 11.6 describes several disorders of sleep.

PRACTICE

25 What are the major functions of the thalamus? of the hypothalamus?

26 How may the limbic system influence a person's behavior?

27 Which vital reflex centers are located in the brainstem?

28 What is the function of the reticular formation?

29 Describe two types of sleep.

TABLE **11.6** | Sleep Disorders

Disorder	Symptoms	Percent of Population
Fatal familial insomnia	Inability to sleep, emotional instability, hallucinations, stupor, coma, death within thirteen months of onset around age fifty, both slow-wave and REM sleep abolished.	Very rare
Insomnia	Inability to fall or remain asleep.	10%
Narcolepsy	Abnormal REM sleep causes extreme daytime sleepiness, begins between ages of fifteen and twenty-five.	0.02–0.06%
Obstructive sleep apnea syndrome	Upper airway collapses repeatedly during sleep, blocking breathing. Snoring and daytime sleepiness.	4–5%
Parasomnias	Sleepwalking, sleeptalking, and night terrors.	<5% of children
REM-sleep behavior disorder	Excessive motor activity during REM sleep, which disturbs continuous sleep.	Very rare
Restless legs syndrome	Brief, repetitive leg jerks during sleep. Leg pain forces person to get up several times a night.	5.5%
Sleep paralysis	Inability to move for up to a few minutes after awakening or when falling asleep.	Very rare

Cerebellum

The **cerebellum** (ser″ĕ-bel′um) is a large mass of tissue inferior to the occipital lobes of the cerebrum and posterior to the pons and medulla oblongata (see fig. 11.15). It consists of two lateral hemispheres partially separated by a layer of dura mater called the *falx cerebelli*. A structure called the *vermis* connects the cerebellar hemispheres at the midline.

Like the cerebrum, the cerebellum is primarily composed of white matter with a thin layer of gray matter, the **cerebellar cortex,** on its surface. This cortex doubles over on itself in a series of complex folds that have myelinated nerve fibers branching into them. A cut into the cerebellum reveals a treelike pattern of white matter, called the *arbor vitae*, surrounded by gray matter. A number of nuclei lie deep within each cerebellar hemisphere. The largest and most important is the *dentate nucleus.*

The cerebellum communicates with other parts of the CNS by means of three pairs of nerve tracts called **cerebellar peduncles** (ser″ĕ-bel′ar pe-dung′kls) (fig. 11.22). One pair, the *inferior peduncles*, brings sensory information concerning the position of body parts such as limbs and joints to the cerebellum via the spinal cord and medulla oblongata. The *middle peduncles* transmit information from the cerebral cortex about the desired position of these body parts. After integrating and analyzing the information from these two sources, the cerebellum sends correcting impulses from the dentate nucleus via the *superior peduncles* to the thalamus and eventually motor cortex (fig. 11.22). These

