

Fundamentals of the Nervous System and Nervous Tissue

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◀ *Branching nerve fiber and astrocyte cells from the mammalian cortex
(immunofluorescent light micrograph 2000×).*

As you are driving down the freeway, a horn blares on your right, and immediately you swerve to your left. Charlie's note on the kitchen table reads, "See you later—I will have the stuff ready at six"; you know that the "stuff" is chili with taco chips, and your mouth waters in anticipation. While you are dozing, your infant son cries out softly, and instantly you awaken. What do these events have in common? All are everyday examples of the function of your nervous system, which has the cells in your body humming with activity nearly all the time.

The nervous system is the master control and communications system of the body. Every thought, action, instinct, and emotion reflects its activity. Its cells communicate through electrical signals, which are rapid and specific and usually produce almost immediate responses.

This chapter begins with an overview of the functions and the divisions of the nervous system. It then focuses on the functional anatomy of nervous tissue, especially of the nerve cells, or *neurons*, which are the key to the efficient system of neural communication. Finally, the chapter addresses how the arrangement of neurons determines the structural organization of the nervous system.

THE FUNCTIONAL ORGANIZATION OF THE NERVOUS SYSTEM

- List the main functions of the nervous system.
- Explain the structural and functional divisions of the nervous system.

Functions of the Nervous System

The nervous system has three overlapping functions (Figure 12.1): (1) It uses its millions of *sensory receptors* to monitor changes occurring both inside and outside the body. Each of these changes is called a *stimulus*, and the gathered information is called **sensory input**. (2) It processes and interprets the sensory input and makes decisions about what should be done

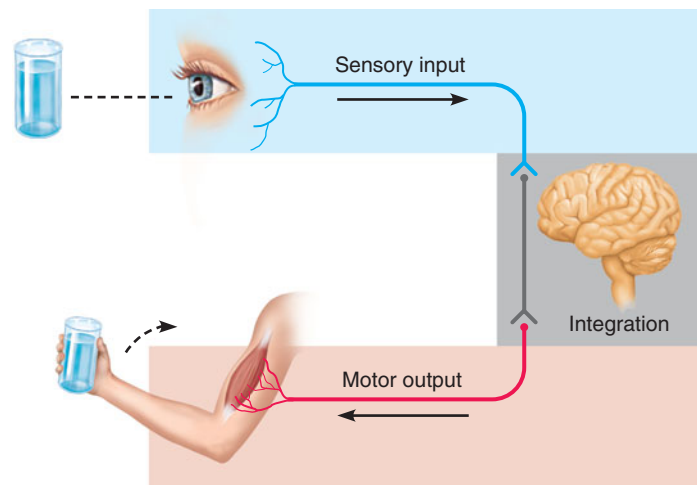


FIGURE 12.1 The nervous system's functions.

at each moment—a process called **integration**. (3) It dictates a response by activating the *effector organs*, our muscles or glands; the response is called **motor output**. Some examples illustrate how these functions work together. When you are driving and hear a horn to your right, your nervous system integrates this information (a horn signifies danger), and your arm muscles contract to turn the wheel to the left (motor output). As another example, when you taste food your nervous system integrates this sensory information and signals your salivary glands to secrete more saliva into your mouth.

Basic Divisions of the Nervous System

Humans have only one, highly integrated nervous system. However, for the sake of convenience you can think of it as having two anatomical parts: the central nervous system and the peripheral nervous system (Figure 12.2). The **central nervous system (CNS)** consists of the *brain* and the *spinal cord*, which occupy the cranium and the vertebral canal, respectively. The CNS is the integrating and command center of the nervous system: It receives incoming sensory signals, interprets these signals, and dictates motor responses based on past experiences, reflexes, and current conditions. The **peripheral nervous system (PNS)**, the part of the nervous system outside the CNS, consists mainly of the *nerves* that

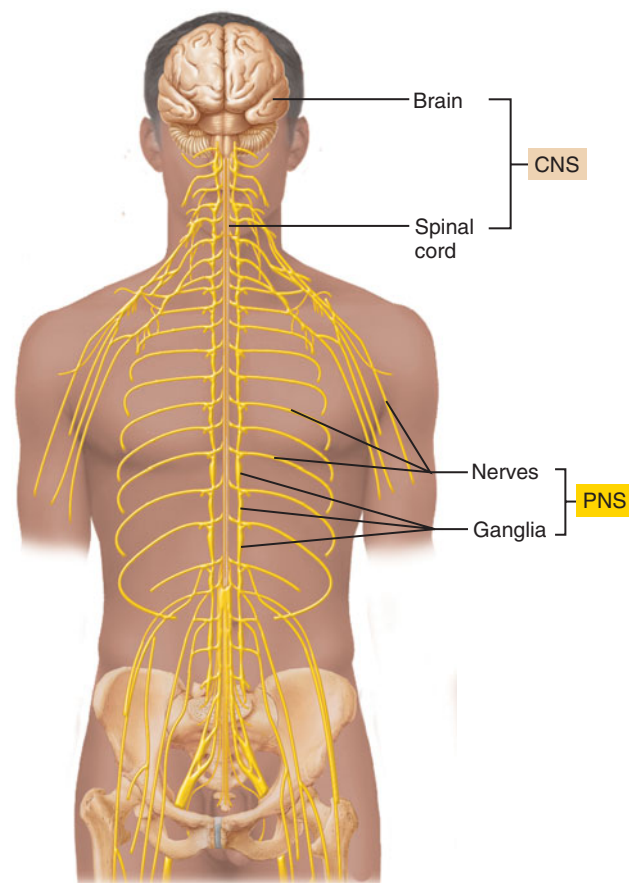


FIGURE 12.2 Divisions of the nervous system: the central nervous system (CNS) and the peripheral nervous system (PNS).

extend from the brain and spinal cord. *Cranial nerves* carry signals to and from the brain, whereas *spinal nerves* carry signals to and from the spinal cord. These peripheral nerves serve as communication lines that link all regions of the body to the central nervous system. Also included in the PNS are **ganglia**, areas where the cell bodies of neurons are clustered.

As mentioned, the nervous system receives sensory inputs and dictates motor outputs (**Figure 12.3**). **Sensory**, or **afferent** (af'er-ent), signals are picked up by sensory receptors located

throughout the body and carried by nerve fibers of the PNS into the CNS (*afferent* means “carrying toward”). **Motor**, or **efferent** (ef'er-ent), signals are carried away from the CNS by nerve fibers of the PNS to innervate the muscles and glands, causing these organs either to contract or to secrete (*efferent* means “carrying away”). Both the sensory inputs and the motor outputs are further divided according to the body regions they serve: The *somatic body region* consists of the structures external to the ventral body cavity—in other words,

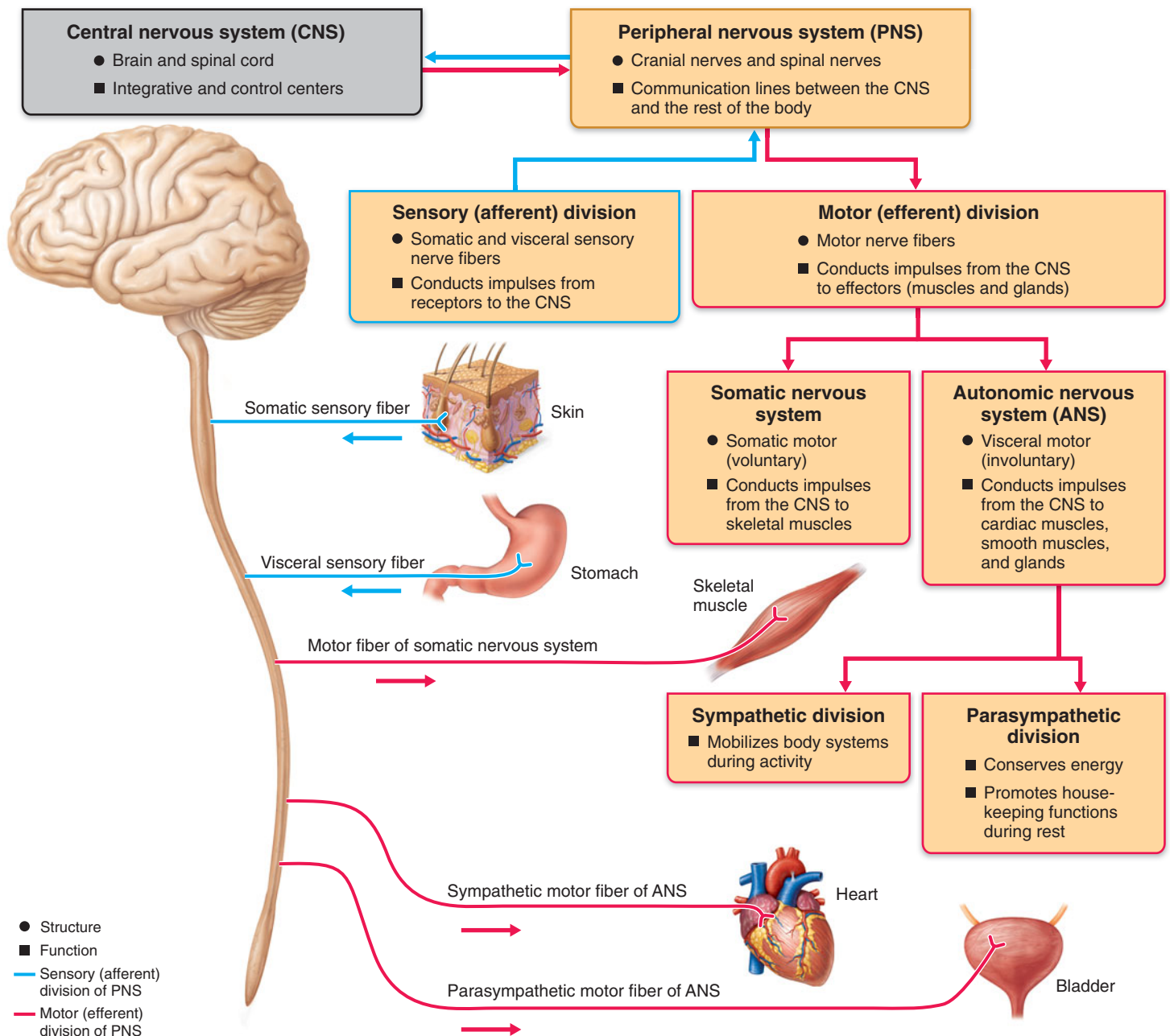


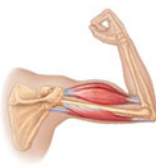

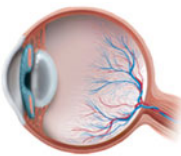



FIGURE 12.3 Schematic of levels of organization in the nervous system.

Visceral organs (located primarily in the ventral body cavity) are innervated by visceral sensory fibers and by motor fibers of the autonomic nervous system. The somatic body regions (limbs and body wall) are innervated by motor fibers of the somatic nervous system and by somatic sensory fibers. Arrows indicate the direction of nerve impulses. (Connections to the spinal cord are not anatomically accurate.)

TABLE 12.1 Types of Sensory and Motor Fibers of the Peripheral Nervous System

Sensory Components		Motor Components	
Somatic Sensory (SS)	Visceral Sensory (VS)	Somatic Motor (SM)	Visceral Motor (VM; Autonomic)
<p>GENERAL: Touch, pain, pressure, vibration, temperature, and proprioception from the skin, body wall, and limbs</p> 	<p>GENERAL: Stretch, pain, temperature, chemical changes, and irritation in viscera; nausea and hunger</p> 	<p>Motor innervation to skeletal muscles</p> 	<p>Motor innervation to smooth muscle, cardiac muscle, and glands</p> 
<p>SPECIAL: Hearing, equilibrium, and vision</p> 	<p>SPECIAL: Taste and smell</p> 		

the structures of the outer tube (skin, skeletal musculature, bones). The *visceral body region* mostly contains the viscera within the ventral body cavity—which means the structures of the body’s inner tube (digestive tube, lungs, heart, bladder, and so on). This scheme results in the four main subdivisions of the PNS: (1) **somatic sensory** (the sensory innervation of the outer tube: skin, body wall, and limbs); (2) **visceral sensory** (the sensory innervation of the viscera); (3) **somatic motor** or voluntary motor (the motor innervation of the outer tube, specifically skeletal muscles); and (4) **visceral motor** also called the **autonomic** (aw-to-nom’ik) **nervous system** (ANS) (the involuntary motor innervation of the inner tube, specifically smooth muscle, cardiac muscle, and glands, as well as some outer tube structures: arrector pili muscles, smooth muscle in the vessels, and sweat glands). Because these subdivisions are essential to understanding the nervous system, we will examine each in greater detail (Table 12.1).

