14

Nervous Tissue

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MODULE 7: NERVOUS SYSTEM

Throughout the day, your body perceives and responds to multiple sensations. You smell spring flowers, feel the touch of a hand on your shoulder, and perceive your limbs moving. You control multiple muscle movements to walk, talk to the person sitting next to you, and hold this textbook. Other muscle movements occur without your voluntary input: Your heart beats, your stomach churns to digest your breakfast, and you jump at the sound of a honking horn. All of these sensations and muscle movements are interpreted and controlled by your **nervous system.** The nervous system is composed of all tissue types, but primarily of **nervous tissue**—neurons and glial cells (see chapter 4). This chapter introduces the study of the nervous system by first describing its overall organization and then investigating the components of nervous tissue.

14.1 Organization of the Nervous System

Learning Objectives:

1. Identify the organs of the CNS and PNS.
2. Understand the general functions of the nervous system.
3. Identify and describe the specific functions of the sensory and motor nervous systems.
4. Compare and contrast the somatic sensory and visceral sensory components.
5. Compare and contrast the somatic motor and autonomic (visceral) motor components.

As the body's primary communication and control system, the nervous system is extremely complex. To describe its interacting structures and functions, anatomists and physiologists have devised specialized terms and organizational systems. For example, the nervous system may be divided into either structural or functional categories, as shown in **table 14.1**. However, always keep in mind that such artificial divisions are merely intended to simplify discussion—there is only one nervous system.

14.1a Structural Organization: Central and Peripheral Nervous Systems

Based on its anatomic components, the nervous system consists of two subdivisions: the central nervous system and the peripheral nervous system **(figure 14.1)**. The **central nervous system (CNS)** is composed of the **brain** and **spinal cord.** The brain is protected and enclosed within the skull, while the spinal cord is housed and protected within the vertebral canal. The **peripheral** (pĕ-rif´-ĕ-răl) **nervous system (PNS)** includes the **cranial nerves** (nerves that extend from the brain), **spinal nerves** (nerves that extend from the spinal cord), and **ganglia** (gang´glē-ă; sing., *ganglion* = swelling), which are clusters of neuron cell bodies located outside the CNS.

14.1b Functional Organization: Sensory and Motor Nervous Systems

Together, the CNS and PNS perform three general functions:

- **Collecting information.** Specialized PNS structures called **receptors** (dendrite endings of sensory neurons or cells) detect changes in the internal or external environment and pass them on to the CNS as sensory input (discussed in chapter 19).
- **Processing and evaluating information.** After processing sensory input, the CNS determines what, if any, response is required.
- **Responding to information.** After selecting an appropriate response, the CNS initiates specific nerve impulses (rapid movements of an electrical charge along the neuron's plasma membrane), called motor output. Motor output travels through structures of the PNS to **effectors** (the cells that receive impulses from motor neurons: muscles or glands).

There are two functional divisions of the nervous system: the sensory nervous system and the motor nervous system **(figure 14.2)**.

WHAT DO YOU THINK?

1. Why is the term *visceral* sometimes used to describe certain parts of the sensory and motor nervous systems?

Table 14.1	Structural and Functional Divisions of the Nervous System	
Nervous System Organization	**Anatomic Components**	**Description**
STRUCTURAL DIVISIONS		
Central nervous system (CNS)	Brain and spinal cord	Command center of nervous system that integrates and processes nervous information
Peripheral nervous system (PNS)	Nerves (cranial and spinal) and ganglia	Projects information to and receives information from CNS; mediates some reflexes
FUNCTIONAL DIVISIONS		
Sensory nervous system	Some CNS and PNS components (including sensory neurons)	Consists of all axons that transmit a nerve impulse *from* a peripheral structure *to* the CNS; includes pain, touch, temperature, and pressure ("input" information)
Somatic sensory		Transmits input from skin, fascia, joints, and skeletal muscle
Visceral sensory		Transmits input from viscera
Motor nervous system	Some CNS and PNS components (including motor neurons)	Consists of all axons that transmit a nerve impulse *from* the CNS *to* a muscle or gland ("output" information)
Somatic motor (somatic nervous system; SNS)		Voluntary control of skeletal muscle
Autonomic motor (autonomic nervous system; ANS)		Involuntary control of smooth muscle, cardiac muscle, and glands
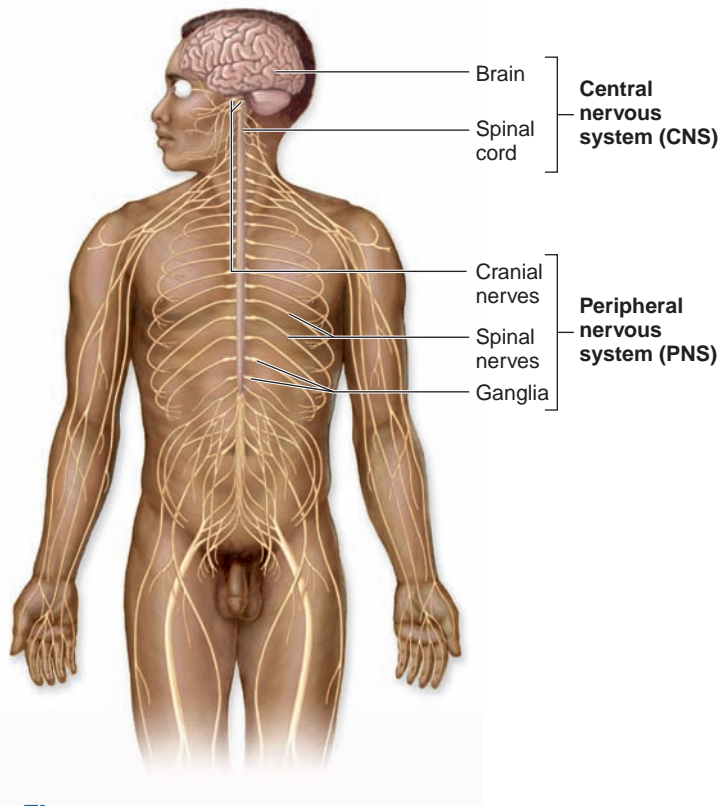
Figure 14.1

Organization of the Nervous System. The central nervous system (CNS) is composed of the brain and spinal cord. The peripheral nervous system (PNS) is composed of cranial nerves, spinal nerves, and ganglia.

Sensory Nervous System

The **sensory** (or *afferent;* af′er-ent) **nervous system** is responsible for receiving sensory information *from* receptors and transmitting this information *to* the CNS. (The term *afferent* means "inflowing," which indicates that nerve impulses are transmitted to the CNS.) Thus, the sensory nervous system is responsible for
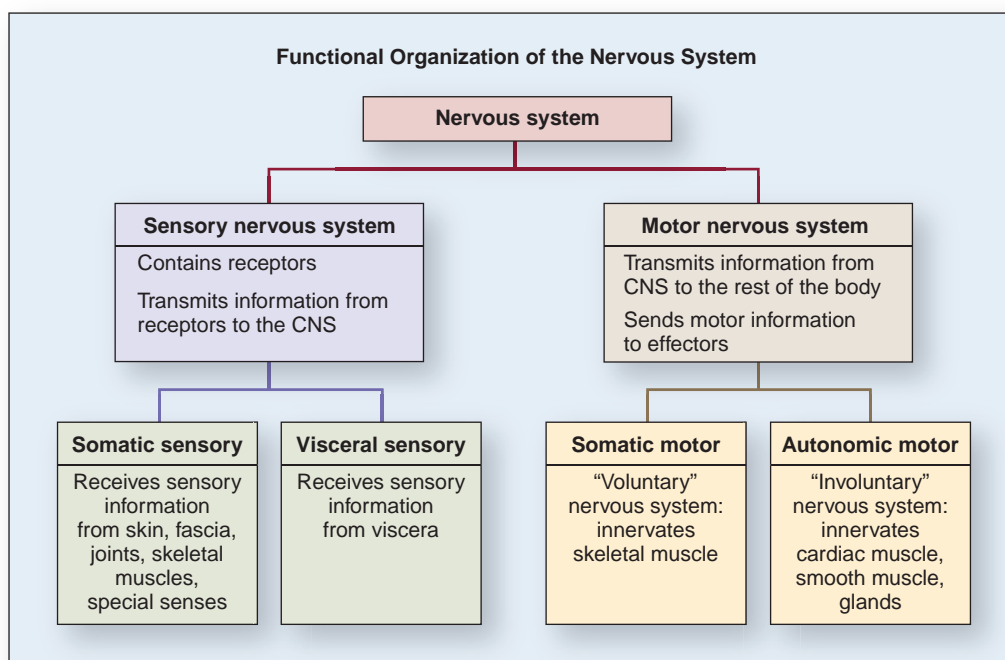
input. The sensory nervous system contains both PNS and CNS components: Nerves of the PNS transmit the sensory information, and certain parts of the brain and spinal cord in the CNS interpret this information.

The sensory nervous system has two components: somatic sensory and visceral sensory. The **somatic sensory** components are the general somatic senses—touch, pain, pressure, vibration, temperature, and proprioception (sensing the position or movement of joints and limbs)—and the special senses (taste, vision, hearing, balance, and smell). These functions are considered *voluntary* because we have some control over them and we tend to be conscious of them. The **visceral sensory** components transmit nerve impulses from blood vessels and viscera to the CNS. The visceral senses primarily include temperature and stretch (of muscles of the organ wall). These functions are said to be *involuntary* because most of the time you do not have voluntary control over them and are not conscious of them. However, you may become aware of visceral sensations when they are extreme—for example, if you have eaten too much and your stomach is bloated.

Motor Nervous System

The **motor** (or *efferent;* ef′er-ent) **nervous system** is responsible for transmitting motor impulses *from* the CNS *to* muscles or glands. (The term *efferent* means "conducting outward," which indicates that nerve impulses are transmitted from the CNS.) Thus, the motor nervous system is responsible for **output.** The motor nervous system contains both CNS and PNS components: Parts of the brain and spinal cord (CNS) initiate nerve impulses, which travel through motor nerves that in turn transmit these impulses to effector organs.

The motor division is subdivided into somatic motor and autonomic motor components. The **somatic motor** component **(somatic nervous system; SNS)** conducts nerve impulses from the CNS to the skeletal muscles, causing them to contract. The somatic motor division is often called the *voluntary nervous system* because the contractions of the skeletal muscles are under conscious control; for example, you exert voluntary

Figure 14.2

Functional Organization of the Nervous System. The nervous system is functionally divided into a sensory nervous system and a motor nervous system. Both of these parts of the nervous system contain somatic and visceral components.

control over your leg muscles as you press on the accelerator of your car.

The **autonomic motor** component is often called the **autonomic nervous system (ANS).** Because it innervates internal organs and regulates smooth muscle, cardiac muscle, and glands without our control, it is also known as the *visceral motor system* or the *involuntary nervous system.* For example, we cannot voluntarily make our hearts stop beating, nor can we prevent our stomachs from growling. The autonomic nervous system has two further subdivisions—parasympathetic and sympathetic—which we examine in chapter 18.

WHAT DID YOU LEARN?

1 Together, what three functions do the CNS and PNS perform?

2 Compare and contrast the meanings of afferent and efferent.

14.2 Cytology of Nervous Tissue

Learning Objectives:

1. Identify and describe the basic features common to all neurons.
2. Describe and understand the structural and functional classifications of neurons.
3. Distinguish between the various types of glial cells, and compare their structures and function.

Two distinct cell types form nervous tissue: neurons, which are excitable cells that are able to generate, transmit, and receive nerve impulses, and glial cells, which are nonexcitable cells that support and protect the neurons.

14.2a Neurons

The basic structural unit of the nervous system is the **neuron** (noor′on). Neurons conduct nerve impulses from one part of the body to another. They have several special characteristics:

- Neurons have a high metabolic rate. Their survival depends on continuous and abundant supplies of glucose and oxygen.
- Neurons have extreme longevity. Most neurons formed during fetal development are still functional in very elderly individuals.
- Neurons typically are nonmitotic (unable to divide and produce new neurons). During the fetal development of neurons, mitotic activity is lost, except possibly in certain areas of the brain (see Clinical View: New Neurons in Adults?).

Neuron Structure

Neurons come in all shapes and sizes, but all neurons share certain basic structural features **(figure 14.3)**. A typical neuron has a cell body. Projecting from the cell body are processes called dendrites and an axon.

The **cell body,** also called a *soma,* serves as the neuron's control center and is responsible for receiving, integrating, and sending nerve impulses. The cell body is enclosed by a plasma membrane and contains cytoplasm surrounding a **nucleus.** The nucleus contains a prominent **nucleolus,** reflecting the high metabolic activity of neurons, which require the production of many proteins. Numerous mitochondria are present within this cytoplasm to produce the large amounts of ATP needed by the neuron. Large numbers of free ribosomes and rough ER produce

New Neurons in Adults?

For years, prevailing medical wisdom has maintained that the number of neurons you have shortly after birth is your supply for a lifetime. Recent studies, however, have shown that this is not always the case. Researchers investigating the hippocampus of the brain, the region involved in memory processing (described in chapter 15), have found that mature neurons are indeed "terminally" differentiated, meaning they lack the ability to divide and produce daughter cells. However, there now appears to be a population of immature progenitor cells in the hippocampus that are called *neural stem cells.* These stem cells were once thought to give rise only to new glial cells in adults, but it is now clear that under special circumstances they can mature into neurons. What's more, the new neurons appear able to incorporate themselves, at least to some degree, into the brain circuitry. Researchers have learned that the surrounding glial cells provide the chemical signals that direct a stem cell down the path of nerve cell maturation.

Although excited by these new data, researchers remain divided as to whether the new cells truly function in the same way as the ones that were present all along. It has yet to be conclusively shown that new hippocampal neurons can make all the necessary connections needed to function as fully integrated parts of the brain. One problem hindering medical application of this new information is that stem cells apparently do not mature to neurons uniformly throughout the adult brain. Only a few regions seem to be so lucky, and the hippocampus is one. Even so, understanding the mechanisms that drive this process in the hippocampus greatly expands our knowledge of brain function and may help explain how the brain can continue to function for so many years. Clinicians hope that research in this field will lead to therapies for conditions that cause the loss of neurons.

proteins for the active neuron. Together, both free and bound ribosomes go by two names: **chromatophilic** (krō-mă-tō-fil′ik; *chromo* = color; *phileo* = to love) **substance,** because they stain darkly with basic dyes, or *Nissl bodies,* because they were first described by the German microscopist Franz Nissl. Cytologists believe that the chromatophilic substance together with dendrites and cell bodies account for the gray color of the gray matter, as seen in brain and spinal cord areas containing collections of neuron cell bodies.