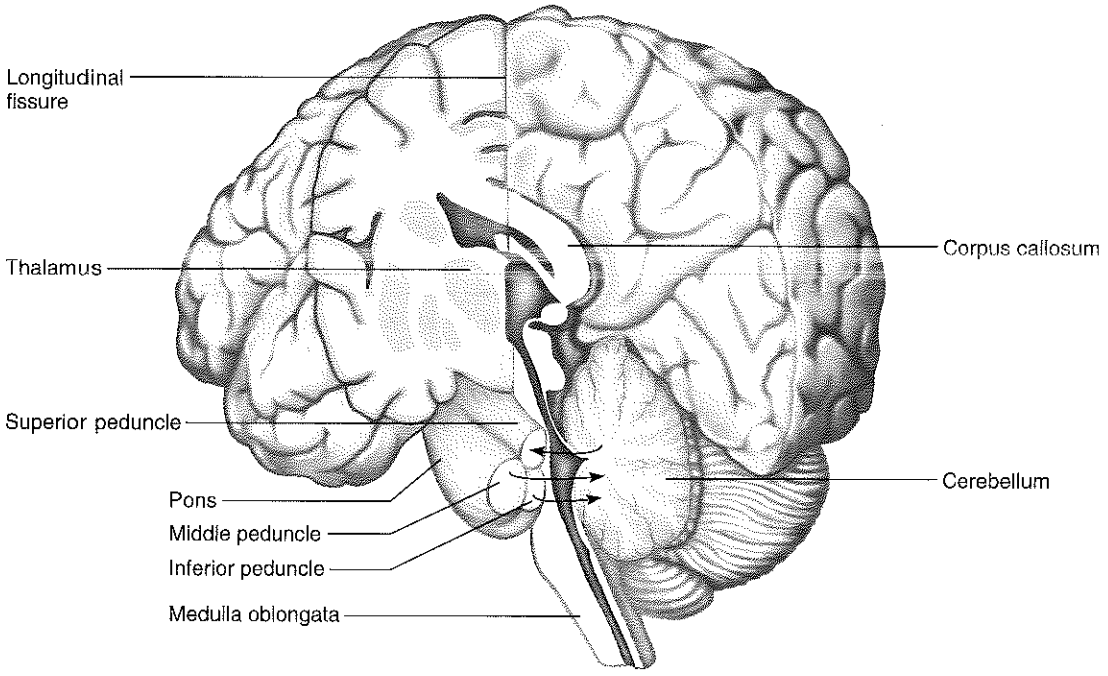


FIGURE 11.22 The cerebellum, located inferior to the occipital lobes of the cerebrum, communicates with other parts of the nervous system by means of the cerebellar peduncles.

TABLE **11.7** | Major Parts of the Brain

Part	Characteristics	Functions
1. Cerebrum	Largest part of the brain; two hemispheres connected by the corpus callosum	Controls higher brain functions, including interpreting sensory impulses, initiating muscular movements, storing memory, reasoning, and intelligence
2. Basal nuclei (basal ganglia)	Masses of gray matter deep within the cerebral hemispheres	Relay stations for motor impulses originating in the cerebral cortex and passing into the brainstem and spinal cord; facilitate and help coordinate voluntary movement
3. Diencephalon	Includes masses of gray matter (thalamus and hypothalamus)	The thalamus is a relay station for sensory impulses ascending from other parts of the nervous system to the cerebral cortex; the hypothalamus helps maintain homeostasis by regulating visceral activities and by linking the nervous and endocrine systems
4. Brainstem	Connects the cerebrum to the spinal cord	
a. Midbrain	Contains masses of gray matter and bundles of nerve fibers that join the spinal cord to higher regions of the brain	Contains reflex centers that move the eyes and head, and maintains posture
b. Pons	A bulge on the underside of the brainstem that contains masses of gray matter and nerve fibers	Relays impulses between the medulla oblongata and cerebrum; helps regulate rate and depth of breathing
c. Medulla oblongata	An enlarged continuation of the spinal cord that extends from the foramen magnum to the pons and contains masses of gray matter and nerve fibers	Conducts ascending and descending impulses between the brain and spinal cord; contains cardiac, vasomotor, and respiratory control centers and various nonvital reflex control centers
5. Cerebellum	A large mass of tissue inferior to the cerebrum and posterior to the brainstem; includes two lateral hemispheres connected by the vermis	Communicates with other parts of the CNS by tracts; integrates sensory information concerning the position of body parts; and coordinates muscle activities and maintains posture

corrections are incorporated into motor impulses that travel downward through the pons, medulla oblongata, and spinal cord to lower motor neurons in the appropriate patterns to move the body in the desired way.

Overall, the cerebellum integrates sensory information concerning the position of body parts and coordinates skeletal muscle activity and maintains posture. It receives sensory impulses from receptors in muscles, tendons, and joints (proprioceptors) and from special sense organs, such as the eyes and ears. For example, the cerebellum uses sensory information from the semicircular canals of the inner ears concerning the motion and position of the head to help maintain equilibrium (see chapter 12, pp. 467–468). Damage to the cerebellum can cause tremors, inaccurate movements of voluntary muscles, loss of muscle tone, a reeling walk, and loss of equilibrium.

Table 11.7 summarizes the characteristics and functions of the major parts of the brain. Clinical Application 11.5 discusses how brain waves reflect brain activity.

PRACTICE

30 Where is the cerebellum located?

31 What are the major functions of the cerebellum?

32 What types of receptors provide information to the cerebellum?

11.6 PERIPHERAL NERVOUS SYSTEM

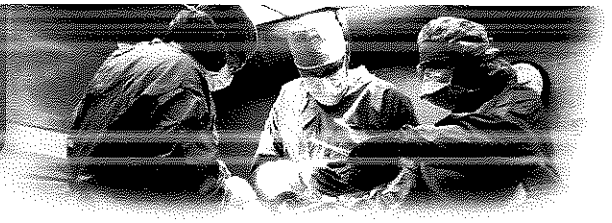
The **peripheral nervous system** consists of the nerves that branch from the CNS, connecting it to other body parts. The PNS includes the *cranial nerves* that arise from the brain and the *spinal nerves* that arise from the spinal cord.