1. **Somatic sensory.** The **general somatic senses** are the senses whose receptors are spread widely throughout the outer tube of the body (in this context, the term *general* means “widespread”). These include the many senses experienced on the skin and in the body wall, such as touch, pain, pressure, vibration, and temperature. The gritty texture of sandpaper, the heat from a mug of hot chocolate, and the pain from a bruise or a pulled muscle are all examples of general somatic sensation.
- Another type of general somatic sensation is **proprioception** (pro”pre-o-sep’shun; “sensing one’s own body”), a sense that detects the amount of stretch in muscles, tendons, and joint capsules. Proprioception informs

you of the position and movement of your body in space, giving you a “body sense.” To demonstrate proprioception, flex and extend your fingers without looking at them—you will be able to feel exactly which joints are moving.

The **special somatic senses** are the somatic senses whose receptors are confined to relatively small areas rather than spread widely throughout the body (in this context, the term *special* means “localized”). Most special senses are confined to the head, including hearing and balance, or **equilibrium** (with receptors in the inner ear), and vision (with receptors in the eye).

2. **Visceral sensory.** The **general visceral senses** include stretch, pain, and temperature, which can be felt widely in the digestive and urinary tracts, reproductive organs, and other viscera. Sensations such as hunger and nausea are also general visceral sensations.
- Taste and smell are considered **special visceral senses**. These senses, referred to also as the chemical senses, have their sensory receptors localized to the tongue and nasal cavity, respectively.
3. **Somatic motor.** The **somatic motor** part of the PNS stimulates contraction of the skeletal muscles in the body. Because we have voluntary control over the contraction of our skeletal muscles, the somatic motor system is often called the *voluntary nervous system*.
4. **Visceral motor.** The **visceral motor** part of the PNS regulates the contraction of smooth and cardiac muscle and secretion by the body’s many glands. General visceral motor neurons make up the *autonomic nervous system*

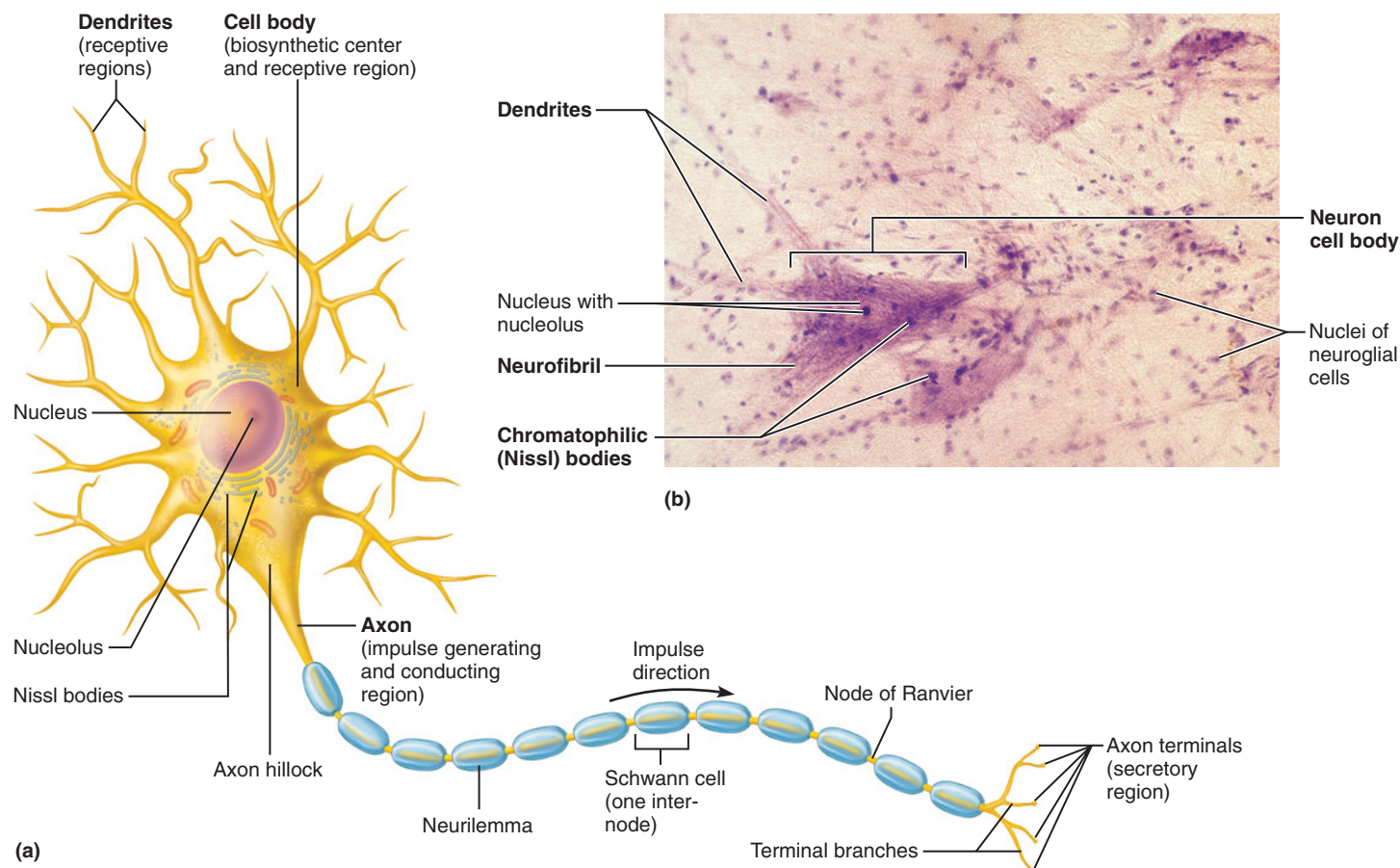


FIGURE 12.4 Structure of a typical neuron (a motor neuron). (a) Diagram of a motor neuron. The arrows indicate directions in which signals travel. The axon of this particular neuron is covered by a myelin sheath. (b) Micrograph of neural tissue from the spinal cord showing neuronal cell bodies and surrounding neuroglial cells.

(ANS), which controls the function of the visceral organs (see Figure 12.3). Because we generally have no voluntary control over such activities as the pumping of the heart and movement of food through the digestive tract, the ANS is also called the *involuntary nervous system*. The autonomic nervous system is divided into the sympathetic division, which gets the body ready for activity (“fight or flight”); and the parasympathetic division, which conserves energy and promotes digestion (“rest and digest”).

You will find it useful to return to this basic discussion of the organization of the nervous system as you work through the details of structure and function of this body system.

check your understanding

1. In which direction are afferent signals carried? What type of information do these signals contain?
2. What subdivision of the nervous system regulates contraction of the muscle tissue in the heart?
3. What type of sensation is (a) pain from a pulled muscle, (b) nausea, (c) taste?

For answers, see Appendix B.

NERVOUS TISSUE

The nervous system consists mostly of **nervous tissue**, whose cells are densely packed and tightly intertwined. Although exceedingly complex, nervous tissue is made up of just two main types of cells: (1) *neurons*, the excitable nerve cells that transmit electrical signals, and (2) *neuroglia*, nonexcitable supporting cells that surround and wrap the neurons. Both of these cell types develop from the same embryonic tissues: neural tube and neural crest (see p. 52).

The Neuron

- Define neuron, describe its structural components, and relate each structure to its functional role.
- Describe the structure of a synapse.
- Classify neurons both structurally and functionally.

The human body contains many billions of **neurons**, or **nerve cells** (Figure 12.4), which are the basic structural units of the nervous system. Neurons are highly specialized cells that conduct electrical signals from one part of the body to another. These signals are transmitted along the plasma membrane in the form of **nerve impulses**, or **action potentials**.

Basically, an impulse is a reversal of electrical charge that travels rapidly along the neuronal membrane. In addition to their ability to conduct electrical signals, neurons have other special characteristics:

1. They have *extreme longevity*. Neurons can live and function for a lifetime, over 100 years.
2. They *do not divide*. As the fetal neurons assume their roles as communication links in the nervous system, they lose their ability to undergo mitosis. There can be a high price for this characteristic of neurons, for they cannot replace themselves if destroyed. There are some exceptions to this rule; neural stem cells have been identified in certain areas of the CNS.
3. They have an exceptionally *high metabolic rate*, requiring continuous and abundant supplies of oxygen and glucose. Neurons cannot survive for more than a few minutes without oxygen.

Neurons typically are large, complex cells. Although they vary in structure, they all have a *cell body* from which one or more *processes* project (Figure 12.4).

The Cell Body

The **cell body** is also called a *soma* (= body). Although the cell bodies of different neurons vary widely in size (from 5 to 140 μm in diameter), all consist of a single nucleus surrounded by cytoplasm. In all but the smallest neurons, the nucleus is spherical and clear and contains a dark nucleolus near its center (Figure 12.4a and b).

The cytoplasm contains all the usual cellular organelles as well as distinctive **chromatophilic (Nissl) bodies** (kro-mah'to-fil-ic). These bodies, whose name means “color-loving” or “easily stained,” are large clusters of rough endoplasmic reticulum and free ribosomes that stain darkly with basic dyes. These cellular organelles continually renew the membranes of the cell and the protein part of the cytosol. **Neurofibrils** are bundles of intermediate filaments (*neurofilaments*) that run in a network between the chromatophilic bodies. Like all other intermediate filaments (see p. 34), neurofilaments keep the cell from being pulled apart when it is subjected to tensile forces.

The cell body is the focal point for the outgrowth of the neuron processes during embryonic development. In most neurons, the plasma membrane of the cell body acts as a receptive surface that receives signals from other neurons.

Most neuron cell bodies are located within the CNS. However, clusters of cell bodies called **ganglia** (singular: **ganglion**, gang'le-on; “knot in a string”), lie along the nerves in the PNS (see Figure 12.2).

Neuron Processes

Armlike **processes** extend from the cell bodies of all neurons. These processes are of two types, *dendrites* and *axons* (Figure 12.4), which differ from each other both in structure and in the functional properties of their plasma membranes. The cell processes of neurons are described here using a motor neuron as an example of a typical neuron. Motor neurons do indeed resemble most neurons in the arrangement of

their processes, but sensory neurons and some tiny neurons differ from the “typical” pattern presented here.

Dendrites Most neurons have numerous **dendrites**, processes that branch from the cell body like the limbs on a tree (*dendro* = tree). Virtually all organelles that occur in the cell body also occur in dendrites, and chromatophilic bodies extend into the basal part of each dendrite. Dendrites function as *receptive sites*, providing an enlarged surface area for receiving signals from other neurons. By definition, dendrites conduct electrical signals *toward* the cell body.

Axons A neuron has only one **axon** (ak'son; “axis, axle”), which arises from a cone-shaped region of the cell body called the **axon hillock** (“little hill”). Axons are thin processes of uniform diameter throughout their length. By definition, axons are impulse generators and conductors that transmit nerve impulses *away* from their cell body.

Chromatophilic bodies and the Golgi apparatus are absent from the axon and the axon hillock alike. In fact, axons lack ribosomes and all organelles involved in protein synthesis, so they must receive their proteins from the cell body. Neurofilaments, actin microfilaments, and microtubules are especially evident in axons, where they provide structural strength. These cytoskeletal elements also aid in the transport of substances to and from the cell body as the axonal cytoplasm is continually recycled and renewed. This movement of substances along axons is called axonal transport.

The axon of some neurons is short, but in others it can be extremely long. For example, the axons of the motor neurons that control muscles in the foot extend from the lumbar region of the spine to the sole, a distance of a meter or more (3–4 feet). Any long axon is called a **nerve fiber**.

Axon diameter varies considerably among the different neurons of the body. Axons with larger diameters conduct impulses faster than those with smaller diameters because of a basic law of physics: The resistance to the passage of an electrical current decreases as the diameter of any “cable” increases.