Dendrites (den′drīt; *dendrites* = relating to a tree) tend to be shorter, smaller processes that branch off the cell body. Some neurons have only one dendrite, while others have many. Dendrites conduct nerve impulses toward the cell body; in essence, they receive input and then transfer it to the cell body for processing. The more dendrites a neuron has, the more nerve impulses that neuron can receive from other cells.
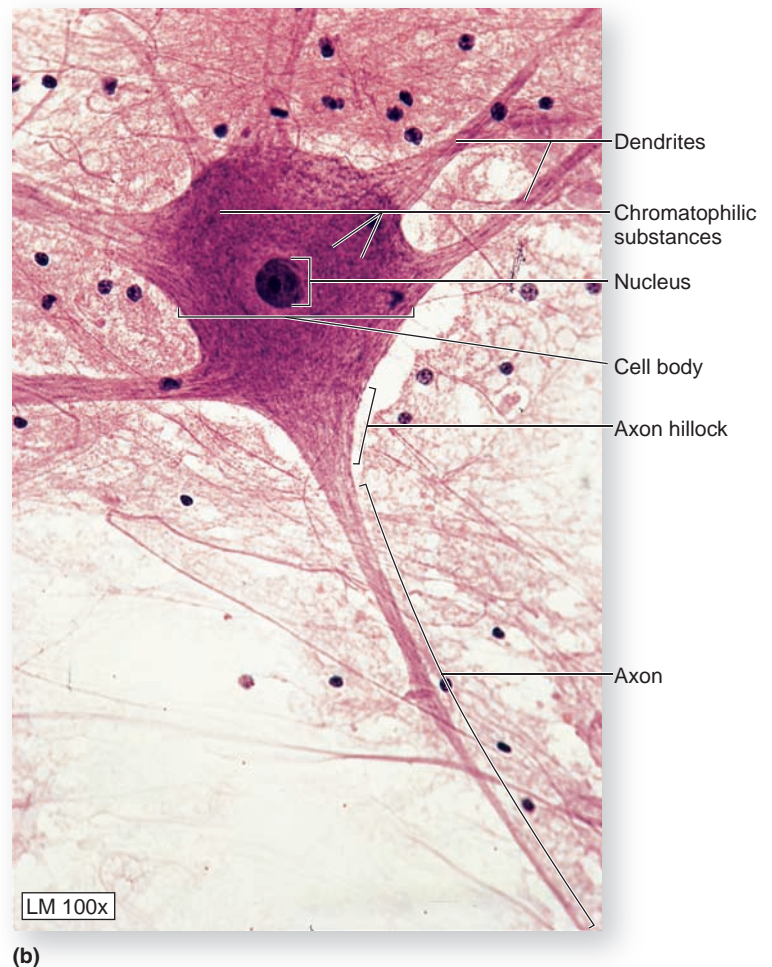
The typically longer nerve cell process emanating from the cell body is the **axon** (ak′son; *axon* = axis), sometimes called a *nerve fiber.*

Neurons have either one axon or no axon at all (neurons with only dendrites and no axons are called **anaxonic** [an-aks-on-ic; *an* = without]. They are small neurons that provide no clues to
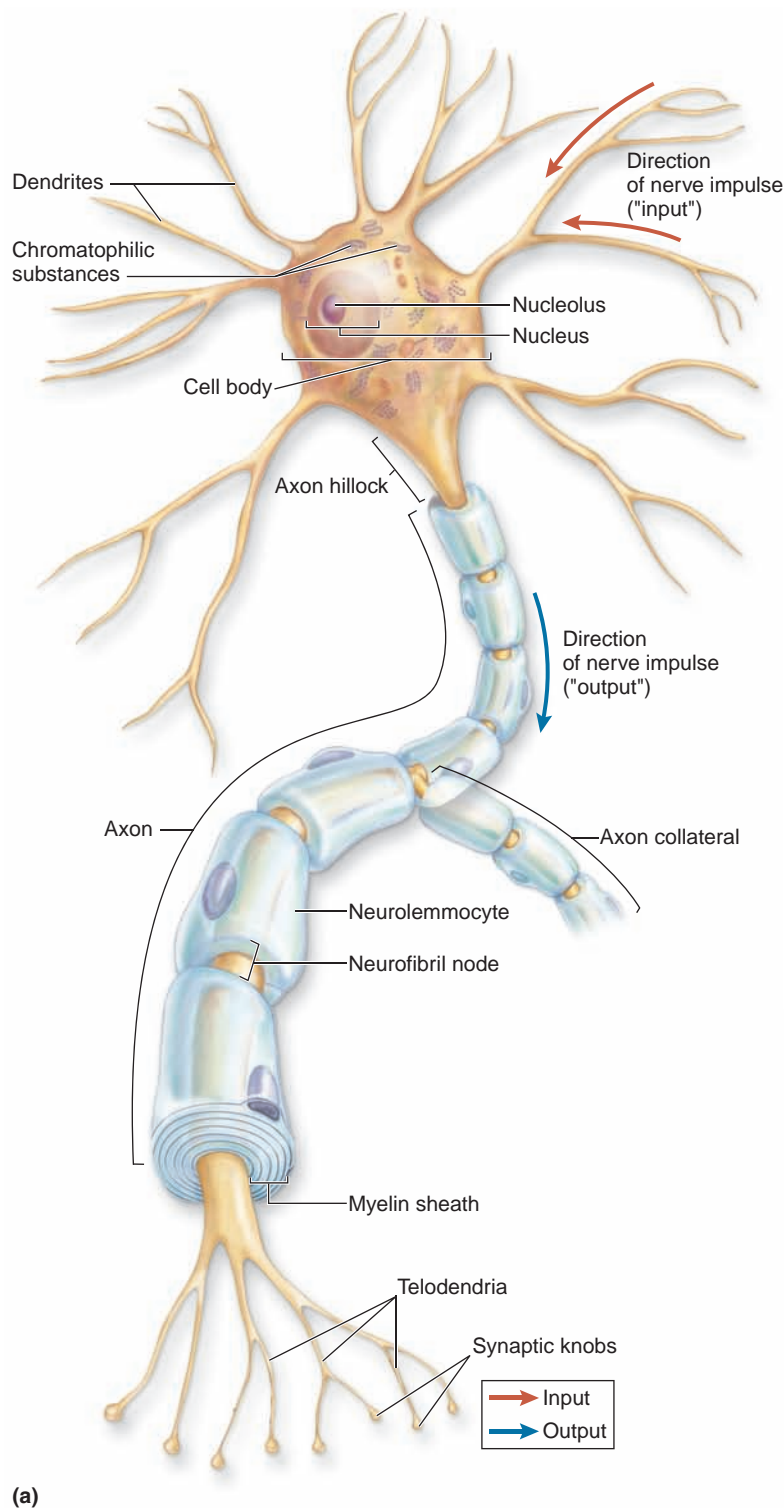
(a)

(b)

Figure 14.3

Structures in a Typical Neuron. (*a*) Input information (red arrows) flows through dendrites to the cell body; output information (blue arrows) flows through the axon to the next cell. (*b*) Photomicrograph of a large motor neuron. AP|R

distinguish axon from dendrite; they are only found in CNS; they are uncommon and their function is unknown.) Most neurons, however, have a single axon. The axon transmits a nerve impulse away from the cell body toward another cell; in essence, the axon transmits output information to other cells. The axon connects to the cell body at a triangular region called the **axon hillock** (hil′lok). Unlike the rest of the cell body, the axon hillock is devoid of chromatophilic substance, and so it lacks those dark-staining regions when viewed under the microscope. Although an axon remains relatively unbranched for most of its length, it may give rise to a few side branches called **axon collaterals.** Most axons and their collaterals branch extensively at their distal end into an array of fine terminal extensions called **telodendria** (tel-

ō-den′dria; sing., telodendrion; *telos* = end), or *axon terminals.* The extreme tips of these fine extensions are slightly expanded regions called **synaptic** (si-nap′tik) **knobs** (also called *end bulbs* or *terminal boutons*).

Special terms denote other internal structures of a neuron. The cytoplasm within the cell body is called the **perikaryon** (per-i-kar′ē-on; *peri* = around, *karyon* = kernel), although some anatomists use that term to describe the whole cell body. The microtubules that form the cytoskeleton are called neurotubules. **Neurofilaments** (noor-ō-fil′ă-ment; *filamentum* = thread) are intermediate filaments that aggregate to form bundles called **neurofibrils** (noor-ō-fī′bril; *fibrilla* = fiber). Neurofibrils extend as a complex network into both the dendrites and axons, where their

Table 14.2	Parts of a Neuron
Category/Structure	**Description**
Neuron	Structural and functional cell of the nervous system; sometimes called a nerve cell
Cell body	Nucleus and surrounding cytoplasm of a neuron (excluding its dendrites and axon)
Perikaryon	Most often refers to the cytoplasm within the cell body. Sometimes used to describe the entire cell body
Neurotubules	Microtubules that form the cytoskeleton
Neurofilaments	Intermediate filaments that aggregate to form bundles called neurofibrils
Neurofibrils	Aggregates of neurofilaments that extend as a complex network into dendrites and axons, their tensile strength provides support for these processes
Dendrites	Neuron processes that conduct information *to* the cell body ("input")
Axon	Neuron process that conducts nerve impulses *away* from the cell body ("output")
Axon hillock	Triangular region connecting axon to cell body
Axon collaterals	Side branches of an axon
Telodendria	Fine terminal branches of an axon or axon collateral
Synaptic knobs	Slightly expanded regions at the tips of telodendria

(a) Unipolar neuron

(b) Bipolar neuron

(c) Multipolar neurons

Figure 14.4

Structural Classification of Neurons. Neurons can be classified according to the number of processes extending directly from the cell body. (*a*) A unipolar neuron has a single process that divides into a peripheral process and a central process. (*b*) A bipolar neuron has two processes. (*c*) A multipolar neuron has three or more processes.

tensile strength provides support for these processes. **Table 14.2** reviews some of the terms used to describe neuron structures.
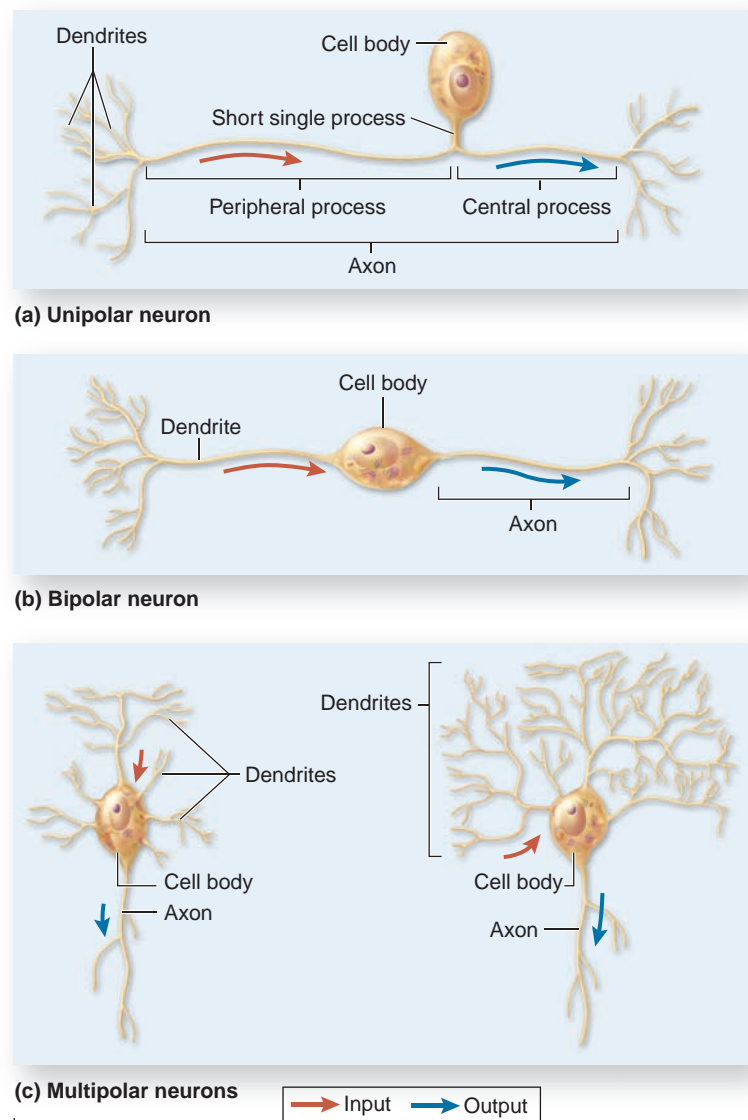
Neuron Classification

Neurons vary widely in morphology and location. They can be classified according to either their structure or their function **(table 14.3)**.

Structural Classification   Structurally, neurons are classified into three types, based on the number of neuron processes emanating directly from the cell body: unipolar, bipolar, or multipolar **(figure 14.4)**.

Unipolar neurons have a single, short neuron process that emerges from the cell body and branches like a T. These neurons are also called *pseudounipolar* (soo′dō-oo-nē-pō-lăr; *pseudo* = false, *uni* = one) because they start out as bipolar neurons during development, but their two processes fuse into a single process. The naming of the branched processes in unipolar neurons has been a source of confusion as it relates to the common definitions of dendrites and axons. It seems most appropriate to call the short, multiple-branched receptive endings dendrites. The combined **peripheral process** (from dendrites to the cell body) and **central process** (from the cell body into the CNS) together denote the axon, because these processes generate and conduct impulses and are often myelinated. Most sensory neurons of the PNS are unipolar neurons.

Bipolar neurons have two neuron processes that extend from the cell body—one axon and one dendrite. These neurons are relatively uncommon in humans and primarily limited to some of the special senses. For example, bipolar neurons are located in the olfactory epithelium of the nose and in the retina of the eye.

Multipolar neurons are the most common type of neuron. Multiple neuron processes—many dendrites and a single axon—

extend from the cell body. Examples of multipolar neurons include motor neurons that innervate muscle and glands. **AP|R**

Functional Classification   Functionally, neurons are classified as one of three types according to the direction the nerve impulse travels relative to the CNS: sensory neurons, motor neurons, or interneurons **(figure 14.5)**.

Sensory neurons, or *afferent neurons,* transmit nerve impulses *from* sensory **receptors** *to* the CNS. These neurons are specialized to detect changes in their environment called **stimuli** (sing., *stimulus*). Stimuli can be in the form of touch, pressure, heat, light, or chemicals. Most sensory neurons are unipolar, although a few are bipolar (e.g., those in the olfactory epithelium of the nose and the retina of the eye, as previously mentioned). The cell bodies of unipolar sensory neurons are located outside the CNS and housed within structures called posterior (dorsal) root ganglia.

Motor neurons, or *efferent neurons,* transmit nerve impulses *from* the CNS *to* muscles or glands. They are called motor neurons because most of them extend to muscle cells, and the nerve

Table 14.3	Structural and Functional Classifications of Neurons	
Structural Classification	**Description**	**Functional Example**
Unipolar neuron	Common type of sensory neuron; single short cell process extends directly from the cell body and looks like a T as a result of the fusion of two processes into one long axon	Most sensory neurons (detect stimuli in the form of touch, pressure, temperature, or chemicals)
Bipolar neuron	Relatively uncommon; two nerve cell processes extend directly from the cell body	Some special sense neurons (e.g., in olfactory epithelium of nose, retina of eye)
Multipolar neuron	Most common type of neuron; multiple nerve cell processes extend from cell body; typically one axon and many dendrites	Interneurons, motor neurons
Functional Classification	**Description**	**Structural Example**
Sensory	Conducts nerve impulses *from* body *to* CNS	Most sensory neurons are unipolar; a few (e.g., some in olfactory epithelium and retina) are bipolar
Motor	Conducts nerve impulses *from* CNS *to* muscles or glands	Multipolar
Interneuron	Found only in CNS; facilitates communication between motor and sensory neurons	Multipolar

impulses they transmit cause these cells to contract. The muscle and gland cells that receive nerve impulses from motor neurons are called effectors, because their stimulation produces a response or effect. The cell bodies of most motor neurons lie in the spinal cord, whereas the axons primarily travel in cranial or spinal nerves to muscles and glands. All motor neurons are multipolar.

Study Tip!

It is sometimes difficult to remember the relationships between "afferent and sensory" and "efferent and motor" and their general locations. This mnemonic will help keep them straight in your mind: "SAME DAVE" (**S**ensory-**A**fferent, **M**otor-**E**fferent; **D**orsal-**A**fferent, **V**entral-**E**fferent). Don't forget that dorsal is posterior and ventral is anterior in humans.