The PNS can also be subdivided into somatic and autonomic nervous systems. Generally, the **somatic nervous system** consists of the cranial and spinal nerve fibers that connect the CNS to the skin and skeletal muscles, so it oversees conscious activities. The **autonomic nervous system** (aw"to nom'ik ner'vus sis'tem) includes fibers that connect the CNS to viscera such as the heart, stomach, intestines, and various glands. The autonomic nervous system controls subconscious actions. Table 11.8 outlines the subdivisions of the nervous system.

TABLE **11.8** | Subdivisions of the Nervous System

1. Central nervous system (CNS)
   a. Brain
   b. Spinal cord
2. Peripheral nervous system (PNS)
   a. Cranial nerves arising from the brain
      (1) Somatic fibers connecting to the skin and skeletal muscles
      (2) Autonomic fibers connecting to viscera
   b. Spinal nerves arising from the spinal cord
      (1) Somatic fibers connecting to the skin and skeletal muscles
      (2) Autonomic fibers connecting to viscera

11.5 CLINICAL APPLICATION



Brain Waves

Brain waves are recordings of fluctuating electrical changes in the brain. To obtain such a recording, electrodes are positioned on the surface of a surgically exposed brain (an electrocorticogram, ECoG) or on the outer surface of the head (an electroencephalogram, EEG). These electrodes detect electrical changes in the extracellular fluid of the brain in response to changes in potential among large groups of neurons. The resulting signals from the electrodes are amplified and recorded. Brain waves originate from the cerebral cortex but also reflect activities in other parts of the brain that influence the cortex, such as the reticular formation. Because the intensity of electrical changes is proportional to the degree of neuronal activity, brain waves vary markedly in amplitude and frequency between sleep and wakefulness.

Brain waves are classified as alpha, beta, theta, and delta waves (fig. 11F). *Alpha waves* are recorded most easily from the posterior regions of the head and have a frequency of 8–13 cycles per second. They occur when a person is awake but resting, with the eyes closed. These waves disappear during sleep, and if the wakeful person's eyes open, higher-frequency beta waves replace the alpha waves.

Beta waves have a frequency of more than 13 cycles per second. Most are recorded in the anterior region of the head. They occur when a person is actively engaged in mental activity or is under tension.

Theta waves have a frequency of 4–7 cycles per second and occur mainly in the parietal and temporal regions of the cerebrum. They are normal in children but do not usually occur in adults. However, some adults produce theta waves in early stages of sleep or at times of emotional stress.

Delta waves have a frequency below 4 cycles per second and happen during sleep. They originate from the cerebral cortex when the reticular formation is not activating it.

Brain wave patterns can be useful for diagnosing disease conditions, such as distinguishing types of seizure disorders (epilepsy) and locating brain tumors. Brain waves are also used to detect *brain death*, in which neuronal activity ceases. In some countries including the United States, an EEG that lacks waves (isoelectric EEG) verifies brain death. However, drugs that greatly depress brain functions must be excluded as the cause of the flat EEG pattern before confirming brain death. ■