Although axons branch far less frequently than dendrites, occasional branches do occur along their length. These branches, called **axon collaterals**, extend from the axon at more or less right angles. Whether an axon remains undivided or has collaterals, it usually branches profusely at its terminus (end): Ten thousand of these **terminal branches** per neuron is not unusual. They end in knobs called **axon terminals** (Figure 12.4a), or *boutons* (boo-tonz'; “buttons”).

A nerve impulse is typically generated where the axon extends from the axon hillock and is conducted along the axon to the axon terminals, where it causes the release of chemicals called *neurotransmitters* into the extracellular space. The neurotransmitters excite or inhibit the neurons or target organ with which the axon terminals are in close contact.

Synapses

The site at which neurons communicate is called a **synapse** (sin'aps; “union”) (Figure 12.5a). Most synapses in the nervous system transmit information through chemical messengers. However, some neurons in certain areas of the CNS

transmit signals electrically through gap junctions. Because signals pass across most synapses in one direction only, synapses determine the direction of information flow through the nervous system.

The neuron that conducts signals toward a synapse is called the **presynaptic neuron**; the neuron that transmits signals away from the synapse is called the **postsynaptic neuron** (Figure 12.5a). Most neurons in the CNS function as both presynaptic (information-sending) and postsynaptic (information-receiving) neurons, getting information from some neurons and dispatching it to others.

There are two main types of synapses. Most synapses occur between the axon terminals of one neuron and the dendrites of another neuron; these are called **axodendritic synapses**. However, many synapses also occur between axons and neuron cell bodies; these are called *axosomatic synapses*.

Structurally, synapses are elaborate cell junctions. This section focuses on the axodendritic synapse (Figure 12.5b) because its structure is representative of both types of synapses. On the presynaptic side, the axon terminal contains **synaptic vesicles**. These are membrane-bound sacs filled with neurotransmitters, the molecules that transmit signals across the synapse. Mitochondria are abundant in the axon terminal because the secretion of neurotransmitters requires a great deal of energy. At the synapse, the plasma membranes of the two neurons are separated by a **synaptic cleft**.

How does a synapse function? When an impulse travels along the axon of the presynaptic neuron, the impulse stimulates the synaptic vesicles to fuse with the presynaptic membrane. The fused area then ruptures, causing the vesicles to release their neurotransmitter molecules, which diffuse across the synaptic cleft and bind to the postsynaptic membrane. This binding changes the membrane charge on the postsynaptic neuron, influencing the membrane's ability to generate a nerve impulse.

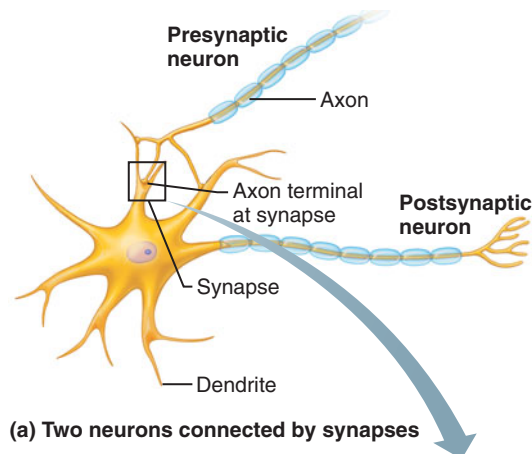
Classification of Neurons

Neurons may be classified both by structure and by function.

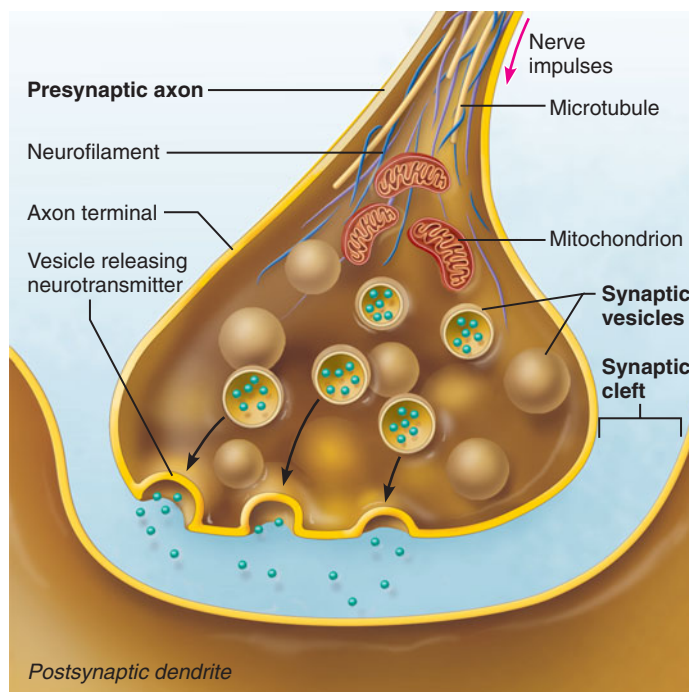
Structural Classification of Neurons Neurons are grouped structurally according to the number of processes that extend from the cell body. By this classification, neurons are *multipolar*, *bipolar*, or *unipolar* (*polar* = ends, poles). See **Table 12.2**.

Most neurons are **multipolar neurons**; that is, they have more than two processes (Table 12.2, first column). Usually, multipolar neurons have numerous dendrites and a single axon. However, some small multipolar neurons have no axon and rely strictly on their dendrites for conducting signals. Well over 99% of neurons in the body belong to the multipolar class.

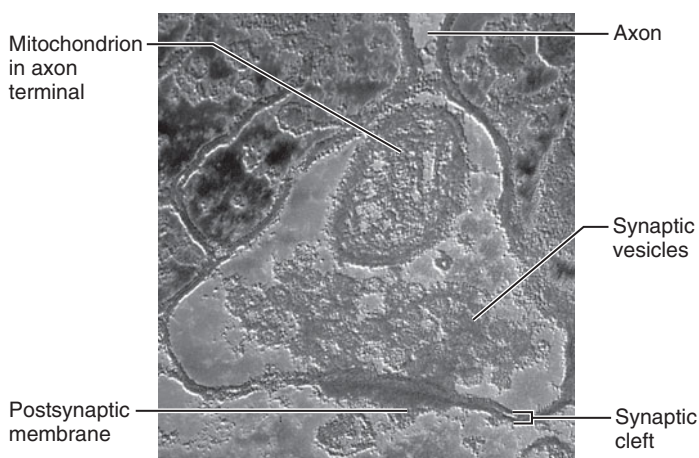
Bipolar neurons have two processes that extend from opposite sides of the cell body (Table 12.2, middle column). These very rare neurons occur in some of the special sensory organs (inner ear, olfactory epithelium of the nose, retina of the eye), where they mostly serve as sensory neurons.



(a) Two neurons connected by synapses



(b) Enlarged view of the synapse



(c) TEM of the synapse (8000 \times)

FIGURE 12.5 Structure of an axodendritic synapse.

TABLE 12.2 Comparison of Structural Classes of Neurons

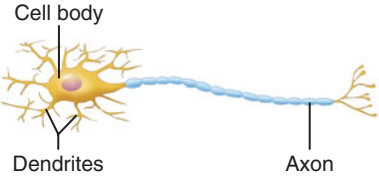
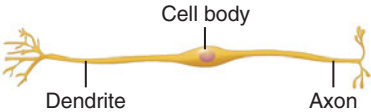
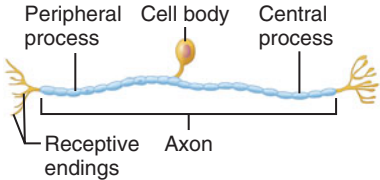



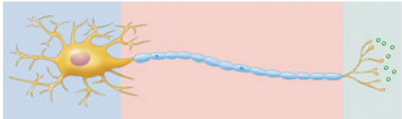
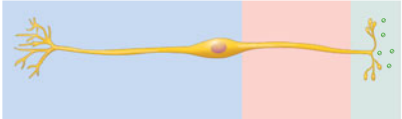
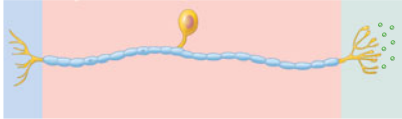
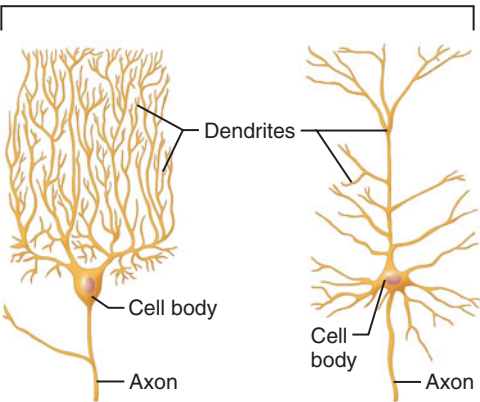
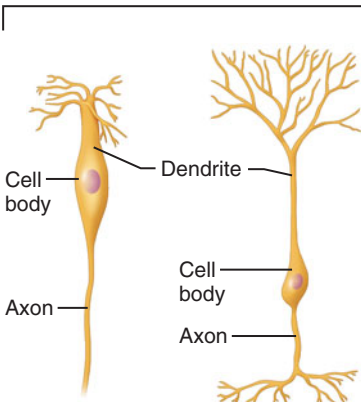
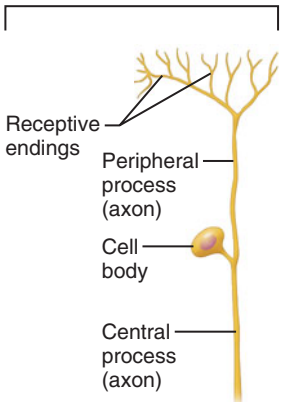
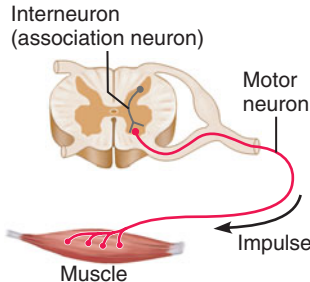
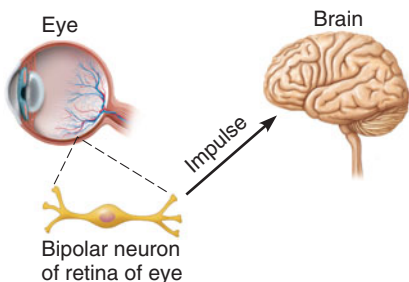
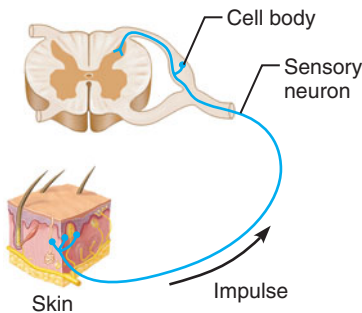
Neuron Type		
Multipolar	Bipolar	Unipolar (Pseudounipolar)
STRUCTURAL CLASS: NEURON TYPE ACCORDING TO THE NUMBER OF PROCESSES EXTENDING FROM THE CELL BODY		
Many processes extend from the cell body; all are dendrites except for a single axon.	Two processes extend from the cell body: One is a fused dendrite; the other is an axon.	One process extends from the cell body and forms central and peripheral processes, which together comprise an axon.
		
RELATIONSHIP OF ANATOMY TO THE THREE FUNCTIONAL REGIONS		
 Receptive region (receives stimulus).	 Conducting region (generates/transmits nerve impulse).	 Secretory region (axon terminals release neurotransmitters).
		