Interneurons, or *association neurons,* lie entirely within the CNS and are multipolar structures. They receive nerve impulses from many other neurons and carry out the integrative function of the nervous system—that is, they retrieve, process, and store information and "decide" how the body responds to stimuli. Thus, interneurons facilitate communication between sensory and motor neurons. Figure 14.5 shows a sensory neuron transmitting stimuli (sensory information) to an interneuron, which then processes that information and signals the appropriate motor neuron(s) to transmit a nerve impulse to the muscle. Interneurons outnumber all other neurons in both their total number and different types; it is estimated that 99% of our neurons are interneurons. The number of interneurons activated during processing or storing increases dramatically with the complexity of the response.
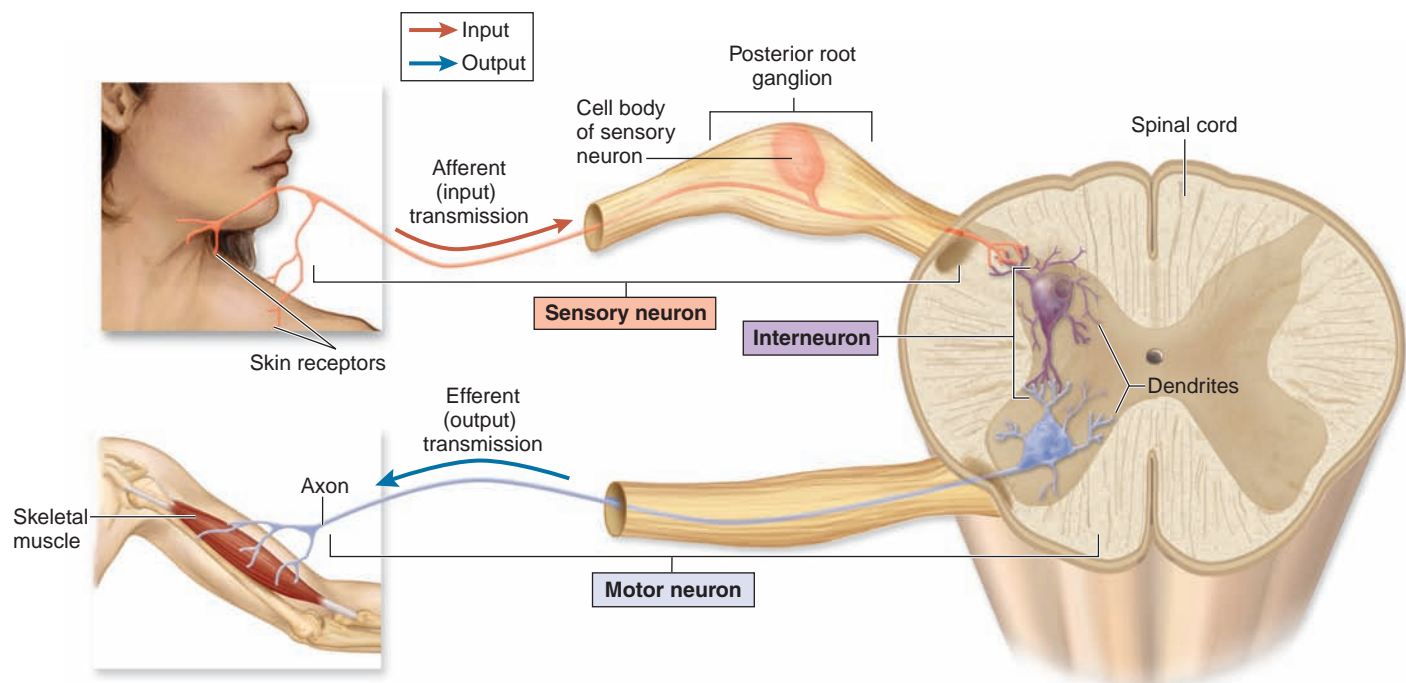
Figure 14.5

Functional Classification of Neurons. Sensory neurons carry afferent (input) signals to the central nervous system. Interneurons process information in the CNS. Motor neurons transmit efferent (output) impulses from the CNS to effectors. AP|R
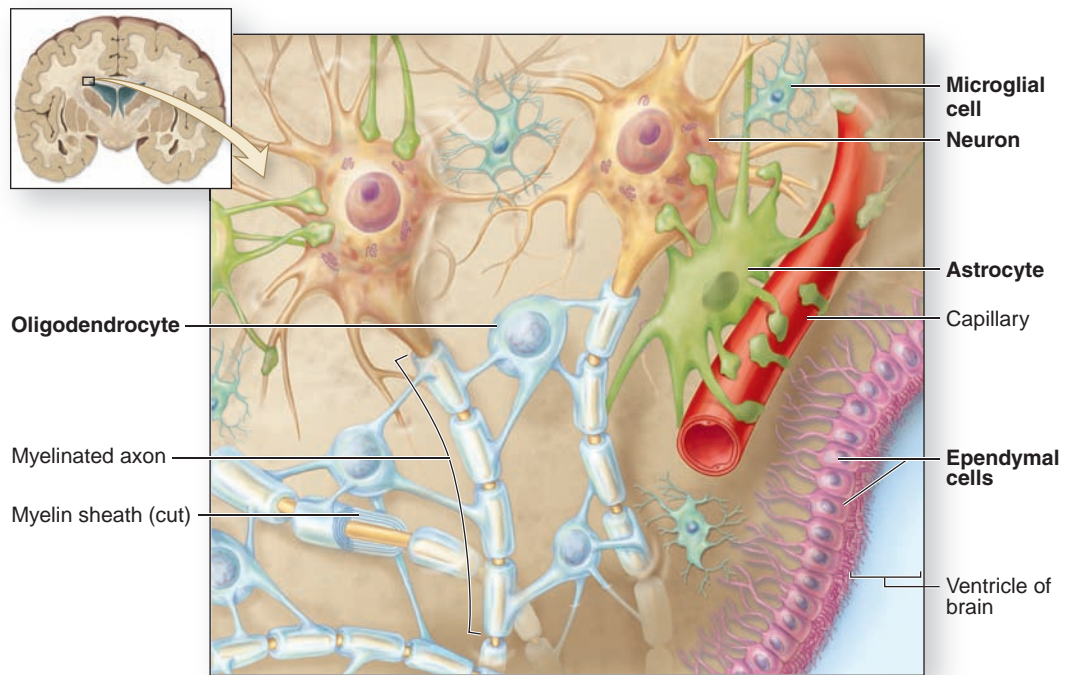
Figure 14.6

Cellular Organization of Nervous Tissue Within the CNS. The four types of glial cells in the CNS are shown in relationship to a neuron.

14.2b Glial Cells

Glial (glī′ăl) **cells,** sometimes referred to as *neuroglia* (noo-rog′lē-a; *glia* = glue) occur within both the CNS and the PNS. Glial cells differ from neurons in that they are smaller and capable of mitosis. Glial cells do not transmit nerve impulses, but they do assist neurons with their functions. Collectively, the glial cells physically protect and help nourish neurons, and provide an organized, supporting framework for all the nervous tissue. During development, glial cells form the framework that guides young migrating neurons to their destinations.

Glial cells far outnumber neurons. The nervous tissue of a young adult may contain 35 to 100 billion neurons and 100 billion to 1 trillion glial cells. Collectively, glial cells account for roughly half the volume of the nervous system. **AP|R**

WHAT DO YOU THINK?

2   If a person has a "brain tumor," is it more likely to have developed from neurons or from glial cells? Why?

Glial Cells of the CNS

Four types of glial cells are found in the central nervous system: astrocytes, ependymal cells, microglial cells, and oligodendrocytes **(figure 14.6)**. They can be distinguished on the basis of size, intracellular organization, and the presence of specific cytoplasmic processes **(table 14.4)**.
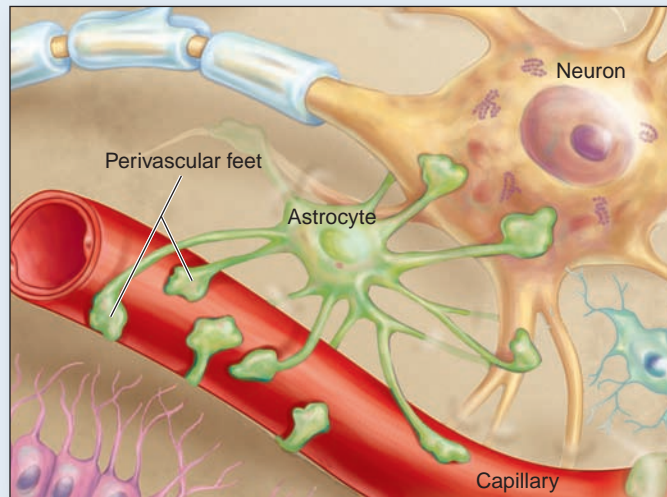
Astrocytes   **Astrocytes** (as′trō-sīt; *astron* = star) exhibit a starlike shape due to many projections from their surface **(figure 14.7a)**.

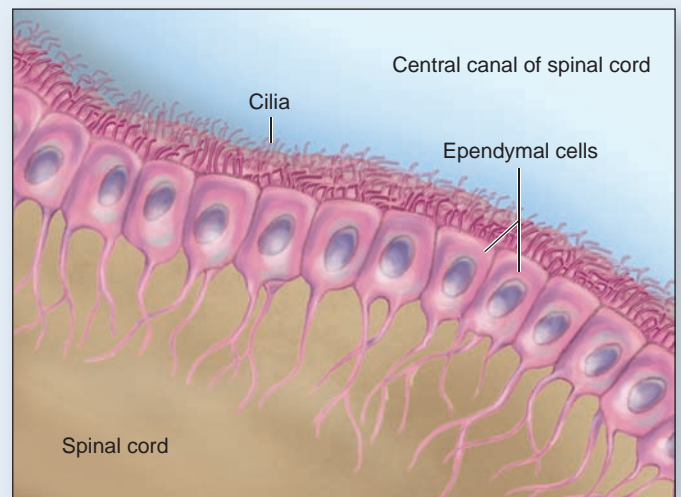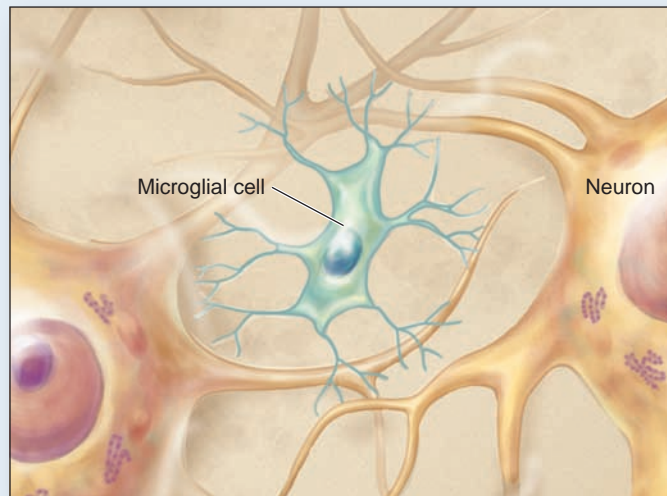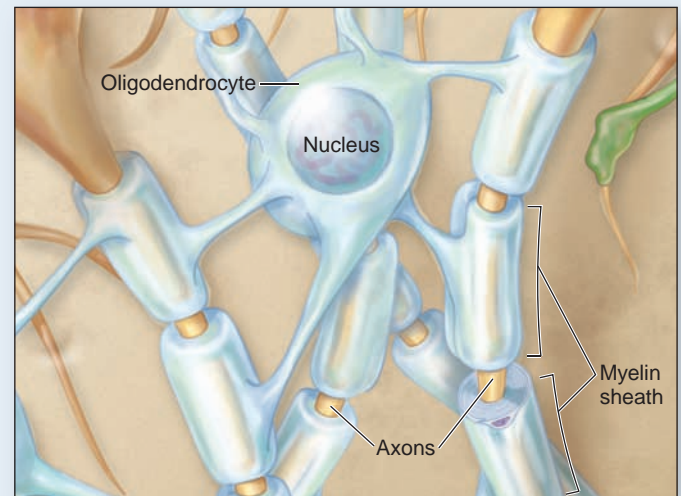| Table 14.4	Glial Cells	
Cell Type	**Appearance**	**Functions**
CENTRAL NERVOUS SYSTEM		
Astrocyte	Large cell with numerous cell processes; in contact with neurons and capillaries; most common type of glial cell	Helps form the blood-brain barrier Regulates tissue fluid composition Provides structural support and organization to CNS Replaces damaged neurons Assists with neuronal development
Ependymal cell	Simple cuboidal epithelial cell lining cavities in brain and spinal cord; cilia on apical surface	Lines ventricles of brain and central canal of spinal cord Assists in production and circulation of CSF
Microglial cell	Small cell with slender branches from cell body; least common type of glial cell	Defends against pathogens Removes debris Phagocytizes wastes
Oligodendrocyte	Rounded, bulbous cell with slender cytoplasmic extensions; extensions wrap around CNS axons	Myelinates and insulates CNS axons Allows faster nerve impulse conduction through the axon
PERIPHERAL NERVOUS SYSTEM		
Satellite cell	Flattened cell clustered around neuronal cell bodies in a ganglion	Protects and regulates nutrients for cell bodies in ganglia
Neurolemmocyte	Flattened cell wrapped around a portion of an axon in the PNS	Myelinates and insulates PNS axons Allows for faster nerve impulse conduction through the axon

CNS Glial Cells

Neuron

Perivascular feet

Astrocyte

Capillary

(a) Astrocyte

Central canal of spinal cord

Cilia

Ependymal cells

Spinal cord

(b) Ependymal cells

Microglial cell

Neuron

(c) Microglial cell

Oligodendrocyte

Nucleus

Myelin sheath

Axons

(d) Oligodendrocyte

PNS Glial Cells

Posterior root ganglion

Satellite cells

Axon

Cell body of sensory neuron

Posterior root

(e) Satellite cells

Neurofibril nodes

Axon

Nucleus

Neurolemmocyte

Myelin sheath
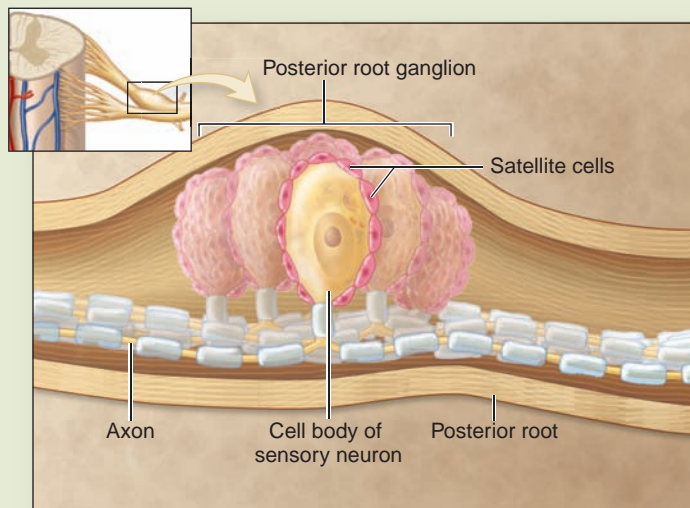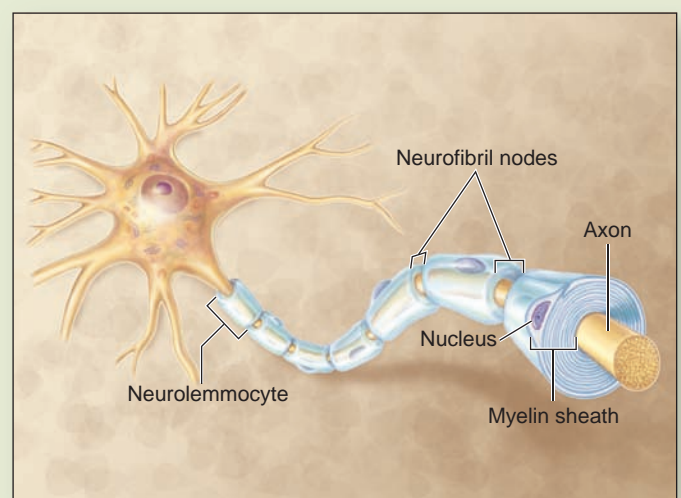
(f) Neurolemmocytes

Figure 14.7

Glial Cells. (*a*) Astrocytes have perivascular feet (only a few are shown here to appreciate their morphology) that wrap completely around capillaries in the CNS. (*b*) Ependymal cells line the fluid-filled spaces in the brain and spinal cord. (*c*) Microglial cells phagocytize damaged neurons and cellular debris. (*d*) Oligodendrocytes myelinate axons in the CNS. (*e*) In the PNS, satellite cells surround neuron cell bodies in ganglia, such as the posterior root ganglion. (*f*) Neurolemmocytes myelinate axons in the PNS.
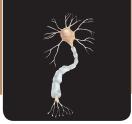
These numerous cell processes touch both capillary walls and different parts of neurons. Astrocytes are the most abundant glial cell in the CNS, and they constitute over 90% of the nervous tissue in some areas of the brain. Their functions include:

- **Helping form the blood-brain barrier.** Ends of astrocyte processes called perivascular feet wrap completely around and cover the outer surface of capillaries in the brain. Together, the perivascular feet and the brain capillaries, which are less "leaky" than other capillaries in the body, contribute to a **blood-brain barrier (BBB)** that strictly controls substances entering the nervous tissue in the brain from the bloodstream. This blood-brain barrier protects the delicate brain from toxins (such as certain waste products and drugs in the blood), but allows needed nutrients to pass through. Sometimes this barrier is detrimental; for example, some medications are not allowed to exit the capillaries and enter the nervous tissue in the brain.
- **Regulating tissue fluid composition.** Astrocytes help regulate the chemical composition of the interstitial fluid within the brain by controlling movement of molecules from the blood to the interstitial fluid.
- **Forming a structural network.** The cytoskeleton in astrocytes strengthens and organizes nervous tissue in the CNS.
- **Replacing damaged neurons.** When neurons are damaged and die, the space they formerly occupied is often filled by cells produced by astrocyte division, a process termed *astrocytosis.*
- **Assisting neuronal development.** Astrocytes help direct the development of neurons in the fetal brain by secreting chemicals that regulate the connections between neurons.