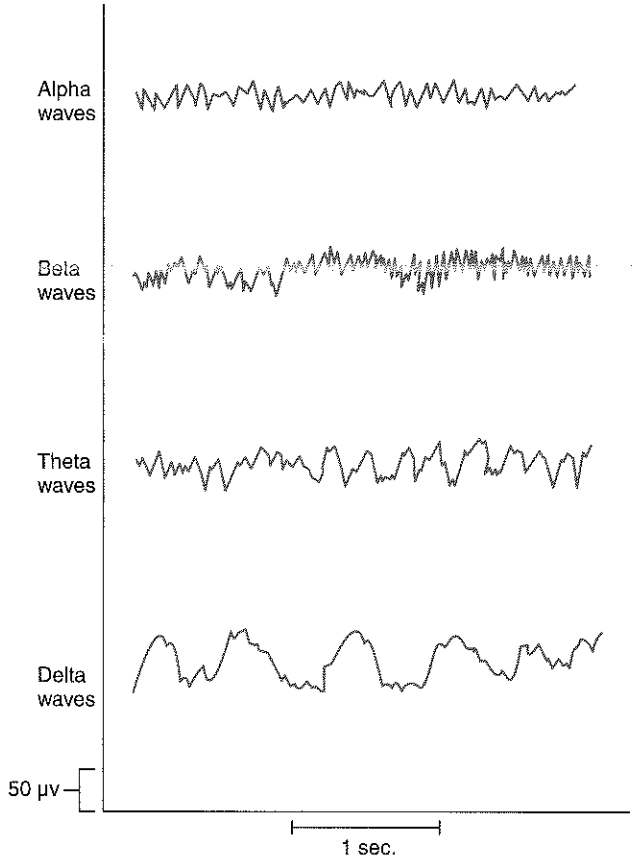


FIGURE 11F Brain waves record fluctuating electrical changes in the brain.

Structure of Peripheral Nerves

A peripheral nerve consists of connective tissue surrounding bundles of nerve fibers. The outermost layer of the connective tissue, called the *epineurium*, is dense and includes many collagenous fibers. Each bundle of nerve fibers (fascicle) is, in turn, enclosed in a sleeve of looser connective tissue called the *perineurium*. A small amount of loose connective tissue called *endoneurium* surrounds individual nerve fibers (figs. 11.23 and 11.24). Blood vessels in the epineurium and perineurium give rise to a network of capillaries in the endoneurium that provides oxygen and nutrients to the neurons.

The term "muscle fiber" refers to an entire muscle cell, whereas the term "nerve fiber" refers to an axon. The terminology for the connective tissue holding them together, however, is similar. In both cases, for example, fibers are bundled into fascicles, whereas epineurium in nerves corresponds to epimysium in muscles, and so forth (see figs. 11.23, 11.24, 9.2, p. 294 and 9.3, p. 295).

Nerve and Nerve Fiber Classification

Recall that nerves are bundles of nerve fibers, or axons. Nerves that have only fibers of sensory neurons, conducting impulses into the brain or spinal cord, are called **sensory nerves.** Nerves that have only fibers involved in motor control are **motor nerves.** Most nerves include both sensory and motor fibers and are called **mixed nerves.**

Nerves originating from the brain that communicate with other body parts are called cranial nerves, whereas

FIGURE 11.23 The structure of a peripheral mixed nerve.

Q: *In the axons found in a mixed nerve, in which direction are the impulses conducted?*

Answer can be found in Appendix G on page 938.