RELATIVE ABUNDANCE AND LOCATION IN HUMAN BODY		
Most abundant in body. Major neuron type in the CNS.	Rare. Found in some special sensory organs (olfactory mucosa, eye, ear).	Found mainly in the PNS. Common only in dorsal root ganglia of the spinal cord and sensory ganglia of cranial nerves.
STRUCTURAL VARIATIONS		
<div>Multipolar</div>  <div>Purkinje cell of cerebellum Pyramidal cell</div>	<div>Bipolar</div>  <div>Olfactory cell Retinal cell</div>	<div>Unipolar</div>  <div>Dorsal root ganglion cell</div>

TABLE 12.2 *continued*

Neuron Type		
Multipolar	Bipolar	Unipolar (Pseudounipolar)
FUNCTIONAL CLASS: NEURON TYPE ACCORDING TO DIRECTION OF IMPULSE CONDUCTION		
<p>1. Most multipolar neurons are interneurons (association neurons) that conduct impulses within the CNS, integrating sensory input or motor output; may be one of a chain of CNS neurons, or a single neuron connecting sensory and motor neurons.</p> <p>2. Some multipolar neurons are motor neurons that conduct impulses along the efferent pathways from the CNS to an effector (muscle/gland).</p>	<p>Essentially all bipolar neurons are sensory neurons that are located in some special sense organs. For example, bipolar cells of the retina are involved with the transmission of visual inputs from the eye to the brain (via an intermediate chain of neurons).</p>	<p>Most unipolar neurons are sensory neurons that conduct impulses along afferent pathways to the CNS for interpretation. (These sensory neurons are called primary or first-order sensory neurons.)</p>
		

Unipolar neurons have a short, single process that emerges from the cell body and divides like an inverted T into two long branches (Table 12.2, last column). Most unipolar neurons start out as bipolar neurons whose two processes fuse together near the cell body during development. Therefore, they are more properly called *pseudounipolar neurons* (*pseudo* = false). Unipolar neurons are found in sensory ganglia in the PNS, where they function as sensory neurons. The short, single process near the neuron cell body divides into two longer branches. One of these branches runs centrally into the CNS and is called the **central process**, whereas the other branch extends peripherally to the receptors and is called the **peripheral process**.

Are the processes of sensory neurons dendrites, or are they axons? The central process is clearly an axon because it (1) carries a nerve impulse and (2) carries that impulse away from the cell body—the two criteria that define an axon (p. 352). The peripheral process, by contrast, is ambiguous: It carries nerve impulses, as does an axon, but these signals travel *toward* the cell body, a fundamental feature of dendrites. Despite this functional similarity to dendrites, however, the peripheral process is called an *axon* because its fine structure is identical to that of true axons. Unipolar neurons, therefore, do not have dendrites; receptive endings at the terminal end of the peripheral axon receive sensory stimuli and transmit signals through the peripheral axon toward the cell body.

Functional Classification of Neurons Neurons are grouped functionally according to the direction the nerve

impulse travels relative to the CNS. Based on this criterion, there are *sensory neurons*, *motor neurons*, and *interneurons* (Table 12.2, last row).

Sensory neurons, or *afferent neurons*, make up the sensory division of the PNS (see Figure 12.3). They transmit impulses *toward* the CNS from sensory receptors in the PNS. Virtually all sensory neurons are pseudounipolar, and their cell bodies are in ganglia outside the CNS. The peripheral process extends from a sensory receptor; the central process terminates in the CNS. These two processes function as one, carrying impulses directly from the peripheral receptors to the CNS.

Motor neurons, or *efferent neurons*, make up the motor division of the PNS (see Figure 12.3). These neurons carry impulses *away* from the CNS to effector organs (muscles and glands). Motor neurons are multipolar, and their cell bodies are located in the CNS (except for some neurons of the autonomic nervous system). Motor neurons form junctions with effector cells, stimulating muscles to contract or glands to secrete.

Interneurons, or *association neurons*, lie between motor and sensory neurons. These multipolar neurons are confined entirely to the CNS (Table 12.2). Interneurons link together into chains that form complex neuronal pathways. The fact that interneurons make up 99.98% of the neurons of the body reflects the vast amount of information processed in the human CNS. These multipolar neurons show great diversity in size and in the branching patterns of their processes, as shown in Table 12.2, “Structural Variations.”

check your understanding

- Which type of neuron process receives stimuli?
- Describe how the electrical impulse from one neuron is passed to another neuron.
- What is the structural classification of most sensory neurons?
- What structural type is most abundant? What neurons in the PNS are of this type?

For answers, see Appendix B.

Supporting Cells

- List the six types of supporting cells in nervous tissue, and distinguish them by location and function.
- Describe the structure of myelin sheaths.

All neurons associate closely with non-nervous supporting cells called **neuroglia** (nu-rog'le-ah; “nerve glue”), or **glial** (gle'al) **cells**. There are six types of neuroglia—four in the CNS and two in the PNS (Figure 12.6). Each type has a unique function, yet in general, these cells provide a supportive scaffolding for neurons. Furthermore, they cover all non-synaptic parts of the neurons, thereby insulating the neurons and keeping the electrical activities of adjacent neurons from interfering with each other.

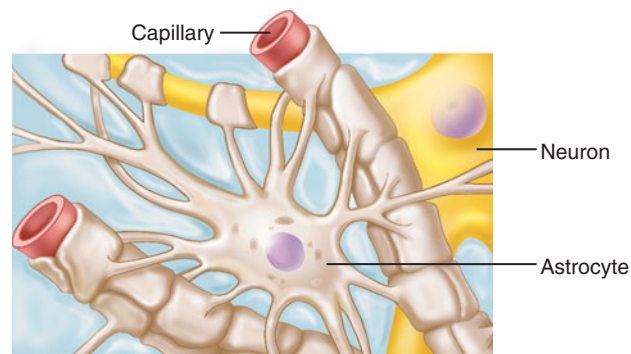
Neuroglia in the CNS

Like neurons, most neuroglial cells of the CNS have branching processes and a central cell body (Figure 12.6a–d). Neuroglia can be distinguished from neurons, however, by the much smaller size of neuroglia and by their darker-staining nuclei (see Figure 12.4). They outnumber neurons in the CNS by about 10 to 1, and they make up about half the mass of the brain. Unlike neurons, glial cells can divide throughout life.

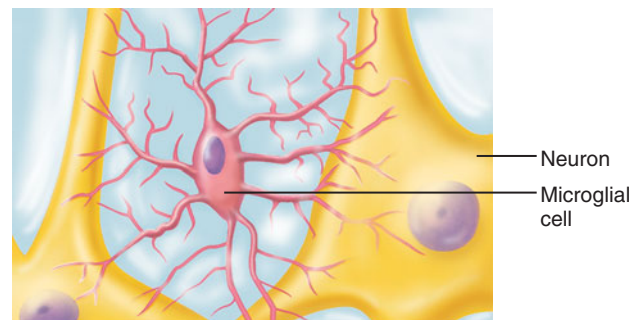
GLIOMAS Because glial cells can divide, they accumulate the “mistakes” in DNA replication that may transform them into cells that proliferate abnormally. Such an accumulation does not occur in neurons, most of which do not divide. Therefore, most tumors that originate in the brain (60%) are **gliomas**, tumors formed by uncontrolled proliferation of glial cells. Two percent of all cancers are gliomas, and their incidence is increasing. These are difficult cancers to treat, and the one-year survival rate is under 50%.



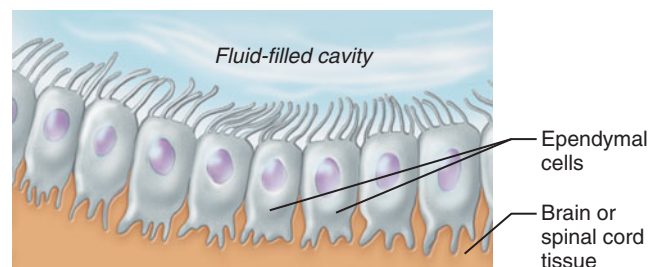
Star-shaped **astrocytes** (as'tro-sītz; “star cells”) are the most abundant glial cells of the CNS (Figure 12.6a). They have many radiating processes with bulbous ends. Some of these bulbs cling to neurons (including the axon terminals), whereas others cling to capillaries. The functions of astrocytes are numerous and not fully understood. Known functions include (1) regulating neurotransmitter levels by increasing the rate of neurotransmitter uptake in regions of high neuronal activity; (2) signaling increased blood flow through capillaries in active



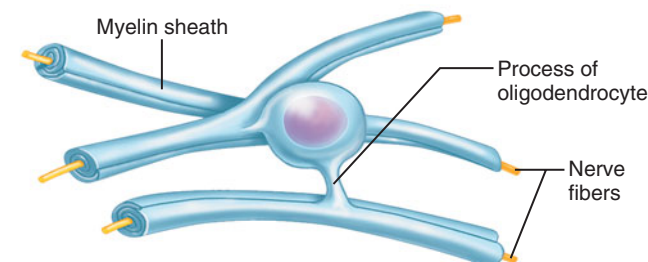
(a) Astrocytes are the most abundant CNS neuroglia.



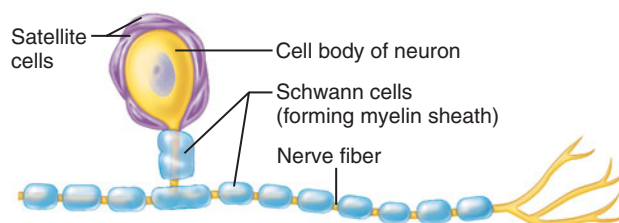
(b) Microglial cells are defensive cells in the CNS.



(c) Ependymal cells line cerebrospinal fluid-filled cavities.



(d) Oligodendrocytes have processes that form myelin sheaths around CNS nerve fibers.



(e) Satellite cells and Schwann cells (which form myelin) surround neurons in the PNS.

FIGURE 12.6 Neuroglia. (a–d) The four types of neuroglial cells in the CNS. (e) Neuroglia of the PNS.

regions of the brain; and (3) controlling the ionic environment around neurons. Astrocytes also help synapses form in developing neural tissue, produce molecules necessary for neural growth (brain-derived trophic factor, BDNF), and propagate calcium signals that may be involved with memory. No longer are these cells considered passive supportive cells for neurons; rather, they appear to have an active role in neural activity. Understanding the activities of these abundant glial cells is an area of ongoing research.

Microglia, the smallest and least abundant neuroglia of the CNS, have elongated cell bodies and cell processes with many pointed projections, like a thorny bush (Figure 12.6b). They are phagocytes, the macrophages of the CNS. They migrate to, and then engulf, invading microorganisms and injured or dead neurons. Unlike other neuroglial cells, microglia do not originate in nervous tissue. Instead, like the other macrophages of the body, they are derived from blood cells called monocytes. The monocytes that become microglia migrate to the CNS during the embryonic and fetal periods.

Recall from Chapter 3 (p. 52) that the CNS originates in the embryo as a hollow neural tube and retains a central cavity throughout life. **Ependymal cells** (ě-pen'dī-mal; “wrapping garment”) form a simple epithelium that lines the central cavity of the spinal cord and brain (Figure 12.6c). Here these cells provide a fairly permeable layer between the *cerebrospinal fluid* that fills this cavity and the tissue fluid that bathes the cells of the CNS. Ependymal cells bear cilia that help circulate the cerebrospinal fluid.

Oligodendrocytes (ol'ī-go-den'dro-sītz) (Figure 12.6d) have fewer branches than astrocytes; indeed, their name means “few-branch cells.” They line up in small groups and wrap their cell processes around the thicker axons in the CNS, producing insulating coverings called *myelin sheaths* (discussed in detail shortly).

Neuroglia in the PNS

The two kinds of neuroglia in the PNS are *satellite cells* and *Schwann cells* (Figure 12.6e), very similar cell types that differ mainly in location. **Satellite cells** surround neuron cell bodies within ganglia. (Their name comes from a fancied resemblance to the moons, or satellites, around a planet.) **Schwann cells** surround all axons in the PNS and form myelin sheaths around many of these axons.

Myelin Sheaths

Myelin sheaths are produced by oligodendrocytes in the CNS and Schwann cells in the PNS. These sheaths are segmented structures that are composed of the lipoprotein **myelin** and surround the thicker axons of the body. Each segment of myelin consists of the plasma membrane of a supporting cell rolled in concentric layers around the axon (Figure 12.7a). Myelin sheaths form an insulating layer that prevents the leakage of electrical current from the axon, increases the speed of impulse conduction along the axon, and makes impulse propagation more energy-efficient.

Myelin Sheaths in the PNS As previously stated, the myelin sheaths in the PNS are formed by Schwann cells (see Figure 12.6e). Myelin sheaths develop during the fetal period

and the first year or so of postnatal life. To form the myelin sheath, the Schwann cells first indent to receive the axon and then wrap themselves around the axon repeatedly, in a jelly-roll fashion (Figure 12.7a ① and ②). Initially the wrapping is loose, but the cytoplasm of the Schwann cell is gradually squeezed outward from between the membrane layers. When the wrapping process is finished, many concentric layers of Schwann cell plasma membrane ensheath the axon in a tightly packed coil of membranes that is the true myelin sheath (Figure 12.7a ③). The nucleus and most of the cytoplasm of the Schwann cell end up just external to the myelin layers. This external material is called the **neurilemma** (“neuron sheath”).