Ependymal Cells   **Ependymal** (ep-en′di-măl) **cells** are cuboidal epithelial cells that line the internal cavities (ventricles) of the brain and the central canal of the spinal cord (figure 14.7*b*). These cells have slender processes that branch extensively to make contact with other glial cells in the surrounding nervous tissue. Ependymal cells and nearby blood capillaries together form a network called the choroid (ko′royd) plexus (see figure 15.7). The choroid plexus produces cerebrospinal fluid (CSF), a clear liquid that bathes the CNS and fills its internal cavities. The ependymal cells have cilia on their apical surfaces that help circulate the CSF. (Chapter 15 describes ependymal cells, the choroid plexus, and CSF in more detail.)

Microglial Cells   **Microglial** (mī-krog′le-ăl; *micros* = small) **cells** represent the smallest percentage of CNS glial cells; some estimates of their prevalence are as low as 5%. Microglial cells are typically small cells that have slender branches extending from the main cell body (figure 14.7*c*). They wander through the CNS and replicate in response to an infection. They perform phagocytic activity and remove debris from dead or damaged nervous tissue. Thus, the activities of microglial cells resemble those of the macrophages of the immune system.

Oligodendrocytes   **Oligodendrocytes** (ol′i-gō-den′drō-sīt; *oligos* = few) are large cells with a bulbous body and slender cytoplasmic extensions or processes (figure 14.7*d*). The processes of oligodendrocytes ensheathe portions of many different axons, each repeatedly wrapping around part of an axon like electrical tape wrapped around a wire. This protective covering around the axon is called a myelin sheath, which we discuss in a later section.

Glial Cells of the PNS

The two glial cell types in the PNS are satellite cells and neurolemmocytes.

Satellite Cells   **Satellite cells** are flattened cells arranged around neuronal cell bodies in ganglia. (Recall that a ganglion is a collection of neuron cell bodies located outside the CNS.) For example, figure 14.7*e* illustrates how satellite cells surround the cell bodies of sensory neurons located in a specific type of ganglion called a posterior root ganglion. Satellite cells physically separate cell bodies in a ganglion from their surrounding interstitial fluid, and regulate the continuous exchange of nutrients and waste products between neurons and their environment.

Neurolemmocytes   **Neurolemmocytes** (noor-ō-lem′ō-sīt), also called *Schwann cells,* are associated with PNS axons (figure 14.7*f*). These cells are responsible for myelinating PNS axons, a process to be discussed in the next section.

Tumors of the Central Nervous System

Neoplasms resulting from unregulated cell growth, commonly known as tumors, sometimes occur in the central nervous system. A tumor that originates within the organ where it is found is called a *primary tumor*. Because mature neurons do not divide and are incapable of giving rise to tumors, primary CNS tumors originate in supporting tissues within the brain or spinal cord that have retained the capacity to undergo mitosis: the meninges (protective membranes of the CNS) or the glial cells. Glial cell tumors, termed **gliomas,** may be either relatively benign and slow-growing or malignant (capable of metastasizing [spreading] to other areas of the body).

A *secondary tumor* is a neoplasm that has originated at one site but subsequently spread to some other organ. For example, lung cancer can metastasize to the nervous system and form additional tumors.
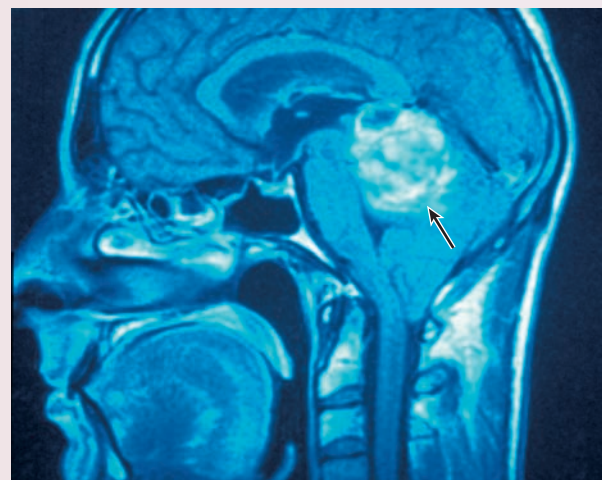
An MRI shows a glioma (arrow).

3 How do dendrites and axons differ in terms of their structure, number, and general function?

4 How do astrocytes participate in the blood–brain barrier?

5 If a person suffers from meningitis (an inflammation of the coverings around the brain), which type of glial cell usually replicates in response to the infection?

6 What are satellite cells, where are they located, and what do they do?

14.3 Myelination of Axons

Learning Objectives:

1. Identify and describe the composition and function of a myelin sheath.
2. Describe and compare nerve impulse propagation in saltatory and continuous conduction.

The main activity of axons is nerve impulse conduction. A **nerve impulse** is the rapid movement of an electrical charge along a neuron's plasma membrane. A nerve impulse is also known as an *action potential,* because a nerve impulse is caused by an actual voltage (potential) change that moves along the plasma membrane of the axon. The nerve impulse's ability to travel along an axon is affected by a process called myelination.
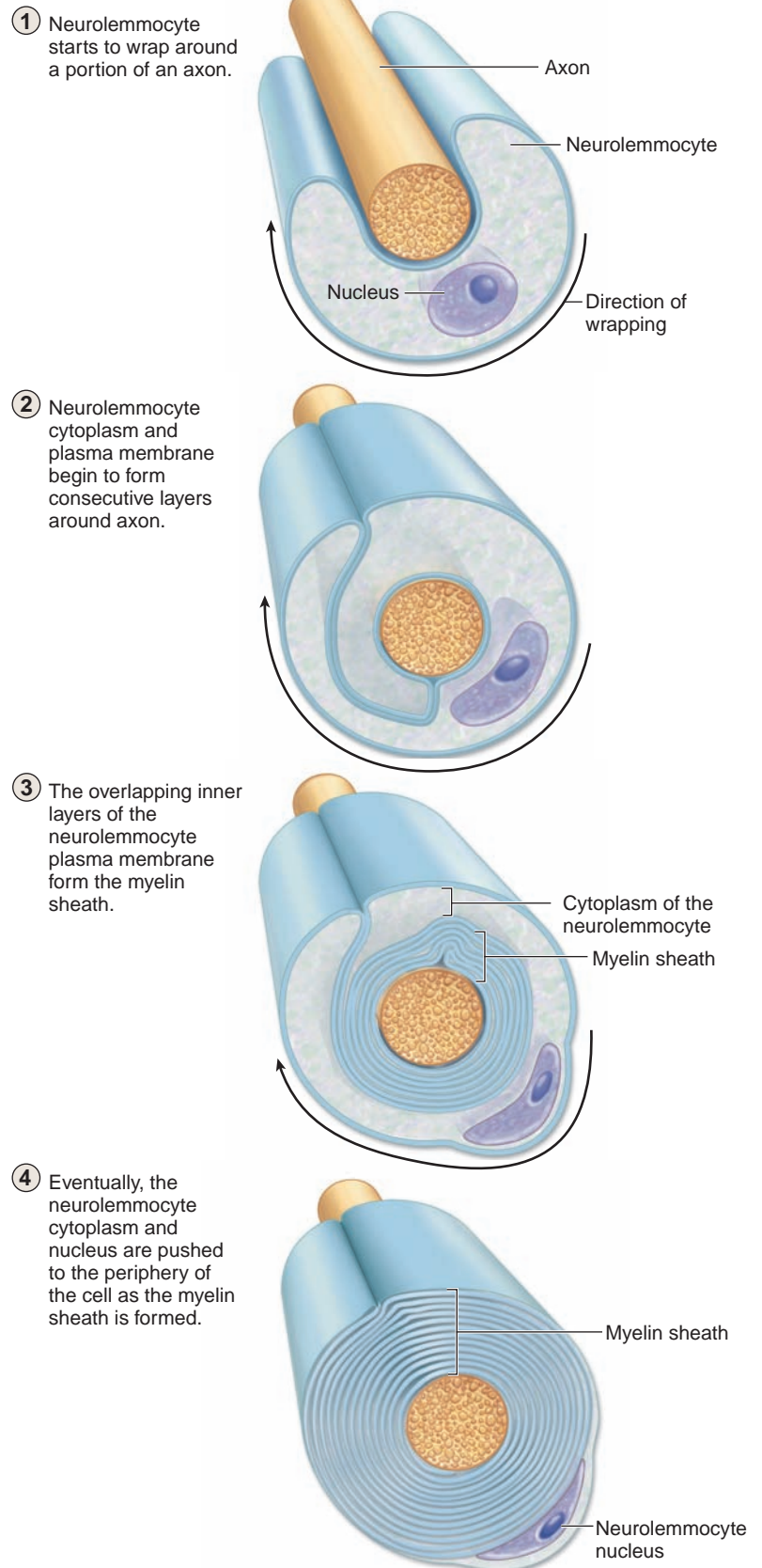
14.3a Myelination

Myelination is the process by which part of an axon is wrapped with a **myelin sheath,** the insulating covering around the axon consisting of concentric layers of myelin. In the CNS, a myelin sheath forms from oligodendrocytes, and in the PNS, it forms from neurolemmocytes. Therefore, myelin mainly consists of the plasma membranes of these glial cells and contains a large proportion of fats and a lesser amount of proteins. The high lipid content of the myelin sheath gives the axon a distinct, glossy-white appearance.

Figure 14.8 illustrates the process of myelinating a PNS axon. The neurolemmocyte starts to encircle a 1 millimeter (mm) portion of the axon, much as if you were wrapping a piece of tape around a portion of your pencil. As the neu-rolemmocyte continues to wrap around the axon, its cyto-plasm and nucleus are squeezed to the periphery (the outside edge). The overlapping inner layers of the plasma membrane form the myelin sheath. Sometimes the name **neurilemma** is used to describe this delicate, thin outer membrane of the neurolemmocyte.

In the CNS, an oligodendrocyte can myelinate a 1 milli-meter portion of *many* axons, not just one. **Figure 14.9a** shows oligodendrocytes myelinating portions of three different axons. The cytoplasmic extensions of the oligodendrocyte wrap successively around a portion of each axon, and successive plasma membrane layers form the myelin sheath.

In the PNS, a neurolemmocyte can myelinate a 1 milli-meter portion of a single axon only (figure 14.9b). Thus, if an axon is longer than 1 millimeter (and most PNS axons are), it takes many neurolemmocytes to myelinate the entire axon. Figure 14.3a shows an axon that has seven neurolemmocytes wrapped around it. The axons in many of the nerves in the body have hundreds or thousands of neurolemmocytes covering their entire length.

1 Neurolemmocyte starts to wrap around a portion of an axon.

Axon

Neurolemmocyte

Nucleus — Direction of wrapping

2 Neurolemmocyte cytoplasm and plasma membrane begin to form consecutive layers around axon.

3 The overlapping inner layers of the neurolemmocyte plasma membrane form the myelin sheath.

Cytoplasm of the neurolemmocyte

Myelin sheath

4 Eventually, the neurolemmocyte cytoplasm and nucleus are pushed to the periphery of the cell as the myelin sheath is formed.

Myelin sheath

Neurolemmocyte nucleus

Figure 14.8

Myelination of PNS Axons. A myelin sheath surrounds most axons. In the PNS, successive adjacent neurolemmocytes form the myelin sheaths along the length of PNS axons.
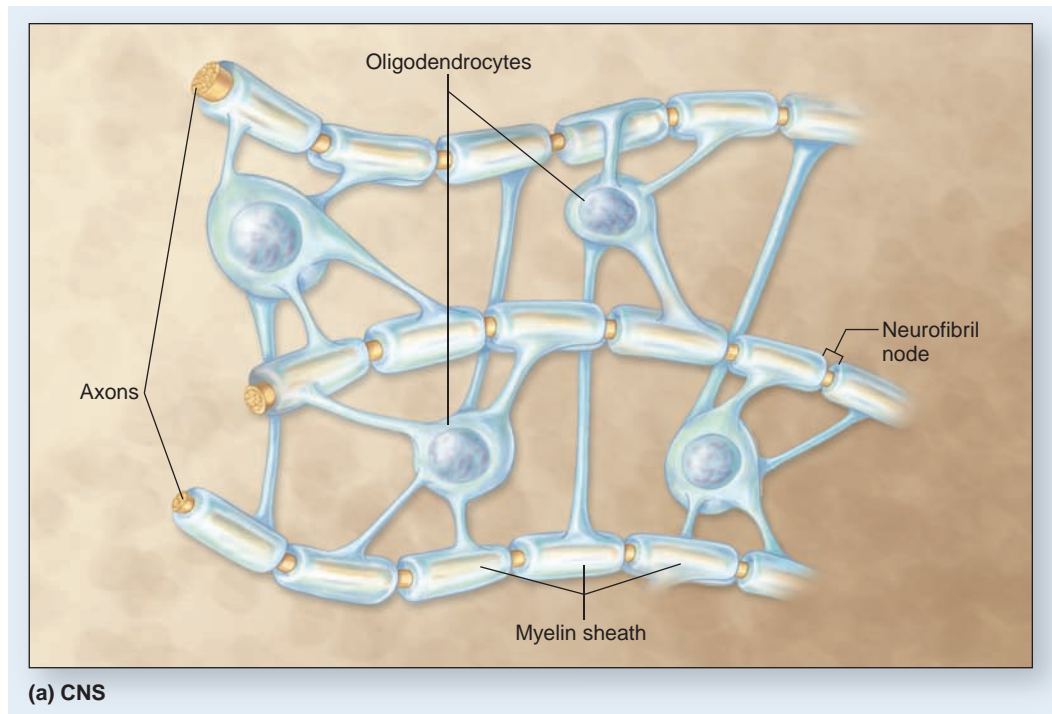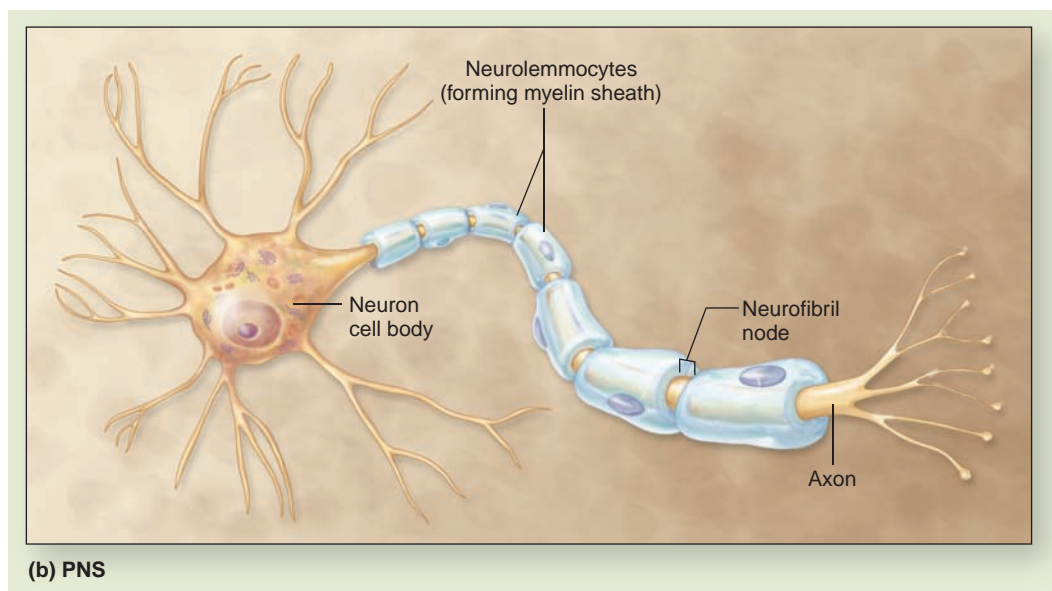
Figure 14.9

Myelin Sheaths in the CNS and PNS.
(*a*) In the CNS, several extensions from an oligodendrocyte wrap around small parts of multiple axons. (*b*) In the PNS, the neurolemmocyte ensheathes only one small part of a single axon. **AP|R**

Not all axons are myelinated. **Unmyelinated axons** in the PNS (shown in **figure 14.10**) are associated with a neurolemmocyte, but no myelin sheath covers them. In other words, the axon merely rests in a portion of the neurolemmocyte rather than being wrapped by successive layers of the plasma membrane. In the CNS, unmyelinated axons are not associated with oligodendrocytes.