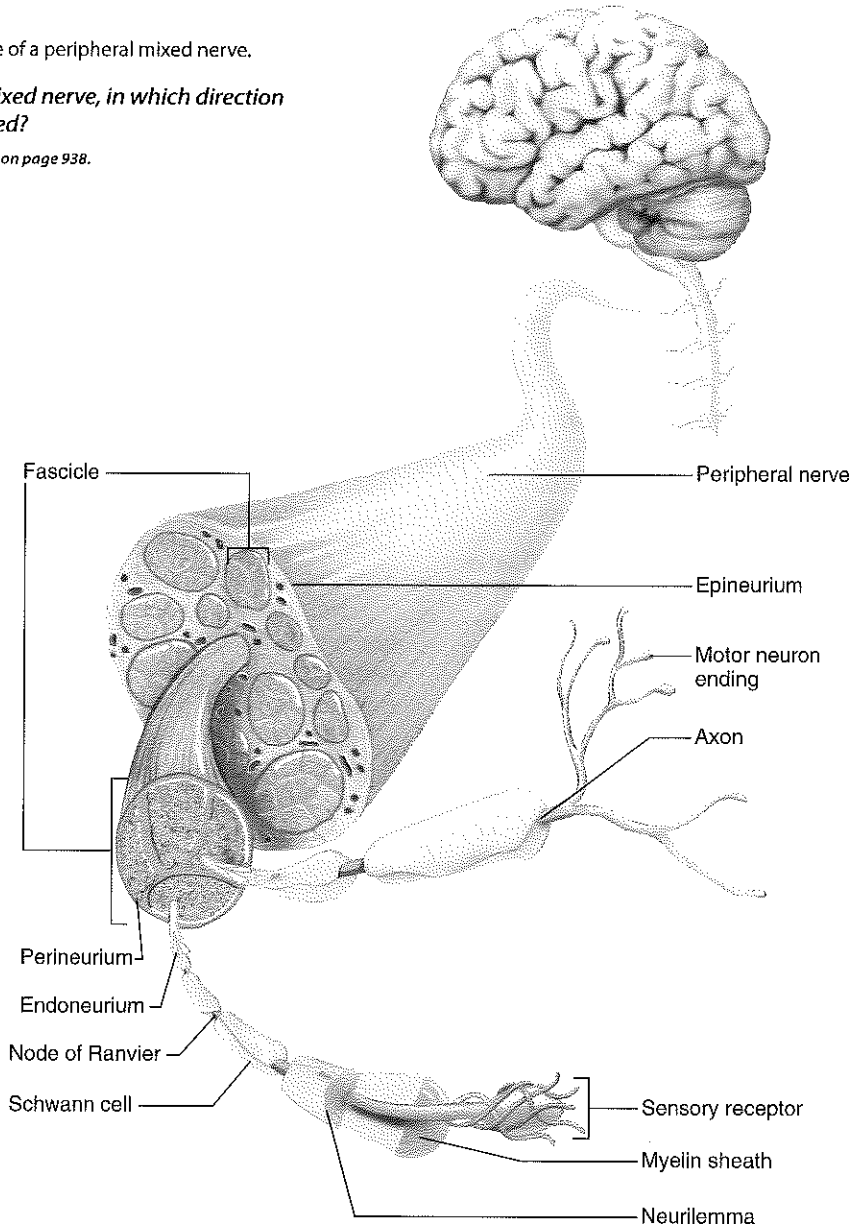
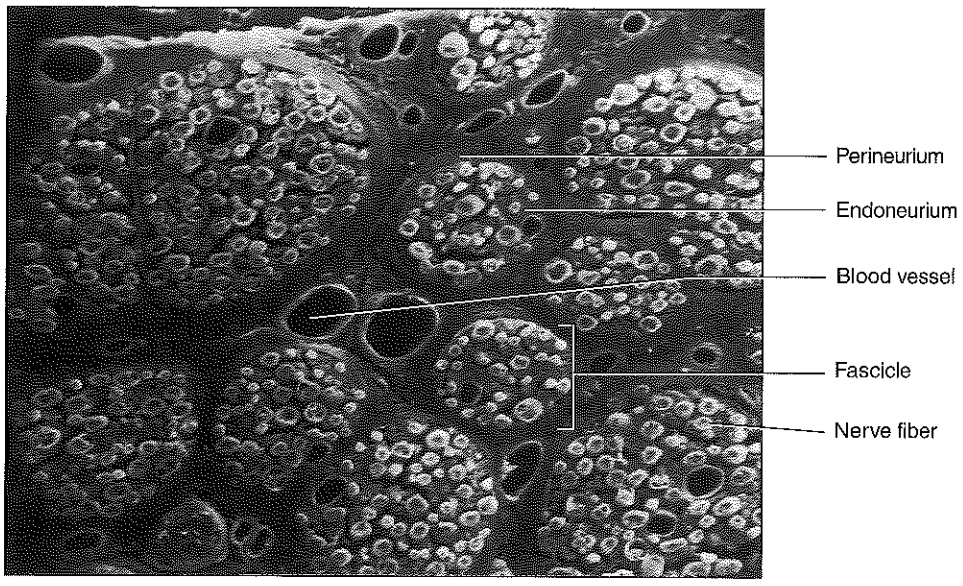


FIGURE 11.24 Scanning electron micrograph of a peripheral nerve in cross section (350×). Note the bundles or fascicles of nerve fibers. Fibers include axons of motor neurons as well as peripheral processes of sensory neurons. Copyright by R. G. Kessel and R. H. Kardon, *Tissues and Organs: A Text-Atlas of Scanning Electron Microscopy,* 1979 (W. H. Freeman & Co.).



those originating from the spinal cord that communicate with other body parts are called **spinal nerves.** The nerve fibers in these structures can be subdivided further into four groups as follows:

1. **General somatic efferent fibers** carry motor impulses outward from the brain or spinal cord to skeletal muscles and stimulate them to contract.
2. **General visceral efferent fibers** carry motor impulses outward from the brain or spinal cord to smooth muscle and glands associated with internal organs.
3. **General somatic afferent fibers** carry sensory impulses inward to the brain or spinal cord from receptors in the skin and skeletal muscles.
4. **General visceral afferent fibers** carry sensory impulses to the CNS from blood vessels and internal organs.