Because the adjacent Schwann cells along a myelinated axon do not touch one another, there are gaps in the myelin sheath (see Figure 12.4a). These gaps, called **nodes of Ranvier**, occur at regular intervals about 1 mm apart. In myelinated axons, nerve impulses do not travel along the myelin-covered regions of the axonal membrane but instead jump from the membrane of one node of Ranvier to the next in a way that greatly speeds impulse conduction.

Only thick, rapidly conducting axons are sheathed with myelin. In contrast, thin, slowly conducting axons lack a myelin sheath and are called **unmyelinated axons** (Figure 12.7b). Schwann cells surround such axons but do not wrap around them in concentric layers of membrane (Figure 12.7b ①). A single Schwann cell can partly enclose 15 or more unmyelinated axons, each of which occupies a separate tubular recess in the surface of the Schwann cell (Figure 12.7b ②). Unmyelinated axons are found in portions of the autonomic nervous system (Chapter 15) and in some sensory fibers.

TIC DOULOUREUX The main sensory nerve of the face, the trigeminal nerve, can be affected by an extremely painful disorder called **tic douloureux** (tik doo'loo-roo; “wincing in pain”), or **trigeminal neuralgia**. Compression of the trigeminal nerve by an adjacent blood vessel causes degeneration and loss of the myelin sheath that surrounds the sensory nerve fibers. Because of the loss of insulation in the nonmyelinated region, impulses in nerve fibers that carry touch sensations stimulate pain fibers in the same nerve (called *cross-talk*), leading to the perception of pain by the brain. Even the softest touch to the face can produce excruciating pain. Although not fatal, this condition is debilitating: The pain is unpredictable and extreme.



Myelin Sheaths in the CNS Oligodendrocytes form the myelin sheaths in the brain and spinal cord (Figure 12.6d). In contrast to Schwann cells, each oligodendrocyte has multiple processes that coil around several different axons. Nodes of Ranvier are present, although they are more widely spaced than those in the PNS.

As in the PNS, the thinnest axons in the CNS are unmyelinated. These unmyelinated axons are covered by the

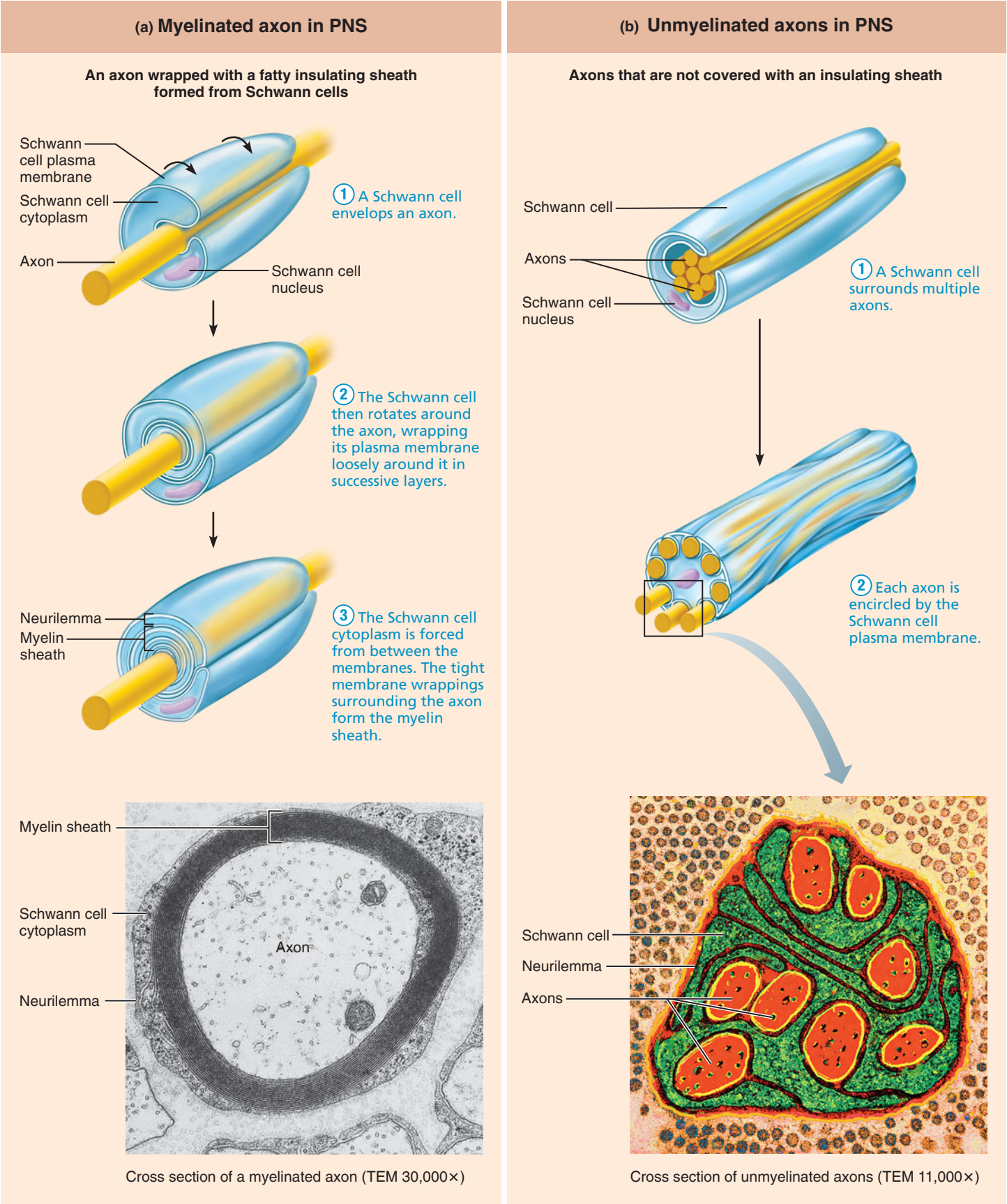


FIGURE 12.7 Schwann cells on myelinated and unmyelinated axons in the PNS.
(a) TEM, 30,000 \times . (b) TEM, 11,000 \times .

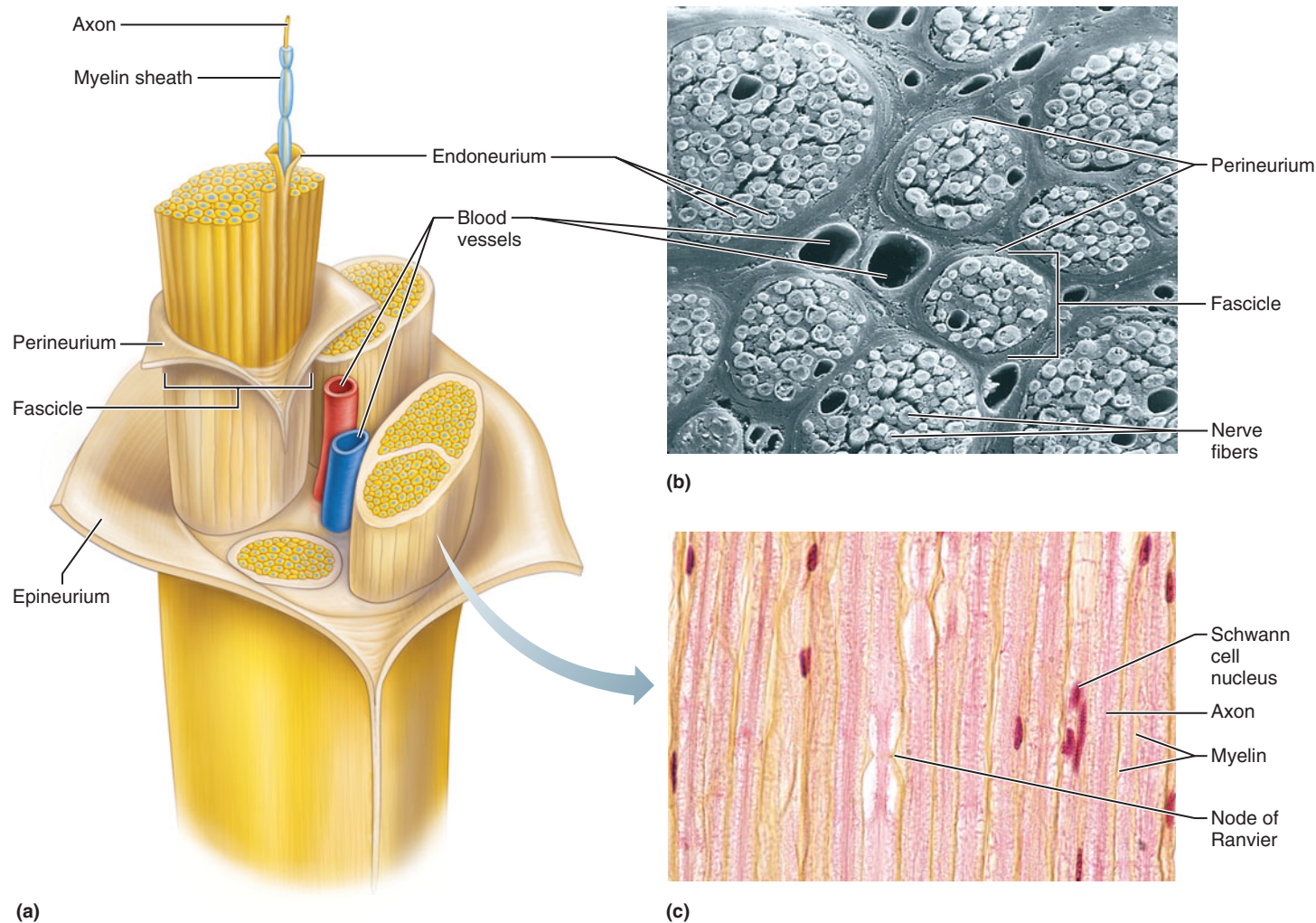


FIGURE 12.8 Structure of a nerve. (a) Three-dimensional view of a portion of a nerve, showing connective tissue wrappings. (b) Scanning electron micrograph of a cross section of portion of a nerve (120 \times). (c) Longitudinal section of a nerve, as viewed by light microscopy (160 \times).

Source: Kessel and Kardon/Visuals Unlimited.

many long processes of glial cells, such as astrocytes, that are so abundant in the CNS.

check your understanding

8. Which neuroglia make myelin in the CNS? In the PNS?
9. Which neuroglia are common in regions where synapses occur?
10. Do Schwann cells cover unmyelinated axons in the PNS?

For answers, see Appendix B.

GROSS ANATOMY OF THE NERVOUS SYSTEM: AN OVERVIEW

- Define nerve and describe the structural components of nerves.
- Distinguish gray matter from white matter in the CNS.

Thus far we have discussed the structure and function of the cells that make up nervous tissue: neurons and neuroglia. Nervous tissue, along with other types of tissues, forms the organs of the nervous system: the brain and spinal cord of the CNS and the nerves and ganglia of the PNS. The basic structural organization of the nerves and CNS is described below. The detailed structure and function of the organs of the CNS are covered in Chapter 13, and those of the PNS are covered in Chapters 14 and 15.

Nerves

A **nerve** is a cablelike organ in the peripheral nervous system (see Figure 12.2). Each nerve consists of many axons (nerve fibers) arranged in parallel bundles and enclosed by successive wrappings of connective tissue (Figure 12.8). Almost all nerves contain both myelinated and unmyelinated sensory and motor fibers.