14.3b Nerve Impulse Conduction

The myelin sheath supports, protects, and insulates an axon. Note in figure 14.9 that small spaces interrupt the myelin sheath between adjacent oligodendrocytes or neurolemmocytes. These gaps are called **neurofibril nodes,** or *nodes of Ranvier.* At these nodes, and only at these nodes, can a change in voltage occur across the plasma membrane and result in the movement of a nerve impulse. Thus, in a myelinated axon, the nerve impulse seems to "jump" from neurofibril node to

neurofibril node, a process called **saltatory conduction.** In an unmyelinated axon, the nerve impulse must travel the entire length of the axon membrane, a process called **continuous conduction. AP|R**

A myelinated axon produces a faster nerve impulse because only the exposed membrane regions are affected as the impulse jumps toward the end of the axon. In an unmyelinated axon, a nerve impulse takes longer to reach the end of the axon because every part of the membrane must be affected by the voltage change. Thus, a myelinated axon also requires less energy in the form of ATP than does an unmyelinated axon. ATP must be used by the cell to reestablish the resting condition that existed prior to the passage of the nerve impulse. Using saltatory conduction, large-diameter, myelinated axons conduct nerve impulses rapidly to the skeletal muscles in the limbs. Using continuous conduction, unmyelinated axons conduct nerve impulses from pain and some cold stimuli.
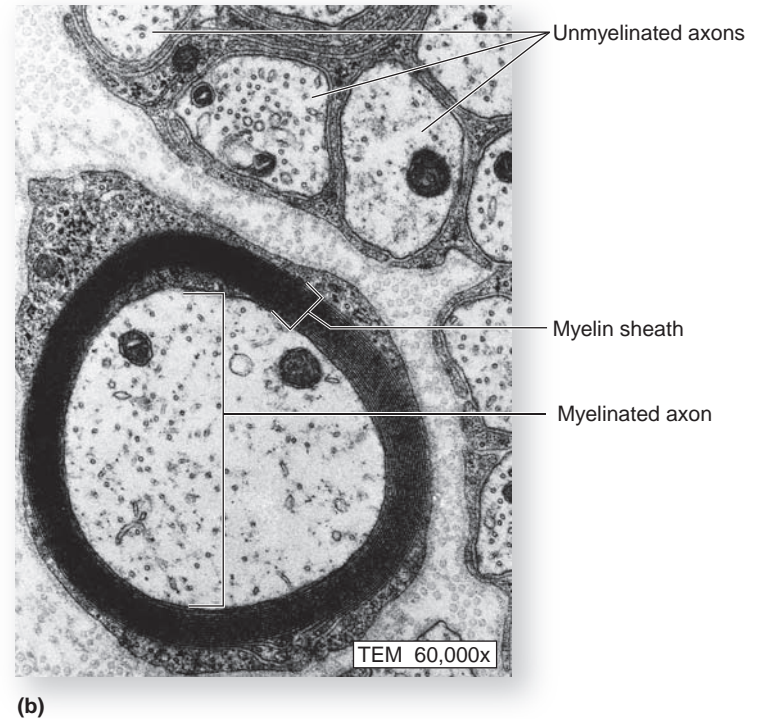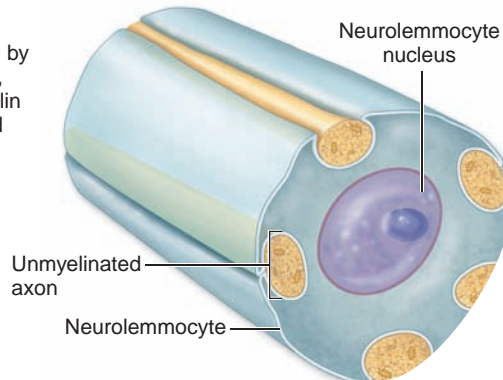
Unmyelinated axons

① Neurolemmocyte starts to envelop multiple axons.
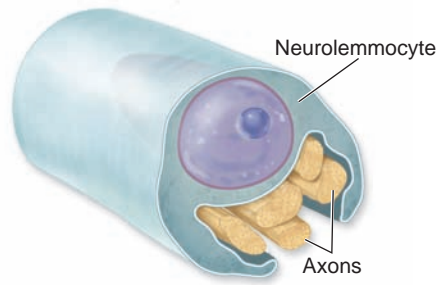
② The unmyelinated axons are enveloped by the neurolemmocyte, but there are *no* myelin sheath wraps around each axon.

Neurolemmocyte

Axons

Neurolemmocyte nucleus

Unmyelinated axon

Neurolemmocyte

(a)

Unmyelinated axons

Myelin sheath

Myelinated axon

TEM 60,000x

(b)

Figure 14.10

Comparison of Unmyelinated and Myelinated Axons. (*a*) Unmyelinated axons are surrounded by a neurolemmocyte but are *not* wrapped in a myelin sheath. (*b*) An electron micrograph shows a myelinated axon and some unmyelinated axons.

Study Tip!

Try using this analogy to help understand the difference between saltatory and continuous conduction: Visualize walking heel-to-toe (continuous conduction) down a path—you move very slowly. Now visualize skipping or running (saltatory conduction) down the same path—you move much more quickly.

WHAT DO YOU THINK?

③ If myelinated axons produce faster nerve impulses than unmyelinated axons, why aren't all axons in the body myelinated?

WHAT DID YOU LEARN?

⑦ What are some differences in the way axons are myelinated in the PNS versus the CNS?

⑧ What are neurofibril nodes, and where are they found?

14.4 Axon Regeneration

Learning Objectives:
1. Describe the conditions under which axons can regenerate.
2. Identify and describe the events that occur after injury to a PNS axon.

PNS axons are vulnerable to cuts, crushing injuries, and other trauma. However, a damaged axon can regenerate if at least some neurilemma remains. PNS axon regeneration depends upon three factors: (1) the amount of damage; (2) neurolemmocyte secretion of nerve growth factors to stimulate outgrowth of severed axons; and (3) the distance between the site of the damaged axon and the effector organ (as the distance to the effector increases, the possibility of repair decreases).

Neurolemmocytes help repair a damaged axon through a regeneration process called **Wallerian** (waw-ler′ē-an) **degeneration,** illustrated in **figure 14.11** and described here:

1. The axon is severed by some type of trauma.
2. The end of the proximal portion of the severed end seals off by membrane fusion and swells. The swelling is a result of cytoplasm flowing from the neuron cell body through the axon. The severed distal portion of the axon and its myelin sheath degenerate; macrophages remove the debris by phagocytosis. The neurolemmocytes in the distal region survive.
3. Neurolemmocytes form a regeneration tube in conjunction with the remaining *endoneurium* (an areolar connective tissue wrapping around axons [see next section]) of the severed axon.
4. The axon regenerates, and remyelination occurs. The regeneration tube guides the axon sprout as it begins to grow rapidly through the regeneration tube at a rate of about 5 millimeters per day under the influence of nerve growth factors released by the neurolemmocytes.
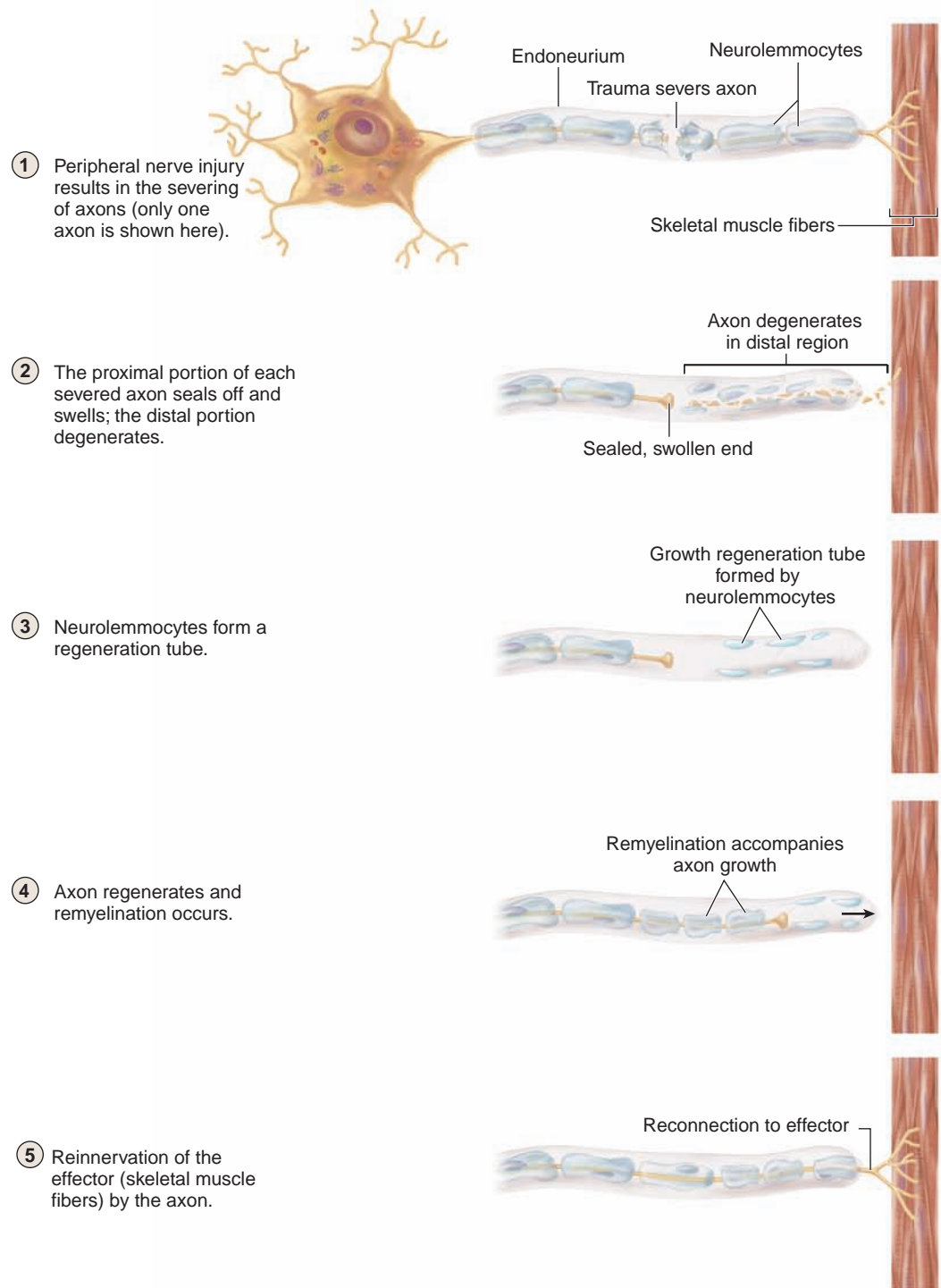5. Innervation is restored as the axon reestablishes contact with its original effector.

Potential regeneration of damaged neurons within the CNS is very limited due to several factors. First, oligodendrocytes do not release a nerve growth factor, and in fact they actively inhibit axon growth by producing and secreting several growth-inhibitory molecules. Second, the large number of axons crowded within the CNS tends to complicate regrowth activities. Finally, both astrocytes and connective tissue coverings may form some scar tissue that obstructs axon regrowth.

WHAT DID YOU LEARN?

⑨ What three factors determine PNS axon regeneration?

Figure 14.11

Wallerian Degeneration. Following injury to a peripheral nerve, the severed axons in the nerve may be repaired and grow out to reinnervate their effector cells. (In this case, one skeletal muscle cell reinnervation is shown.)

① Peripheral nerve injury results in the severing of axons (only one axon is shown here).

Endoneurium   Neurolemmocytes

Trauma severs axon

Skeletal muscle fibers

② The proximal portion of each severed axon seals off and swells; the distal portion degenerates.

Axon degenerates in distal region

Sealed, swollen end

③ Neurolemmocytes form a regeneration tube.

Growth regeneration tube formed by neurolemmocytes

④ Axon regenerates and remyelination occurs.

Remyelination accompanies axon growth

⑤ Reinnervation of the effector (skeletal muscle fibers) by the axon.

Reconnection to effector

14.5 Nerves

Learning Objective:

1. Describe the organization and structure of a nerve.

A **nerve** is a cablelike bundle of parallel axons. While a single axon typically must be viewed using a microscope, a nerve tends to be a macroscopic structure. **Figure 14.12** shows a typical nerve. Like a muscle, a nerve has three successive connective tissue wrappings:

- An individual axon in a myelinated neuron is surrounded by neurolemmocytes and then wrapped in the **endoneurium** (en-dō-noo′rē-ŭm; *endon* = within), a

delicate layer of areolar connective tissue that separates and electrically isolates each axon. Also within this connective tissue layer are capillaries that supply each axon.
- Groups of axons are wrapped into separate bundles called **fascicles** (fas′i-kl) by a cellular dense irregular connective tissue layer called the **perineurium** (per-i-noo′rē-ŭm; *peri* = around). This layer supports blood vessels supplying the capillaries within the endoneurium.
- All of the fascicles are bundled together by a superficial connective tissue covering termed the **epineurium** (ep-i-noo′rē-ŭm; *epi* = upon). This thick layer of dense irregular connective tissue encloses the entire nerve, providing both support and protection to the fascicles within the layer.

CLINICAL VIEW

### Nerve Regeneration and Spinal Cord Injuries

Spinal cord injuries frequently leave individuals unable to walk or paralyzed from the neck down. At one time, people with a spinal injury at the neck level were doomed to die, chiefly because of inadequate stimulation of the diaphragm and subsequent respiratory failure. Today, aggressive and early treatment of spinal cord injuries helps save lives that would have been lost just 5 years ago. Early use of steroids immediately after the injury appears to preserve some muscular function that might otherwise be lost. Early use of antibiotics has substantially reduced the number of deaths caused by pulmonary and urinary tract infections that accompany spinal cord injuries. There is even hope for repair and reconnection of damaged nerves. Recent research with rats has achieved reconnection and partial restoration of function of severed spinal cords. Researchers in several laboratories have devised a method of creating a "bridge" of nervous tissue that spans the injured area and have used transplanted olfactory nerve tissue as a guide for regrowing severed spinal cord axons capable of reaching the correct targets in the rat brain. This procedure has yet to be tried in humans. In addition, other research indicates that neural stem cells may be able to regenerate CNS axons.

Actor Christopher Reeve, known to many as Superman, was injured in a horse-riding accident and was paralyzed inferior to the level of the second cervical vertebra. Reeve became a tireless proponent and fund-raiser for spinal cord injury research. Up until his death in 2004, his own strides in rehabilitation were remarkable and helped advance spinal cord injury treatments for others. Hopefully, research and clinical medicine will lead to further help for the numerous victims of such traumatic injury.

Actor Christopher Reeve was a pioneer in challenging previous conceptions about neuron regeneration.