The term *general* in each of these categories indicates that the fibers are associated with general structures such as the skin, skeletal muscles, glands, and viscera. Three other groups of fibers, found only in cranial nerves, are associated with more specialized, or *special*, structures:

1. **Special somatic efferent fibers** carry motor impulses outward from the brain to the muscles used in chewing, swallowing, speaking, and forming facial expressions.
2. **Special visceral afferent fibers** carry sensory impulses inward to the brain from the olfactory and taste receptors.
3. **Special somatic afferent fibers** carry sensory impulses inward to the brain from the receptors of sight, hearing, and equilibrium.

Cranial Nerves

Twelve pairs of **cranial nerves** arise from the underside of the brain. The first two pairs, which begin in the cerebrum, these nerves originate from the brainstem. They pass from their sites of origin through foramina of the skull and lead to areas of the head, neck, and trunk.

Most cranial nerves are mixed nerves, but some of those associated with special senses, such as smell and vision, have only sensory fibers. Other cranial nerves that innervate muscles and glands are primarily composed of motor fibers and have only limited sensory functions. These are neurons associated with certain receptors *(proprioceptors)* that respond to the rate or degree of contraction of skeletal muscles. Because these fibers contribute directly to motor control, cranial nerves whose only sensory component is from such proprioceptors are usually considered motor nerves. This pertains to cranial nerves III, IV, VI, XI, and XII.

Neuron cell bodies to which the sensory fibers in the cranial nerves attach are outside the brain, and most are in groups called *ganglia* (sing., *ganglion*). On the other hand, most motor neuron cell bodies are in the gray matter of the brain.

Numbers and names designate cranial nerves. The numbers indicate the order in which the nerves arise from the brain, from anterior to posterior. The names describe primary functions or the general distribution of cranial nerve fibers (fig. 11.25).

The first pair of cranial nerves, the **olfactory** (ol-fak'to-re) **nerves** (I), are associated with the sense of smell and include only sensory neurons. These bipolar neurons, in the lining of the upper nasal cavity, serve as *olfactory receptor cells.* Axons

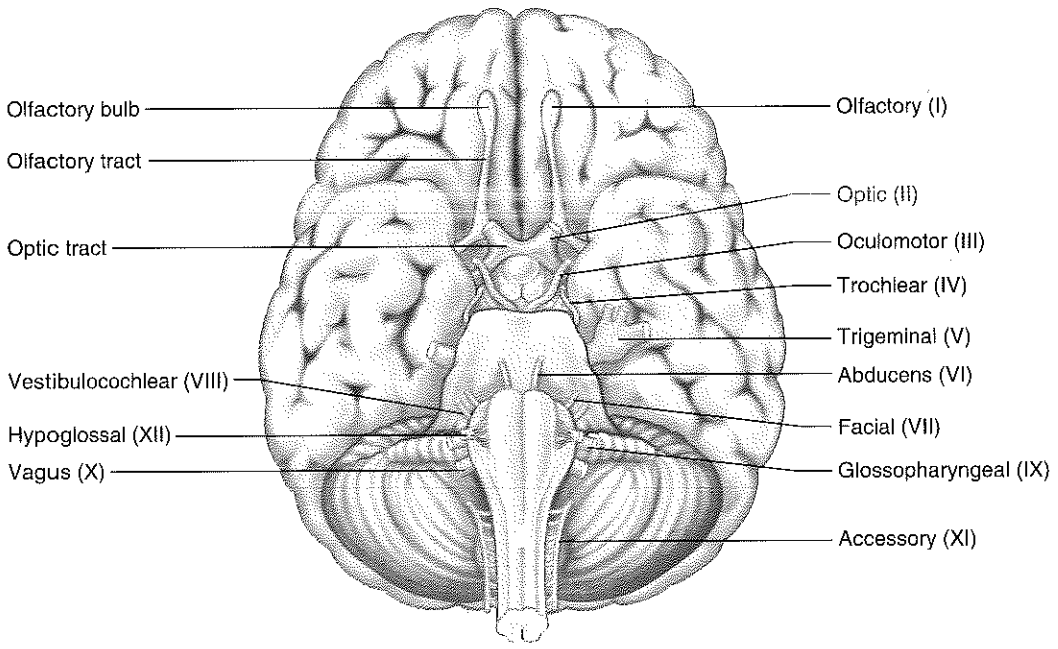


FIGURE 11.25 AP|R The cranial nerves, except for the first two pairs, arise from the brainstem. They are identified either by numbers indicating their order, their function, or the general distribution of their fibers.