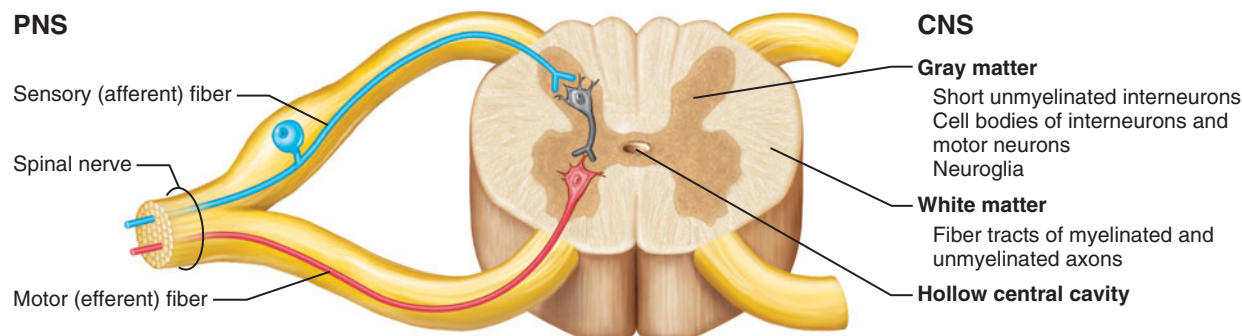


FIGURE 12.9 Cross section through the spinal cord. Linkage between PNS and CNS is illustrated on the left.

Within a nerve, each axon is surrounded by Schwann cells. Covering the Schwann cells is a delicate layer of loose connective tissue called **endoneurium** (en"do-nu're-um). Groups of axons are bound into bundles called nerve **fascicles** by a wrapping of connective tissue called the **perineurium**. Finally, the whole nerve is surrounded by a tough fibrous sheath, the **epineurium**. The three layers of connective tissue in nerves correspond exactly to those in skeletal muscle: the endomysium, perimysium, and epimysium (see p. 242). The connective tissue in a nerve also contains the blood vessels that nourish the axons and Schwann cells, as Figure 12.8 shows.

The terms *neuron*, *nerve fiber*, and *nerve* are easy to confuse. Keep in mind:

- A **neuron** is a nerve cell.
- A **nerve fiber** is a long axon.
- A **nerve** is a collection of nerve fibers in the PNS.

Gray and White Matter of the CNS

The brain and spinal cord have distinct regions of gray and white matter that reflect the arrangement of their neurons. The **gray matter** is a gray-colored zone that surrounds the hollow central cavity of the CNS. In the spinal cord it is a butterfly-shaped region in which the dorsal half contains cell bodies of interneurons and the ventral half contains cell bodies of motor neurons (**Figure 12.9**). Thus, *gray matter is the site where neuron cell bodies are clustered*. More specifically, the gray matter of the CNS is a mixture of neuron cell bodies; dendrites; short, unmyelinated neurons; and neuroglia.

External to the gray matter is **white matter**, which contains no neuron cell bodies but millions of axons. Its white color comes from the myelin sheaths around many of the axons. Most of these axons either ascend from the spinal cord to the brain or descend from the brain to the spinal cord, allowing these two regions of the CNS to communicate with each other. Thus, *white matter consists of axons running between different parts of the CNS*. Within the white matter, axons traveling to similar destinations form axon bundles called **tracts**.

Throughout the CNS white matter is external to gray matter, which surrounds the hollow central cavity. In two regions of the brain (the cerebrum and cerebellum), there is an additional layer of gray matter located superficially, the **cortex**. The anatomy of the CNS and the distribution of gray and white matter are described more completely in Chapter 13.

check your understanding

11. Name the connective tissue wrapping that encloses a bundle of nerve fibers into a fascicle.
12. Where do synapses occur in the CNS, in white matter or in gray matter?
13. Why is white matter white?

For answers, see Appendix B.

NEURONAL INTEGRATION

Integration Between the PNS and CNS

- Describe the structural link between the peripheral nervous system and the central nervous system.
- Define reflex, and list the basic components of a reflex arc. Distinguish monosynaptic reflexes from polysynaptic reflexes.

We divide the nervous system into the PNS and CNS to simplify the discussion of each component. Yet it is important to remember that these two divisions of the nervous system are functionally and structurally linked.

The PNS is composed of the axons of sensory (afferent) and motor (efferent) neurons (nerve fibers) bundled together as nerves (**Figure 12.9**). These nerves function as information pathways to and from the periphery of the body: The afferent fibers respond to sensory stimuli and carry that information to the CNS; the efferent fibers transmit motor stimuli from the CNS to muscles and glands, causing them to function (contract or secrete).

The CNS is composed of interneurons that (1) process received sensory information, (2) direct this information to

specific regions of the CNS, (3) initiate the appropriate motor response, and (4) transport information (sensory and motor) from one region of the CNS to another. The first three functions are accomplished by interneurons in the gray matter; the fourth occurs via axons in the white matter.

The gray matter of the CNS is like a complex series of highway interchanges: Information enters the gray matter and is rerouted to other regions of the CNS. The neurons of the PNS synapse with neurons in the gray matter, creating a network of ramps that link the roadways of the PNS (the nerves) with the superhighways of the CNS (the white matter). In the gray matter, pathways converge and diverge as information is processed and routed to other regions of the CNS.

The white matter pathways in the CNS are formed by long myelinated axons that extend out from the gray matter. These pathways are the superhighways that carry information (sensory and motor) between the various regions of the CNS for processing in the gray matter.

The structural link between the PNS and the CNS occurs in the gray matter of the CNS. The simplest example of neuronal integration is the reflex arc.

Reflex Arcs

Reflex arcs are simple chains of neurons that cause our simplest, reflexive behaviors and reflect the basic structural plan of the nervous system. Reflex arcs account for **reflexes**, which are defined as rapid, automatic *motor* responses to stimuli. Reflexes are unlearned, unpremeditated, and involuntary. Examples are jerking away your hand after it accidentally touches a hot stove and vomiting in response to some food that irritates your stomach. As you can see from these examples, reflexes are either *somatic reflexes* resulting in the contraction of skeletal muscles or *visceral reflexes* activating smooth muscle, cardiac muscle, or glands.

Every reflex arc has five essential components, each of which activates the next (Figure 12.10):

1. The *receptor* is the site where the stimulus acts. Receptors are located at the terminal end of the peripheral process of a sensory neuron.
2. The *sensory neuron* transmits the afferent impulses to the CNS.
3. The *integration center* consists of one or more synapses in the gray matter of the CNS (represented by the spinal cord in Figure 12.10). In the simplest reflex arcs, the integration center is a single synapse between a sensory neuron and a motor neuron. In more complex reflexes, it can involve multiple synapses that send signals through long chains of interneurons to other portions of the CNS, for instance, to portions of the brain.
4. The *motor neuron* conducts efferent impulses from the integration center to an effector.
5. The *effector* is the muscle or gland cell that responds to the efferent impulses by contracting or secreting.

Figure 12.11 illustrates the simplest of all reflexes, the **monosynaptic reflex** (mon'ō-sī-nap'tik; "one synapse").

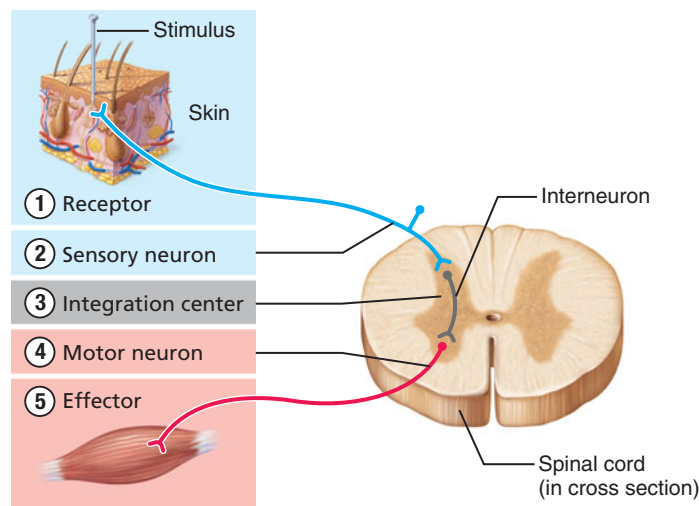


FIGURE 12.10 Components of a reflex arc. Receptors detect changes in the internal or external environment. Effectors are muscles or glands.

In a monosynaptic reflex there is no interneuron between the sensory neuron and the motor neuron; thus, as its name implies, there is only one synapse in this reflex arc. The example shown is the familiar “knee-jerk” reflex: The impact of a hammer on the patellar ligament stretches the quadriceps muscles of the thigh. This stretching initiates an impulse in a sensory neuron that directly activates a motor neuron in the spinal cord, which then signals the quadriceps muscle to contract. This contraction counteracts the original stretching caused by the hammer.

Many skeletal muscles of the body participate in such monosynaptic *stretch reflexes*, which help maintain equilibrium and upright posture. In these reflexes, the sensory neurons sense the stretching of muscles that occurs when the body starts to sway, and then the motor neurons activate muscles that adjust the body’s position to prevent a fall. Because they contain just one synapse, stretch reflexes are the fastest of all reflexes—and speed is essential to keep one from falling to the ground.

Far more common are **polysynaptic reflexes**, in which one or more interneurons are part of the reflex pathway between the sensory and motor neurons. The presence of even one interneuron means that there have to be at least two synapses in this type of reflex arc, thus the name polysynaptic. Most of the simple reflex arcs in the body contain a single interneuron and therefore have a total of three neurons. *Withdrawal reflexes*, by which we pull away from danger, are three-neuron polysynaptic reflexes (Figure 12.11b). Pricking a finger with a tack initiates an impulse in the sensory neuron, which activates the interneuron in the CNS. The interneuron then signals the motor neuron to contract the muscle that withdraws the hand.

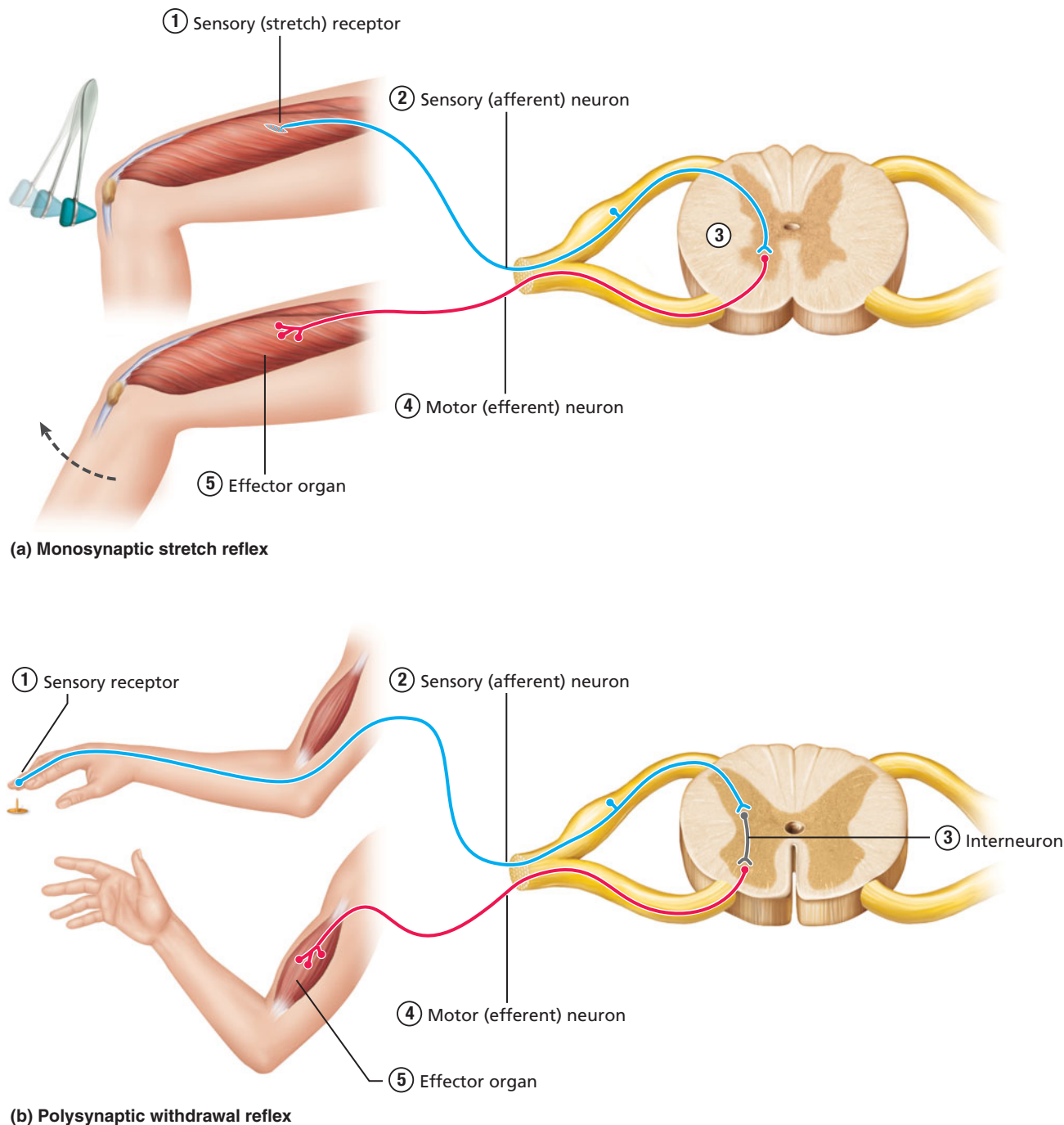


FIGURE 12.11 Types of reflex arcs. (a) A monosynaptic reflex arc has two neurons and a single synapse. (b) A polysynaptic reflex arc has more than two neurons (in this case, three) and therefore has at least two synapses. The five components of a reflex arc are indicated by number.