(a)

(b)

(c)
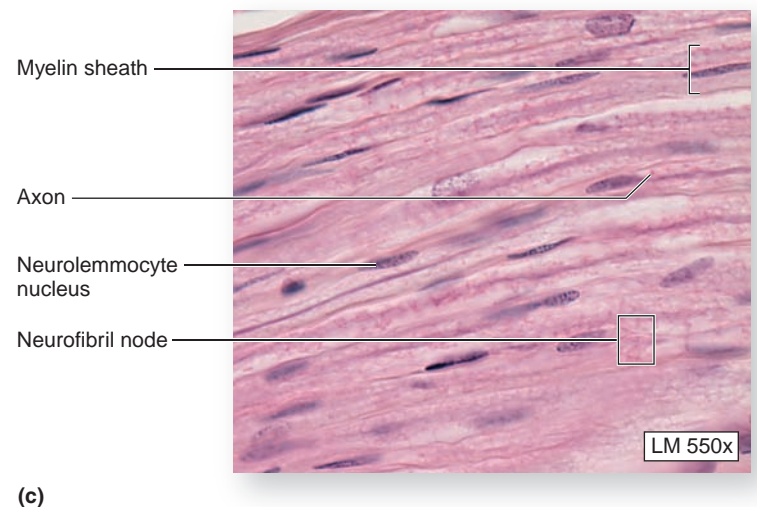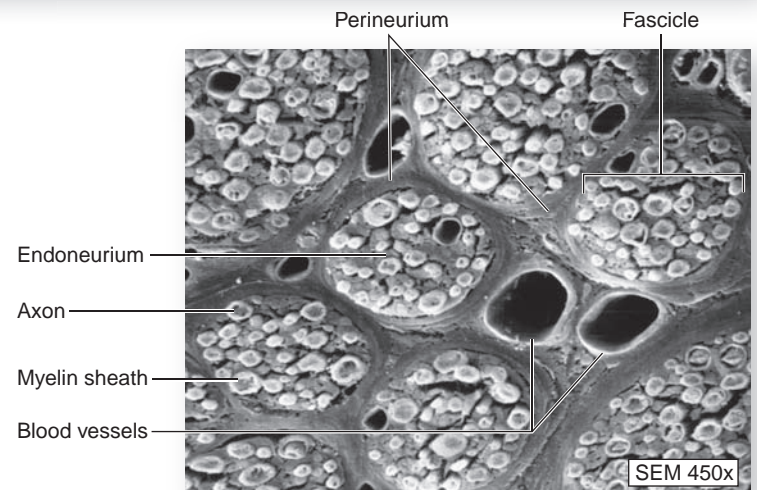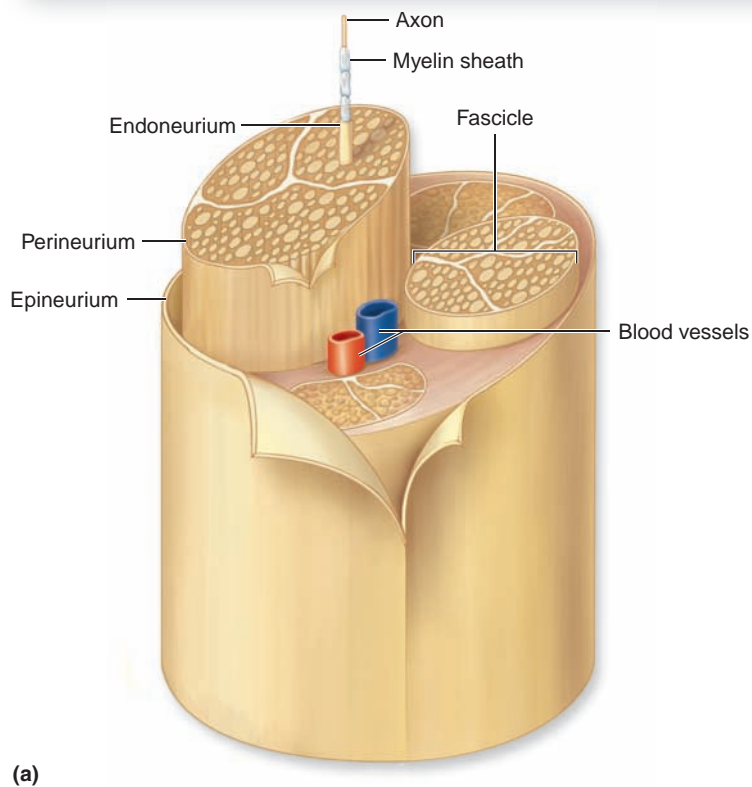
Figure 14.12

Nerve Structure. (*a*) A nerve is formed from many parallel axons wrapped by successive connective tissue layers. (*b*) SEM shows a cross section of a nerve. (*c*) A photomicrograph shows a longitudinal section of a nerve.

Nerves are a component of the peripheral nervous system. Sensory neurons convey sensory information to the central nervous system, motor neurons convey motor impulses from the central nervous system to the muscles and glands. Mixed nerves convey both types of information.
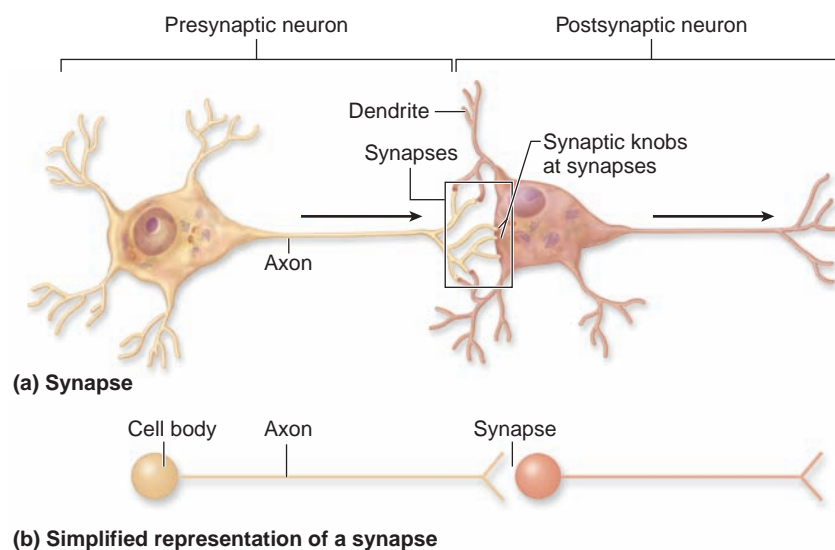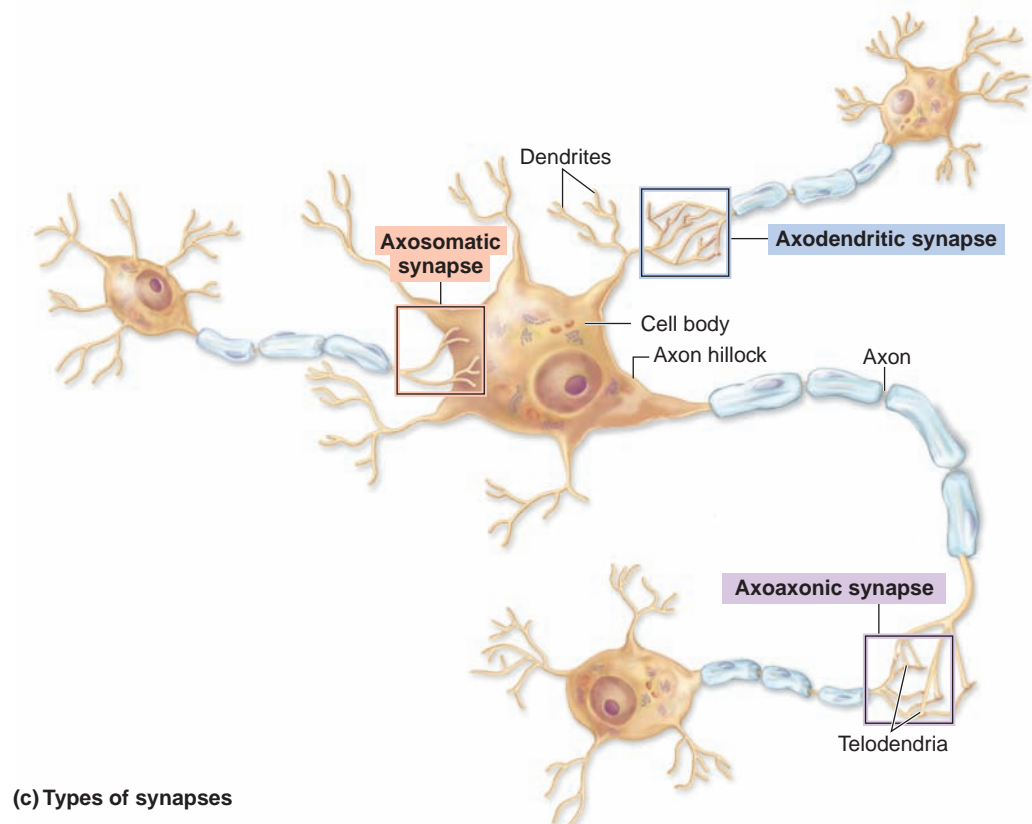
14.6 Synapses

Learning Objectives:

1. Describe the components of the various types of synapses.
2. Summarize and explain the events that occur during the conduction of nerve impulses in electrical and chemical synapses.

Axons terminate as they contact other neurons, muscle cells, or gland cells at specialized junctions called **synapses** (sin′aps; *syn* = together, *hapto* = to clasp) where the nerve impulse is transmitted to the other cell. **Figure 14.13a** shows an axon transmitting a nerve impulse to another neuron at a synapse. As the axon approaches the
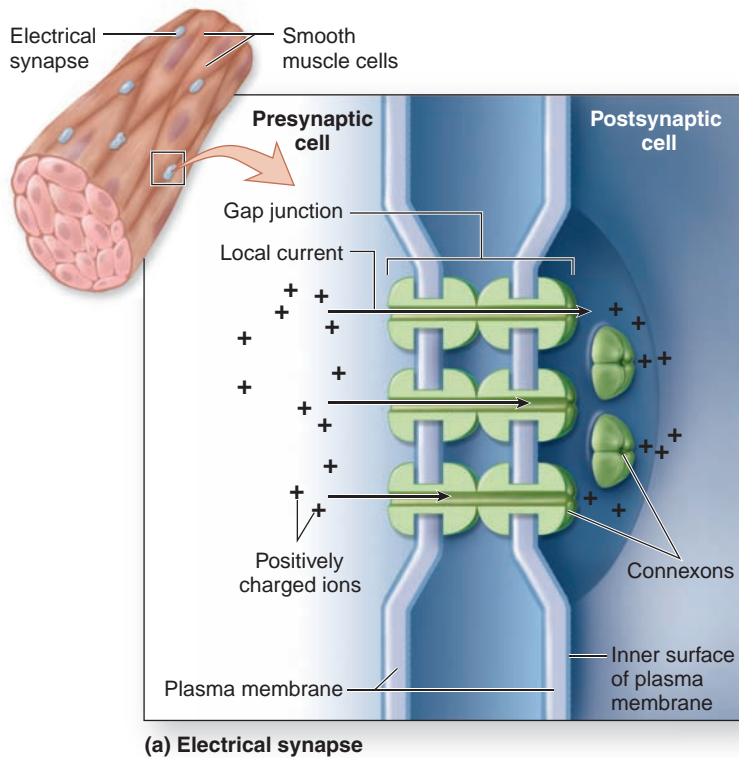

(a) **Synapse**

(b) **Simplified representation of a synapse**

(c) **Types of synapses**

Figure 14.13

Synapses. Synapses are intercellular junctions where two excitable cells come in contact to exchange information. (*a*) A synapse occurs where the plasma membrane of a presynaptic neuron synaptic knob comes in close proximity to the plasma membrane of a postsynaptic neuron. Arrows indicate the direction of nerve impulse flow. (*b*) In this simplified representation of a synapse, the spheres represent the cell bodies of the presynaptic and postsynaptic cells, the line represents the axon, and the angled arrow represents the synaptic knobs. (*c*) An axodendritic synapse occurs between an axon and a dendrite; an axosomatic synapse occurs between an axon and a cell body; and an axoaxonic synapse is between an axon and another axon.

Figure 14.14

Electrical and Chemical Synapses. (*a*) In an electrical synapse, ions pass through gap junctions between neurons from the presynaptic to the postsynaptic cell. (*b*) In a chemical synapse, a neurotransmitter is released from the presynaptic neuron to receptors on the membrane of the postsynaptic neuron. **AP|R**
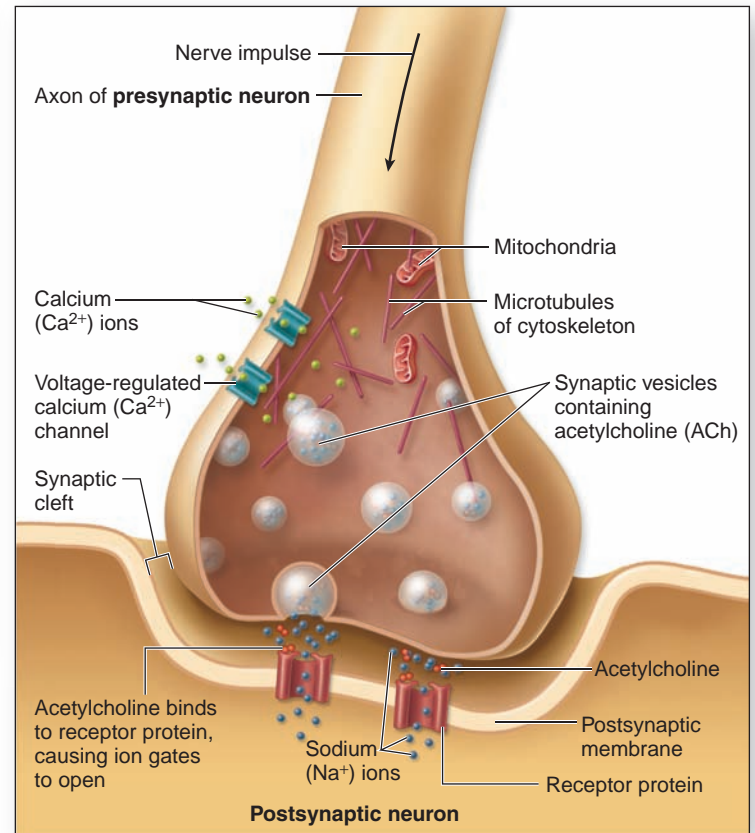
cell onto which it will terminate, it generally branches repeatedly into several telodendria, and each telodendrion loses its myelin covering. Additionally, the synaptic endings usually form swellings called synaptic knobs at the ends of the axon branches. A typical synapse in the CNS consists of the close association of a **presynaptic** (prē-si-nap′tik; *pre* = before) **neuron** and a **postsynaptic** (pōst-si-nap′tik; *post* = after) **neuron** at a region where their plasma membranes are separated by a very narrow space called the **synaptic cleft.** Presynaptic neurons transmit nerve impulses through their axons toward a synapse; postsynaptic neurons conduct nerve impulses through their dendrites and cell bodies away from the synapse.

Figure 14.13*b* shows a simplified diagram of a synapse. Here, the cell body of each neuron is represented by a sphere, and the axon is shown as a straight line. The synaptic knob is represented by an angled arrow attached to the axon, and the space between that angled arrow and the cell body of the next neuron is the synapse.

Axons may establish synaptic contacts with any portion of the surface of another neuron, except those regions covered by a myelin sheath. Three common types of synapses are axodendritic, axosomatic, and axoaxonic (figure 14.13*c*):

- The **axodendritic** (ak′sō-den-drit′ik) **synapse** is the most common type. It occurs between the synaptic knobs of a presynaptic neuron and the dendrites of the postsynaptic neuron. These specific connections occur either on the expanded tips of narrow dendritic spines or on the shaft of the dendrite.
- The **axosomatic** (ak′sō-sō-mat′ik) **synapse** occurs between synaptic knobs and the cell body of the postsynaptic neuron.
- The **axoaxonic** (ak′sō-ak-son′ik) **synapse** is the least common synapse and far less understood. It occurs between

the synaptic knob of a presynaptic neuron and the synaptic knob of a postsynaptic neuron. The action of this synapse appears to influence the activity of the synaptic knob.

14.6a Synaptic Communication

Most neurons exhibit both presynaptic and postsynaptic sides and functions. Synapses may be of two types: electrical or chemical.