Neuronal Circuits

- Describe the roles of interneurons in the CNS.
- Differentiate between serial and parallel processing.
- Define convergent and divergent circuits and give an example of each.

Even though reflex arcs reflect the basic organization of the human nervous system, it is obviously more than just a series of simple reflex arcs. To appreciate its complexity, you must understand the role that interneurons play. More than 99% of all neurons are interneurons, which include not only the intermediate neurons of reflex arcs but also all the neurons that are confined entirely within the CNS. The complexity of the CNS arises from the organization of this vast number of interneurons into neuronal circuits that process information.

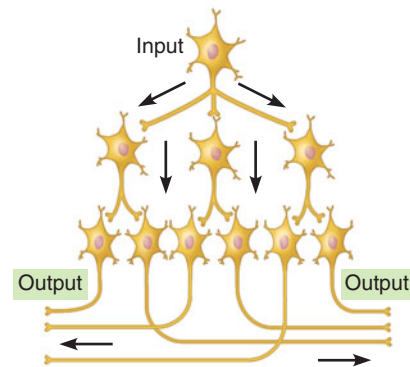
Typically, a single neuron synapses with many other neurons. The interneurons of the CNS may be interconnected in multiple ways. These are referred to as **neuronal circuits** (Figure 12.12). In a **diverging circuit** (Figure 12.12a), one presynaptic neuron synapses with several other neurons. An example of neuronal **divergence** is seen in the stretch reflex previously described. The stretch of a muscle stimulates numerous sensory neurons. Each sensory neuron synapses directly with 100–150 neurons in the gray matter of the spinal cord. Some of these neurons are motor neurons that directly innervate the stretched muscle and stimulate contraction. Others are interneurons that act to inhibit the activity of the antagonistic muscle group, and still others are interneurons that project sensory information to higher regions of the CNS. As a result of divergence, information is distributed through multiple neuronal pathways.

When many neurons synapse on a single postsynaptic neuron, the circuit is a **converging circuit** (Figure 12.12b). For example, **convergence** occurs when a single motor neuron receives both excitatory and inhibitory impulses from many other neurons. These impulses are integrated by the target motor neuron and influence whether it will initiate a nerve impulse. Divergence and convergence are apparent throughout the central nervous system as neurons integrate information.

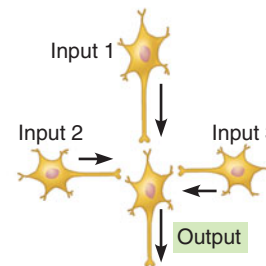
Finally, in a **reverberating circuit**, one neuron in the circuit receives feedback from another neuron in the same circuit. As shown in Figure 12.12c, a branch off the axon of one neuron circles back and synapses with a previous neuron in the circuit. In this pathway, the signal continues to be sent until either synaptic fatigue or inhibition by another signal interrupts the circuit. Reverberating circuits are involved in the control of many rhythmic activities, such as breathing and swinging the arms when walking.

Information is processed in two ways in the nervous system. Neurons that synapse one-on-one in a sequence are said to be joined **in series**, and the processing is called **serial processing**. Neurons linked this way pass their signal along a single pathway from one neuron to the next, like links in a chain. A reflex arc is one example, and a long chain of interneurons carrying a sensory signal to the brain is another (see Figures 12.11 and 12.13).

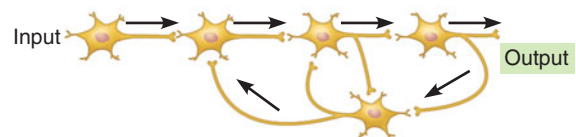
The second way of processing information is along neurons joined **in parallel**. Information from a single neuron is sent along two or more parallel pathways. This is called **parallel processing**. Parallel processing occurs when a single sensory stimulus results in multiple perceptions. For example, as you watch a friend walking toward you, multiple pathways process visual stimuli from your retina in parallel, evaluating the color, shape, spatial location, and movement of your friend. The stimuli are also processed by the parts of your brain associated with recognition and memory from past experiences, enabling you to recognize your friend, recall his name, and remember when you last saw him. For all



(a) Diverging circuit to multiple pathways



(b) Converging circuit



(c) Reverberating circuit

FIGURE 12.12 Types of neuronal circuits.

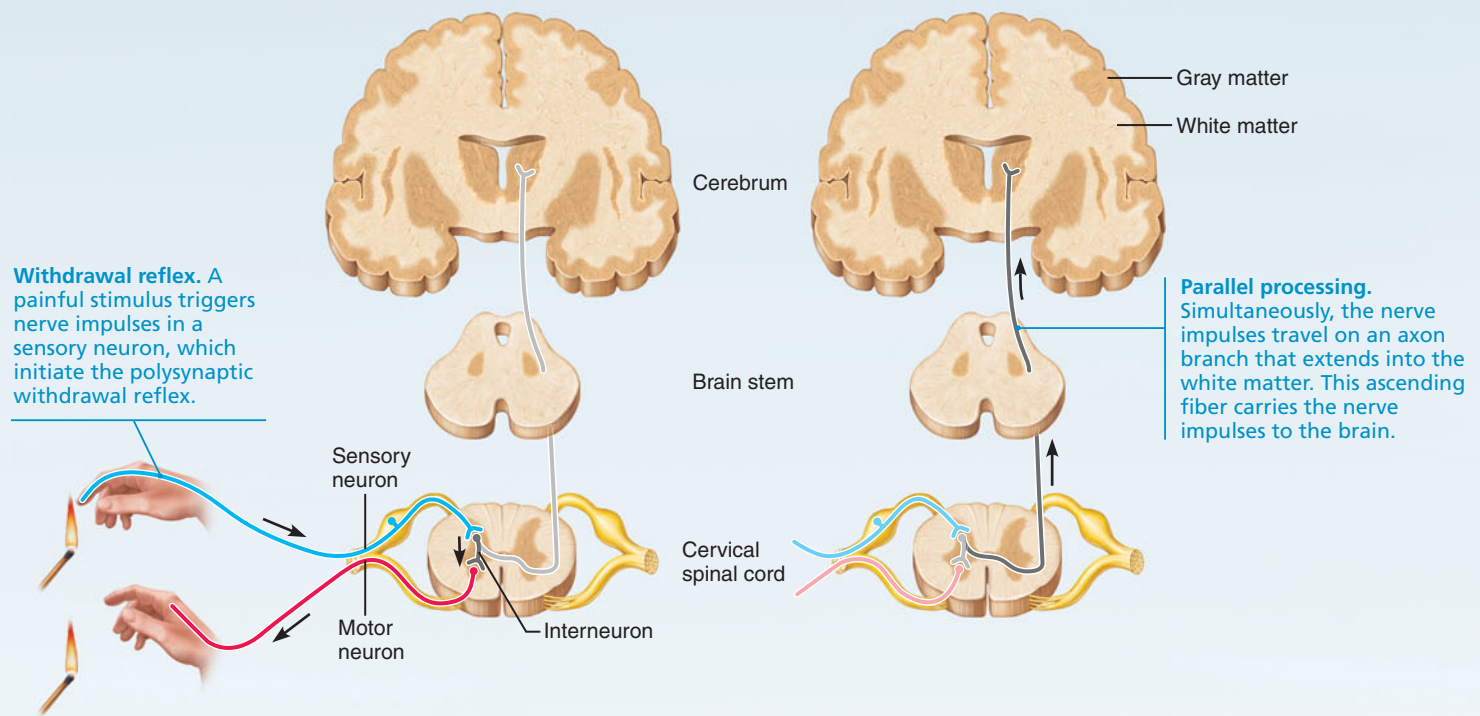
its complexity, parallel processing occurs almost instantaneously. It allows the brain to evaluate stimuli with incredible speed and enables information to be integrated along numerous pathways.

Simplified Design of the Nervous System

Neuronal circuits form chains of interneurons that are interposed between each sensory and motor neuron. Although simplified, *Focus on Neuronal Pathways* (Figure 12.13) is useful for conceptualizing the organization of neurons in the CNS. For example, if you burn your finger, the immediate result is the simple withdrawal reflex of moving your hand away (as shown in the left portion of Figure 12.13).

FIGURE 12.13

► A stimulus elicits signals through several neuronal pathways. The initial reflex arc is followed by slower responses mediated by the interneurons of the CNS. These interneurons integrate sensory input, initiate motor output, and link the different regions of the brain and spinal cord.



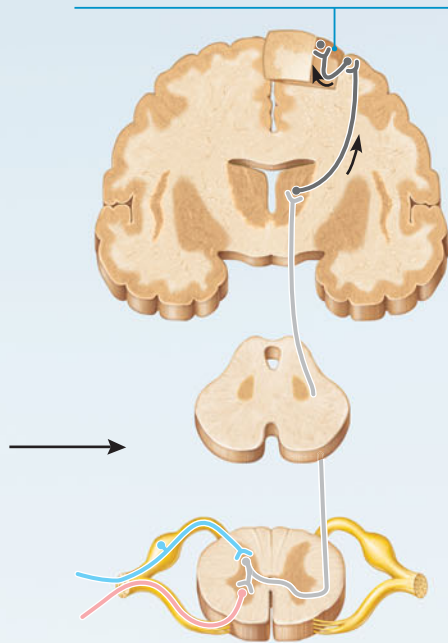
However, the sensory information is passed through a long chain of interneurons to the area of the brain that interprets sensory signals (Figure 12.13, middle two illustrations), and you feel the sensation of pain. You don't generally feel pain until after you have reflexively moved your hand away because the CNS needs time to process the information. In response to the pain, the motor area of your brain may initiate a nonreflexive motor response (shown on the far right in Figure 12.13), for instance, running your finger under cold water. In Chapter 13, you will learn the details of where the sensory signal is interpreted and where a motor response is initiated by the CNS.

check your understanding

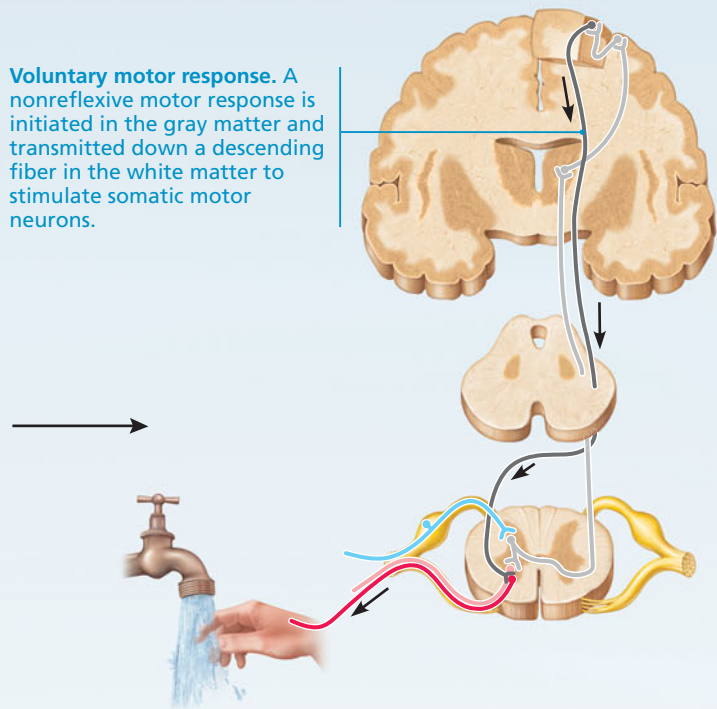
14. If there is no interneuron in a reflex arc, as in the stretch reflex, what functions as the integration center?
15. If you touch a hot stove, you reflexively withdraw your hand. The sensation of pain comes after your hand has moved. Why does it take longer to feel pain than it does to move your hand?
16. What type of neural circuit contains multiple neurons synapsing on a single neuron, altering its potential to produce a nerve impulse?