Electrical Synapses

In an **electrical synapse,** the plasma membranes of the presynaptic and postsynaptic cells are bound tightly together. Electrical synapses are fast and secure, and they permit two-way signaling. At this synapse, **gap junctions** formed by connexons between both plasma membranes (review chapter 4) facilitate the flow of ions, such as sodium ions (Na^+), between the cells **(figure 14.14*a*)**. This causes a local current flow between neighboring cells. Remember that a voltage change caused by movement of charged ions results in a nerve impulse. Thus, these cells act as if they shared a common plasma membrane, and the nerve impulse passes between them with no delay. Electrical synapses are not very common in the brains of mammals. In humans, for example, these synapses occur primarily between smooth muscle cells (such as the smooth muscle in the intestines), where quick, uniform innervation is essential. Electrical synapses are also located in cardiac muscle at the intercalated discs (see chapter 4).

Chemical Synapses

The most numerous type of synapse is the **chemical synapse.** This type of synapse facilitates most of the interactions between neurons and all communications between neurons and effectors. At these junctions, the presynaptic membrane releases a signaling

molecule called a **neurotransmitter.** There are many different neurotransmitters, but acetylcholine (ACh) is the most common neurotransmitter and is our example in figure 14.14b. Some types of neurons use other neurotransmitters. The neurotransmitter molecules are released only from the presynaptic cell. They then bind to receptor proteins found only in the plasma membrane of the postsynaptic cell, and this causes a brief voltage change across the membrane of the postsynaptic cell. Thus, a unidirectional flow of information and communication takes place; it originates in the presynaptic cell and is received by the postsynaptic cell. A very precise sequence of events is required for the conduction of a nerve impulse from the presynaptic neuron to the postsynaptic neuron:

1. A nerve impulse travels through the axon and reaches its synaptic knob.
2. The arrival of the nerve impulse at the synaptic knob causes an increase in calcium ion (Ca^{2+}) movement into the synaptic knob through voltage-regulated calcium ion channels in the membrane.
3. Entering calcium ions cause synaptic vesicles to move to and bind to the inside surface of the membrane; neurotransmitter molecules within the synaptic vesicles are released into the synaptic cleft by exocytosis.
4. Neurotransmitter molecules diffuse across the synaptic cleft to the plasma membrane of the postsynaptic cell.
5. Neurotransmitter molecules attach to specific protein receptors in the plasma membrane of the postsynaptic cell, causing ion gates to open. Note: The time it takes for neurotransmitter release, diffusion across the synaptic cleft, and binding to the receptor is called the **synaptic delay.**
6. An influx of sodium ions (Na^+) moves into the postsynaptic cell through the open gate, affecting the charge across the membrane.
7. Change in the postsynaptic cell voltage causes a nerve impulse to begin in the postsynaptic cell.
8. The enzyme acetylcholinesterase (AChE) resides in the synaptic cleft and rapidly breaks down molecules of ACh

that are released into the synaptic cleft. Thus, AChE is needed so that ACh will not continuously stimulate the postsynaptic cell.

Once a nerve impulse is initiated, two factors influence the rate of conduction of the impulse: the axon's diameter and the presence (or absence) of a myelin sheath. The larger the diameter of the axon, the more rapidly the impulse is conducted because of less resistance to current flow as charged ions move into the axon. Also, as previously mentioned, an axon with a myelin sheath conducts impulses many times faster than an unmyelinated axon because of the differences between saltatory and continuous conduction.
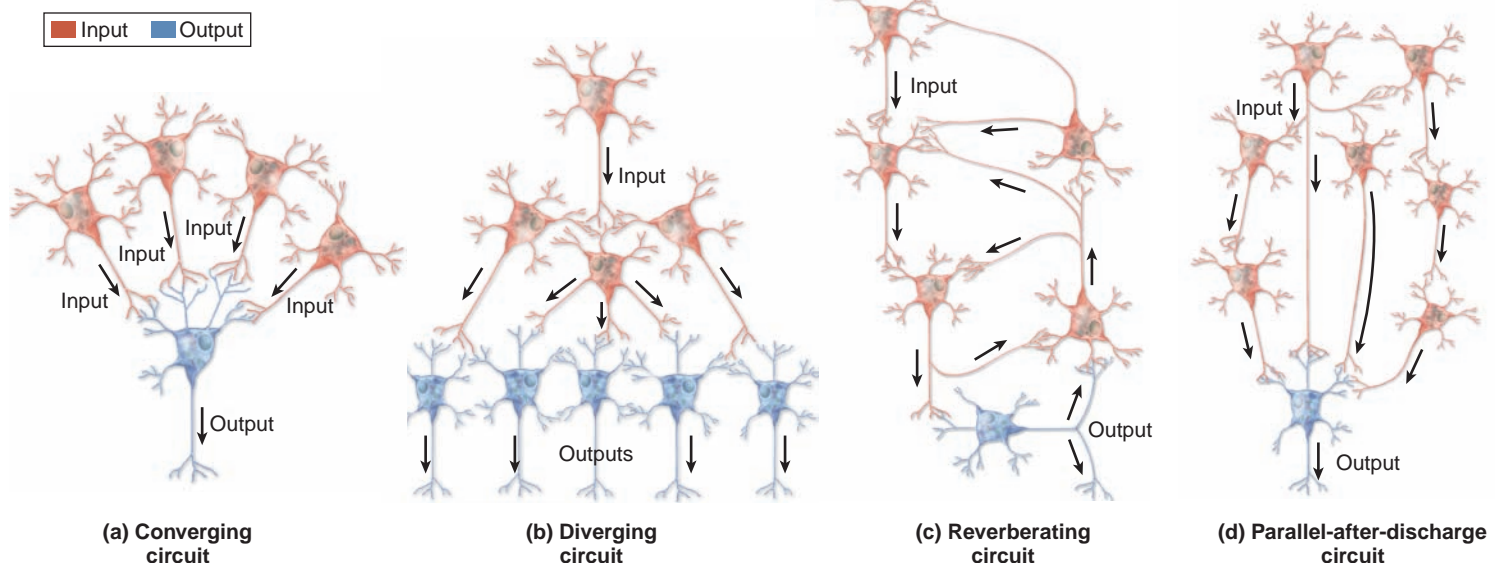
WHAT DID YOU LEARN?

12 What are the two types of synaptic communication?

13 What factors influence the impulse conduction rate?

14.7 Neural Integration and Neuronal Pools

Learning Objective:

1. Identify the four different neuronal circuits, and describe how each one functions.

The nervous system is able to coordinate and integrate nervous activity in part because billions of interneurons within the CNS are grouped in complex patterns called **neuronal pools** (or *neuronal circuits* or *pathways*). Neuronal pools are defined based upon function, not anatomy, into four types of circuits: converging, diverging, reverberating, and parallel-after-discharge **(figure 14.15)**. A pool may be localized, with its neurons confined to one specific location, or its neurons may be distributed in several different regions of the CNS. However, all neuronal pools are restricted in their number of input sources and output destinations.

■ Input ■ Output

(a) **Converging circuit**

(b) **Diverging circuit**

(c) **Reverberating circuit**

(d) **Parallel-after-discharge circuit**

Figure 14.15

Neuronal Pools. Neuronal pools are groups of neurons arranged in specific patterns (circuits) through which impulses are conducted and distributed. Four types of neuronal pools are recognized: (*a*) converging circuit, (*b*) diverging circuit, (*c*) reverberating circuit, and (*d*) parallel-after-discharge circuit.

Nervous System Disorders

Five serious diseases that attack portions of the nervous system are amyotrophic lateral sclerosis, multiple sclerosis, Parkinson disease, Guillain-Barré syndrome, and multifocal motor neuropathy.

Amyotrophic lateral sclerosis (**ALS**; often called *Lou Gehrig disease*) is a well-known motor neuron disease that progresses quickly and is eventually fatal. It affects neurons in both the brain and the spinal cord, leading to progressive degeneration of the somatic motor system. ALS patients generally have weakened and atrophied muscles, especially in the hands and forearms. Additionally, they may experience speech impairment, breathing difficulties, and chewing and swallowing problems that result in choking or excessive drooling. However, the disease does not affect sensory abilities, such as hearing, sight, or smell. No effective treatment or cure exists, and the disease is invariably fatal.

ALS affects both males and females, but it occurs in males more often. About 90% of ALS cases occur in families with no previous history of the disease. In contrast, about 10% of cases are inherited and called *familial* (meaning that more members of the same family are affected than can be accounted for by chance). The inherited form of ALS has been localized to a gene on chromosome 21.

Multiple sclerosis (MS) is progressive demyelination of neurons in the central nervous system accompanied by the destruction of oligodendrocytes. As a result, the conduction of nerve impulses is disrupted, leading to impaired sensory perception and motor coordination. Repeated inflammatory events at myelinated sites cause scarring (sclerosis), and in time some function is permanently lost. The disease usually strikes young adults between the ages of 18 and 40. It is five times more prevalent in whites than in blacks.

Although MS is very disabling, it progresses slowly, and most patients lead productive lives, especially during recurring periods of remission.

Symptoms are diverse because almost any myelinated site in the brain or spinal cord may be affected. Among the typical symptoms are vision problems, muscle weakness and spasms, urinary infections and bladder incontinence, and drastic mood changes.

The most widely held view of the cause of multiple sclerosis is that the body's immune system attacks its own central nervous system, making MS an autoimmune disorder. Treatment depends to some degree on the stage and severity of the disease. Steroids are useful during periods of acute symptoms, whereas interferons (natural proteins produced by the immune system) are used for prolonged therapy. Recent experiments have shown that one form of interferon lowers the activity of immune cells, reducing the number and severity of attacks.

Parkinson disease (*Parkinsonism* or "shaky palsy") is a slowly progressive disorder affecting muscle movement and balance. The condition is characterized by stiff posture, tremors, and reduced spontaneity of facial expressions. It results from loss of cells that produce the neurotransmitter dopamine in a specific region of the brainstem. For further information about Parkinson disease, see Clinical View: In Depth, "Brain Disorders," in chapter 15, page 472.

Guillain-Barré syndrome (GBS) is a disorder of the peripheral nervous system characterized by muscle weakness that begins in the distal limbs, but rapidly advances to involve proximal muscles as well (a condition known as ascending paralysis). At the microscopic level, inflammation causes loss of myelin from the peripheral nerves and spinal nerve roots. Most cases of GBS are preceded by an acute, flulike illness, although no specific infectious agent has ever been identified. In rare instances, the condition may follow an immunization. Even though GBS appears to be an immune-mediated condition, the use of steroids provides little if any measurable improvement. In fact, most people recover almost all neurologic function on their own with little medical intervention. Should hospitalization and treatment be required, therapies fall into four categories: (1) supportive, including breathing assistance if indicated; (2) physical therapy to increase muscle flexibility and strength; (3) injections of high-dose immunoglobulins to "turn off" the production of antibodies causing the disease; and (4) plasmaphoresis, a process of filtering the blood to remove the antibodies that are causing the myelin destruction.

Multifocal motor neuropathy (MMN) is an immune-mediated motor neuropathy that is similar to GBS but less severe. MMN is a demyelinating condition that progresses slowly and usually presents with asymmetric weakness and variable degrees of muscular atrophy in the forearm and hand. It affects men more often than women and, in most cases, will cause symptoms before age 45. The clinical signs of MMN may resemble a motor neuron disease, such as ALS, making diagnosis difficult. Because MMN needs to be treated differently from ALS, an accurate diagnosis is important for proper medical management. Since the body's own antibodies eat away at the myelin sheaths around motor neurons, the typical treatment for MMN is intravenous immunoglobulin (called IVIG) to slow the production of antibodies. IVIG is successful in most cases.

(a)

Individuals with neurodegenerative diseases must overcome physical challenges to carry on the activities of daily life. (a) Amyotrophic lateral sclerosis (scientist and writer Stephen Hawking). (b) Multiple sclerosis.

(b)

In a **converging circuit,** nerve impulses converge (come together) at a single postsynaptic neuron (figure 14.15a). This neuron receives input from several presynaptic neurons. For example, multiple sensory neurons synapse on the neurons in the salivary nucleus in the brainstem, resulting in the production of saliva. The various inputs may originate from more than one stimulus—in this example, smelling food, seeing the time on the clock indicating dinnertime, hearing food preparation activities, or seeing pictures of food in a magazine. These multiple inputs lead to a single output, the production of saliva.

A **diverging circuit** spreads information from one presynaptic neuron to several postsynaptic neurons, or from one pool to multiple pools (figure 14.15b). For example, the few neurons in the brain that control the movements of skeletal muscles in the legs during walking also stimulate the muscles in the back that maintain posture and balance while walking. In this case, a single or a few inputs lead to multiple outputs.

Reverberating circuits utilize feedback to produce a repeated, cyclical stimulation of the circuit, or a reverberation (figure 14.15c). Once activated, a reverberating circuit may continue to function until either inhibitory stimuli or synaptic fatigue breaks the cycle. (**Synaptic fatigue** occurs when repeated stimuli cause temporary inability of the presynaptic cell to meet demands of synaptic transmission as a result of a lack of neurotransmitter production.) The repetitious nature of a reverberating circuit ensures that we continue breathing while we are asleep.

In a **parallel-after-discharge circuit,** several neurons or neuronal pools process the same information at one time. A single presynaptic neuron stimulates different groups of neurons, each of which passes the nerve impulse along a pathway that ultimately synapses with a common postsynaptic cell (figure 14.15d). This type of circuit is believed to be involved in higher-order thinking, such as the type needed to perform precise mathematical calculations.

WHAT DID YOU LEARN?

14   How is a diverging circuit different from a reverberating circuit?
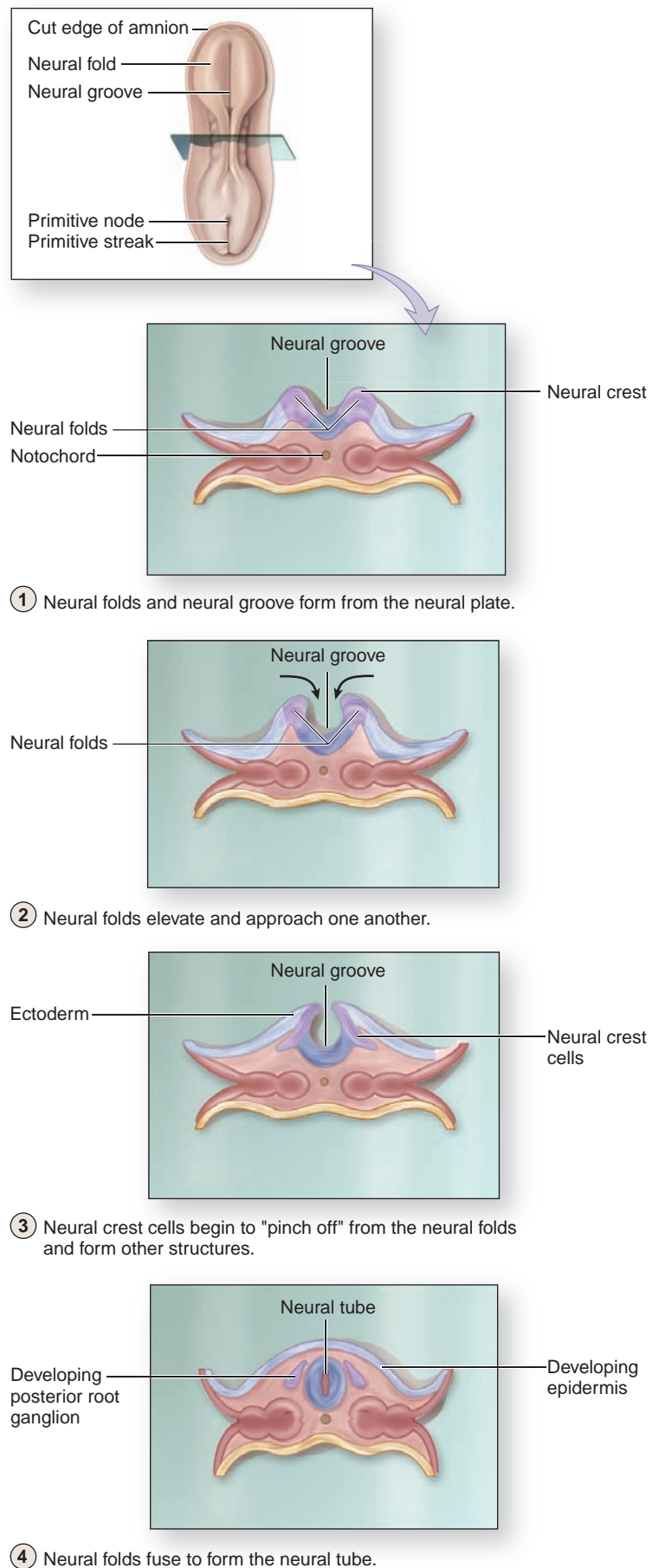
14.8 Development of the Nervous System

Learning Objective:

1. Define and describe the early events in nervous system development.

Nervous tissue development begins in the embryo during the third week when a portion of the ectoderm that overlies the notochord thickens. This thickened ectoderm is called the **neural plate,** and the cells of the plate collectively are called the **neuroectoderm.** The neuroectoderm undergoes dramatic changes, called **neurulation** (noor-oo-lā′shŭn), to form nervous tissue structures. The process of neurulation is shown in **figure 14.16** and explained here:

1. The neural plate develops a central longitudinal indentation called the **neural groove.** As this is occurring, cells along the lateral margins of the neural plate proliferate, becoming the thickened **neural folds.** The tips of the neural folds form the neural crest and are occupied by **neural crest cells** (or simply, the *neural crest*).
2. The neural folds elevate and approach one another as the neural groove continues to deepen. The neural crest cells are

① Neural folds and neural groove form from the neural plate.

② Neural folds elevate and approach one another.

③ Neural crest cells begin to "pinch off" from the neural folds and form other structures.

④ Neural folds fuse to form the neural tube.

Figure 14.16

Nervous System Development. The process of neurulation begins in the third week, and the neural tube finishes closing by the end of week 4.

Neural Tube Defects

Neural tube defects (NTDs) are serious developmental deformities of the brain, spinal cord, and meninges. The two basic categories of NTDs are anencephaly and spina bifida. Both conditions result from localized failure of the developing neural tube to close.

Anencephaly (an′en-sef′ă-lē; *an* = without, *enkephalos* = brain) is the substantial or complete absence of a brain as well as the bones making up the cranium. Infants with anencephaly rarely live longer than a few hours following birth. Fortunately, neural tube defects of this magnitude are rare, and are easily detected with prenatal ultrasound, thus alerting the parents to the condition.

Spina bifida (spī′nă bĭ′fid′ă; *spina* = spine, *bifidus* = cleft in two parts) occurs more frequently than anencephaly. This defect results when the


A newborn with anencephaly.

caudal portion of the neural tube, often in the lumbar or sacral region, fails to close. Two forms of spina bifida occur: the more severe spina bifida cystica and the less severe spina bifida occulta. In spina bifida cystica, almost no vertebral arch forms, so the posterior aspect of the spinal cord in this region is left unprotected (figures *a* and *b*). Typically, there is a large cystic structure in the back, filled with cerebrospinal fluid (CSF) and covered by a thin layer of skin or in some cases only by meninges (protective membranes around the spinal cord). Surgery is generally done promptly to close the defect, reduce the risk of infection, and preserve existing spinal cord function. Paralysis of the lower limbs is often part of the spina bifida syndrome. But even with these problems, most children with spina bifida cystica live well into adulthood.

Spina bifida occulta is less serious, but much more common than the cystica variety. This condition is characterized by a partial defect of the vertebral arch, typically involving the vertebral lamina and spinous process (figure *c*). The bony defect is small, and the spinal cord or meninges does not protrude. Often there is a tuft of hair in the region of the bony defect. Most people with this condition are otherwise asymptomatic, and it is generally detected incidentally during an x-ray for an unrelated reason. Estimates of the incidence of spina bifida occulta range as high as 17% of the population in some x-ray studies.

Although the risk of neural tube defects cannot be eliminated, it can be greatly reduced. Researchers have discovered that increased intake of vitamin B_{12} and the B vitamin **folic acid (folate)** by pregnant women is correlated with a decreased incidence of neural tube defects. Both vitamin B_{12} and folic acid are critical to DNA formation and are necessary for cellular division and tissue differentiation. Thus, pregnant women are encouraged to take prenatal vitamins containing high levels of these chemicals, and the food industry has begun fortifying many breads and grains with folate as well.
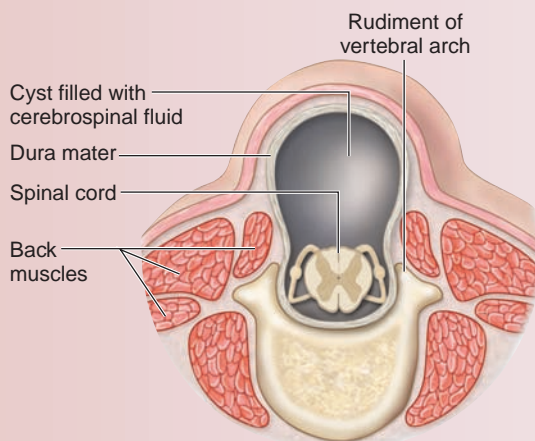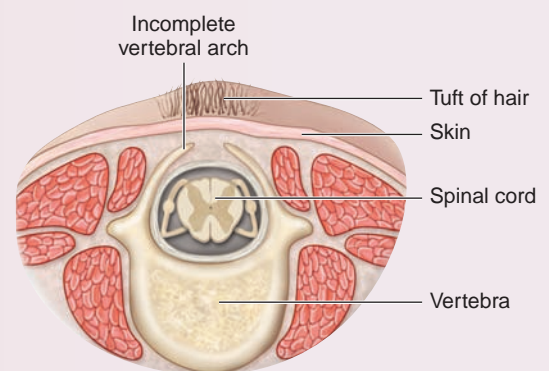

(a) Spina bifida cystica

(b) Child with spina bifida cystica

(c) Spina bifida occulta

Spina bifida is a neural tube disorder that occurs in two forms: (a, b) spina bifida cystica; (c) spina bifida occulta. (See chapter 7 for a description of vertebral development.)

now at the very highest point of the neural groove. When viewed from a superior angle, the neural folds resemble the sides of a hot dog roll, with the neural groove represented by the opening in the roll.

3. The neural crest cells begin to "pinch off" from the neural folds and form other structures.

4. By the end of the third week, the neural folds have met and fused at the midline, and the neural groove starts to form a **neural tube,** which has an internal lumen called the **neural canal.** The neural tube initially fuses at its midline, and later the neural folds slightly superior and inferior to this midline fuse as well. Thus, the neural tube forms as the neural folds "zip" together both superiorly and inferiorly.

For a short time, the neural tube is open at both its ends. These openings, called **neuropores** (noor′ō-pōr), close during the end of the fourth week. The opening closest to the future head is the **cranial neuropore,** while the opening closest to the future buttocks region is the **caudal neuropore.** If these openings do not close, the developing human will have a neural tube defect (see Clinical View). The developing neural tube forms the central nervous system. In particular, the cranial part of the neural tube expands to form the brain (see chapter 15), while the caudal part of the neural tube expands to form the spinal cord (see chapter 16). Also, please refer back to chapter 7 to review vertebral development.

Clinical Terms

demyelination (dē-mī′ĕ-li-nā′shun) Progressive loss or destruction of myelin in the CNS and PNS with preservation of the axons; often leads to loss of sensation and/or motor control.

neuritis (noo-rī′tis) Inflammation of a nerve.

neuropathy (noo-rop′ă-thē) Classical term for a disorder affecting any segment of the nervous system.

neurotoxin (noor-ō-tok′sin) Any poison that acts specifically on nervous tissue.

Chapter Summary

14.1 Organization of the Nervous System 416	■ The nervous system includes all the nervous tissue in the body.
	14.1a Structural Organization: Central and Peripheral Nervous Systems 416
	■ The central nervous system is composed of the brain and the spinal cord.
	■ The peripheral nervous system is composed of the cranial nerves, spinal nerves, and ganglia.
	14.1b Functional Organization: Sensory and Motor Nervous Systems 416
	■ The nervous system is functionally subdivided into a sensory nervous system that conveys sensory information to the CNS, and a motor nervous system that conducts motor commands to muscles and glands.
14.2 Cytology of Nervous Tissue 418	■ Neurons are excitable cells that transmit nerve impulses, and glial cells completely surround neurons and support them.
	14.2a Neurons 418
	■ A generalized neuron has a cell body and processes called dendrites and an axon. They are classified structurally by the number of processes attached to the cell body (unipolar, bipolar, or multipolar) and functionally as sensory neurons, motor neurons, or interneurons.
	14.2b Glial Cells 422
	■ Glial cells support neurons in the CNS. Astrocytes help form the blood-brain barrier and regulate tissue fluid composition; ependymal cells line CNS cavities and produce cerebrospinal fluid; microglial cells act as phagocytes in nervous tissue; and oligodendrocytes myelinate CNS axons.
	■ In the PNS, satellite cells support neuron cell bodies in ganglia, and neurolemmocytes myelinate PNS axons.
14.3 Myelination of Axons 425	■ A nerve impulse is the rapid movement of a charge along a neuron's plasma membrane.
	14.3a Myelination 425
	■ Oligodendrocytes (CNS) and neurolemmocytes (PNS) wrap around axons of neurons, forming a discontinuous myelin sheath along the axon, with small gaps called neurofibril nodes.
	14.3b Nerve Impulse Conduction 426
	■ The myelin sheath insulates the axonal membrane, resulting in faster nerve impulse conduction.
	■ Unmyelinated axons are associated with a neurolemmocyte but not ensheathed by it.
14.4 Axon Regeneration 427	■ Regeneration of damaged neurons is limited to PNS axons that are able to regrow under certain conditions by a process called Wallerian degeneration.
14.5 Nerves 428	■ A nerve is a bundle of many parallel axons organized in three layers: an endoneurium around a single axon, a perineurium around a fascicle, and an epineurium around all of the fascicles.
14.6 Synapses 430	■ The specialized junction between two excitable cells where a nerve impulse is transmitted is called a synapse.
	■ Swellings of axons at their end branches are called synaptic knobs.
	■ The space between the presynaptic and postsynaptic cells is the synaptic cleft.
	■ Synapses are classified according to the point of contact between the synaptic knob and the postsynaptic cell as axodendritic, axosomatic, or axoaxonic.

14.6 Synapses (continued) 430	**14.6a Synaptic Communication** 431 ■ Synapses are termed electrical when a flow of ions passes from the presynaptic cell to the postsynaptic cell through gap junctions; synapses are termed chemical when a nerve impulse causes the release of a chemical neurotransmitter from the presynaptic cell that induces a response, in the postsynaptic cell. ■ A myelinated axon conducts impulses faster than an unmyelinated axon, and the larger the diameter of the axon, the faster is the rate of conduction.
14.7 Neural Integration and Neuronal Pools 432	■ Interneurons are organized into neuronal pools, which are groups of interconnected neurons with specific functions. ■ In a converging circuit, neurons synapse on the same postsynaptic neuron. ■ A diverging circuit spreads information to several neurons. ■ In a reverberating circuit, neurons continue to restimulate presynaptic neurons in the circuit. ■ A parallel-after-discharge circuit involves parallel pathways that process the same information over different amounts of time and deliver that information to the same output cell.
14.8 Development of the Nervous System 434	■ Nervous tissue development begins in the early embryo with the formation of the neural plate. As this plate grows and develops, a neural groove appears as a depression in the plate, prior to the elevation of neural folds along the lateral side of the plate. The fusion of the neural folds gives rise to a neural tube, from which the brain and spinal cord develop. ■ A neural tube defect can result if part of the neural tube fails to fuse.

Challenge Yourself

Matching

Match each numbered item with the most closely related lettered item.

_____ 1. motor nervous system

_____ 2. effector

_____ 3. oligodendrocyte

_____ 4. chromatophilic substance

_____ 5. collaterals

_____ 6. microglial cells

_____ 7. multipolar neurons

_____ 8. interneuron

_____ 9. chemical synapse

_____ 10. dendrite

a. skeletal muscle fiber

b. neuron part that usually receives incoming impulses

c. stain darkly with basic dyes

d. transmits motor information

e. uses a neurotransmitter

f. makes myelin sheaths in CNS

g. neurons with multiple dendrites

h. side branches of axons

i. respond to CNS infection

j. sensory to motor neuron communication

Multiple Choice

Select the best answer from the four choices provided.

_____ 1. The cell body of a mature neuron does not contain
  a. a nucleus.
  b. ribosomes.
  c. a centriole.
  d. mitochondria.

_____ 2. Neurons that have only two processes attached to the cell body are called
  a. unipolar.
  b. bipolar.
  c. multipolar.
  d. efferent.

_____ 3. Which neurons are located *only* within the CNS?
  a. motor neurons
  b. unipolar neurons
  c. sensory neurons
  d. interneurons

_____ 4. A structure or cell that collects sensory information is a
  a. motor neuron.
  b. receptor.
  c. neurolemmocyte.
  d. ganglion.

_____ 5. The glial cells that help produce CSF in the CNS are
  a. satellite cells.
  b. microglial cells.
  c. ependymal cells.
  d. astrocytes.

_____ 6. Which of the following is *not* a part of the CNS?
  a. microglial cell
  b. spinal cord
  c. neurolemmocyte
  d. brain

_____ 7. Which of these cells transmits, transfers, and processes a nerve impulse?
  a. neurolemmocyte
  b. astrocyte
  c. neuron
  d. oligodendrocyte

_____ 8. Which type of neuronal pool utilizes nerve impulse feedback to repeatedly stimulate the circuit?
  a. converging circuit
  b. diverging circuit
  c. reverberating circuit
  d. parallel-after-discharge circuit

_____ 9. At an electrical synapse, presynaptic and postsynaptic membranes interface through
  a. neurofibril nodes.
  b. gap junctions.
  c. telodendria.
  d. neurotransmitters.

_____ 10. The epineurium is
  a. a thick, dense irregular connective tissue layer enclosing the nerve.
  b. a group of axons.
  c. a delicate layer of areolar connective tissue.
  d. a cellular layer of dense regular connective tissue.

Content Review

1. What are the three structural types of neurons? How do they compare to the three functional types of neurons?

2. What is the function of sensory neurons?

3. Identify the principal types of glial cells, and briefly discuss the function of each type.

4. How does the myelin sheath differ between the CNS and the PNS?

5. Describe the procedure by which a PNS axon may repair itself.

6. Describe the arrangement and structure of the three coverings that surround axons in ANS nerves.

7. Clearly distinguish among the following: a neuron, an axon, and a nerve.

8. What are the differences between electrical and chemical synapses? Which is the more common type of synapse in humans?

9. Discuss the similarities and differences between converging and parallel-after-discharge circuits.

10. What are the basic developmental events that occur during neurulation?

Developing Critical Reasoning

1. Over a period of 6 to 9 months, Marianne began to experience vision problems as well as weakness and loss of fine control of the skeletal muscles in her leg. Blood tests revealed the presence of antibodies (immune system proteins) that attack myelin. Beyond the presence of the antibodies, what was the cause of Marianne's vision and muscular difficulties?

2. Surgeons were able to reattach an amputated limb, sewing both the nerves and the blood vessels back together. After the surgery, which proceeded very well, the limb regained its blood supply almost immediately, but the limb remained motionless and the patient had no feeling in it for several months. Why did it take longer to reestablish innervation than circulation?

Answers to "What Do You Think?"

1. The term *visceral* refers to organs, especially thoracic and abdominal organs such as the heart, lungs, and gastrointestinal tract. Therefore, the parts of the sensory and motor nervous systems that innervate these viscera are called the visceral sensory and visceral motor (autonomic) nervous systems.

2. Tumors occur due to uncontrolled mitotic growth of cells. Since glial cells are mitotic and neurons typically are nonmitotic, a "brain tumor" almost always develops from glial cells.

3. A myelinated axon takes up more space than an unmyelinated axon. There simply isn't enough space in the body to hold myelin sheaths for every axon. Thus, the body conserves this space by myelinating only the axons that must transmit nerve impulses very rapidly.