For answers, see Appendix B.

Integration in gray matter. Multiple interneurons process the nerve impulses to localize the stimulus, identify its source, and plan a response. This complex processing is illustrated here in a simplified manner.



Voluntary motor response. A nonreflexive motor response is initiated in the gray matter and transmitted down a descending fiber in the white matter to stimulate somatic motor neurons.



DISORDERS OF NERVOUS TISSUE

- Describe how multiple sclerosis relates to myelin and axon function.
- Describe the process of neuronal regeneration in the peripheral nervous system.

Multiple Sclerosis

Multiple sclerosis (MS) is a progressive disease that destroys patches of myelin in the brain and spinal cord, disrupting neuronal signals in the CNS and leading to sensory disorders and weakened musculature. This disease, which varies greatly in intensity among individuals who have it, is characterized by

periods of relapse (disability) and remission (recovery). Common signs and symptoms, which vary according to which part of the CNS is affected, include numbness or pain on the skin of some part of the body, disturbances of vision, muscle weakness or paralysis, difficulty in maintaining balance, slurred speech, bladder incontinence, fatigue, and depression.

The cause of MS is incompletely understood. It is known to be an autoimmune disease in which the immune system attacks the myelin around axons in the CNS, thereby interfering with the conduction of signals along the axons. The immune system cells called lymphocytes break down the myelin, and then macrophages consume the remains through phagocytosis. The damage is also accompanied by inflammation, which can destroy the axons themselves.

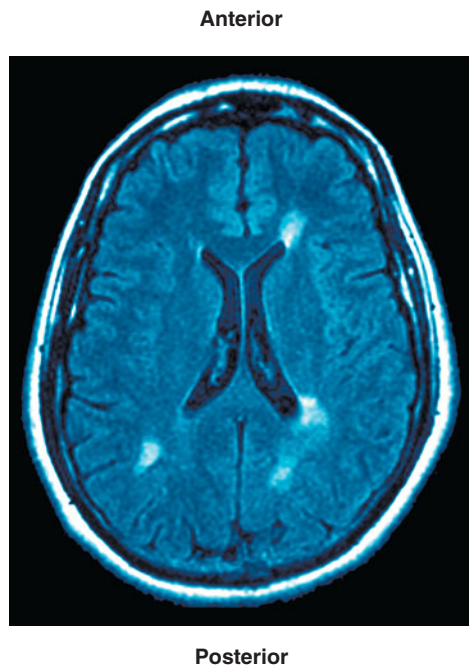


FIGURE 12.14 Multiple sclerosis. MRI of the brain of a patient with MS, transverse section. Lesions appear as bright white spots within the white matter.

MS affects different people in different ways. Some have only a single attack and recover without a recurrence, many have a decade or longer of alternating remissions and relapses, and a few deteriorate rapidly and continuously within the first year. Remission seems to result from an unexplained halting of the immune response, which gives axons time to repair themselves and to recover their functions. However, after 10–15 years of periodic relapses, the accumulated damage to the axons is often too great, and 50% of MS sufferers decline rapidly in their second decade of the disease.

MS is not always easy to recognize. A definitive but invasive test for MS identifies MS-specific antibodies in cerebrospinal fluid taken from the space around the spinal cord. A less invasive approach tests for a delay in the time it takes visual signals to travel from the eye through the brain, as measured by monitoring brain waves detected on the outside of the skull. Finally, magnetic resonance imaging can reveal the disease's characteristic lesions (**Figure 12.14**).

Treatment is directed toward relieving the symptoms. Anti-inflammatory steroid drugs lessen the severity and duration of relapses, but they do not reduce the frequency of attacks. Other drugs, such as interferons and glatiramer acetate, act to control the immune system to decrease the frequency of relapses as well as the appearance of new lesions. Mitoxantrone, a cancer drug that suppresses lymphocyte activity, has been successful in treating more advanced stages of the disease.

Neuronal Regeneration

Because there is no effective replacement of dead or damaged neurons after the fetal period, neural injuries tend to cause per-

manent dysfunction in children and adults. If axons alone are destroyed, however, the cell bodies often survive, and the axons may regenerate (**Figure 12.15**). If a nerve is severed in the PNS, macrophages invade and destroy the axon distal to the injury (**Figure 12.15** ②). Axon filaments can grow peripherally from the injured site at an approximate rate of 1.5 mm a day within regeneration tubes formed by the surviving Schwann cells that surrounded the original axons (**Figure 12.15** ③). Thus, eventual reinnervation of the target organ, with partial recovery of function, is sometimes possible in the PNS (**Figure 12.15** ④). In the CNS, however, the neuroglia never form bands to guide the regrowing axons and even hinder such axons by secreting growth-inhibiting chemicals. Therefore, there is no effective regeneration after injury to the spinal cord or brain.

REGENERATION AND SPINAL CORD INJURIES

Trauma to the spine has left 200,000 living Americans paralyzed with spinal cord injury. To help these people, extensive medical research is being conducted on spinal cord regeneration. The main goals of this research are to (1) identify and block the chemicals that inhibit axonal growth in the injured CNS; (2) add neurotrophins to induce axonal sprouting and remyelination; (3) make the damaged region of the spinal cord more like the PNS by implanting Schwann cells or segments of peripheral nerves, along which the CNS axons may grow; (4) isolate neuronal stem cells and add them to the damaged spinal cord. Currently, the only helpful treatment for spinal injury relies on the fact that much of the axonal damage is secondary—caused by inflammation, production of free radicals, and apoptosis that develop in the cord after the injury. Administering the anti-inflammatory drug methylprednisolone within 8 hours after injury minimizes this secondary damage and improves the prognosis of many patients. (For more on spinal cord injuries, see Chapter 13, p. 418).



check your understanding

- Both peripheral nerves and the white matter of the spinal cord are composed of axonal processes. Why is it possible to regain function after an injury to a peripheral nerve, but not after an injury to the spinal cord?
- From your understanding of the functions of myelin and functions of the white matter tracts of the CNS, explain how the loss of myelination in the CNS, as occurs in multiple sclerosis, can cause the signs and symptoms typical of this disease.

For answers, see Appendix B.

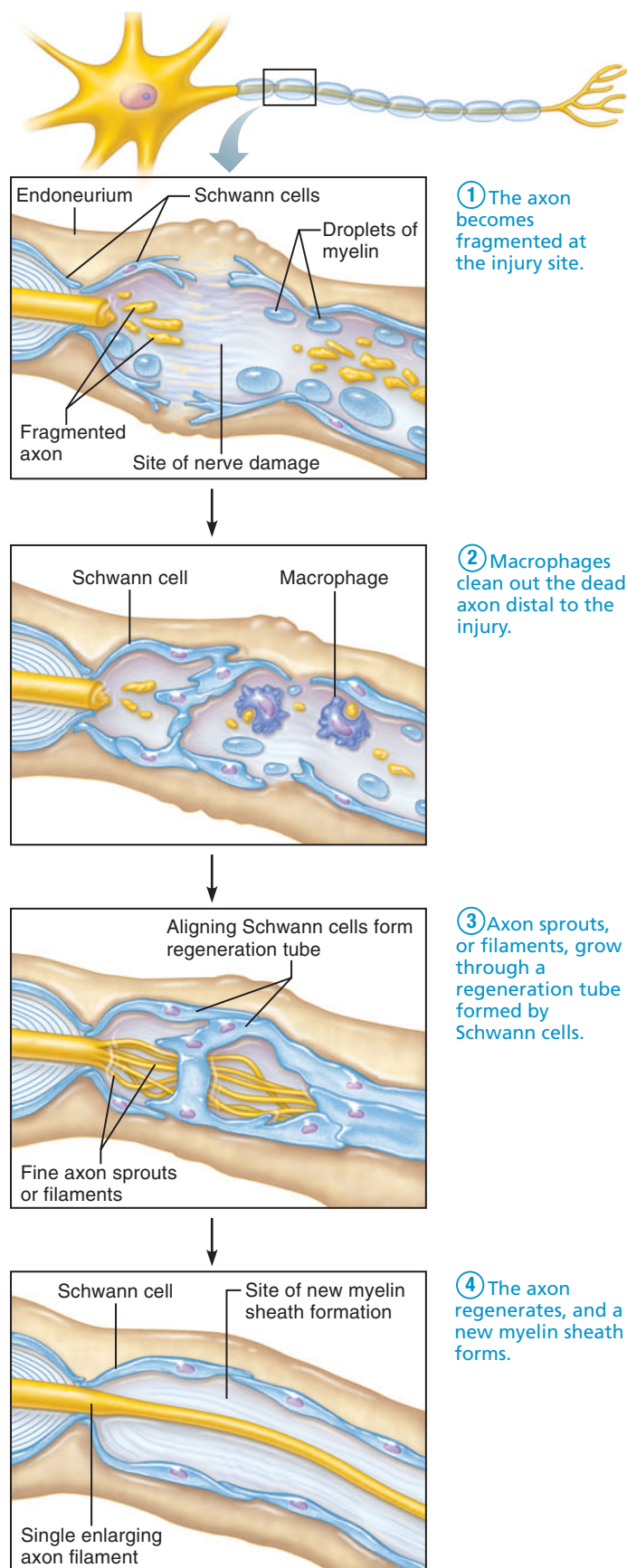


FIGURE 12.15 Regeneration of an axon in a peripheral nerve.

NERVOUS TISSUE THROUGHOUT LIFE

- Describe the development of the nervous system in the embryo.

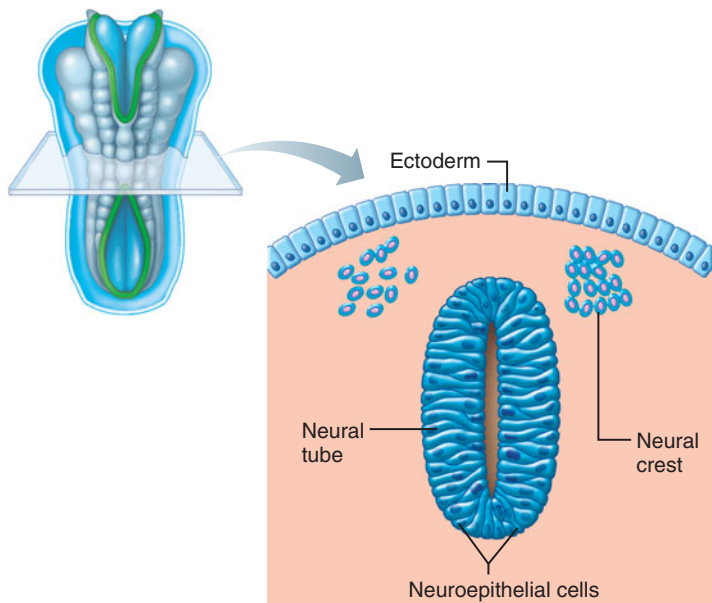
Embryonic Development of Nervous Tissue

Recall from Chapter 3 that the nervous system develops from the dorsal ectoderm, which invaginates to form the neural tube and the neural crest (**Figure 12.16**; see also Figure 3.7 on p. 54). The neural tube, whose walls begin as a layer of pseudostratified **neuroepithelial cells**, becomes the CNS. These cells divide, migrate externally, and become neuroblasts (future neurons), which never again divide, and neuroglial cells (**Figure 12.16b**). The earliest of these glial cells extend outward from the neuroepithelium and provide pathways along which young neurons migrate to reach their final destinations. Just external to the neuroepithelium, the neuroblasts cluster into an **alar plate** and a **basal plate**, the future gray matter (**Figure 12.16c**). Dorsally, the neuroblasts of the alar plate become interneurons, which remain in the CNS. Ventrally, the neuroblasts of the basal plate become motor neurons and sprout axons that grow out to the effector organs. (Some interneurons also form from the basal plate and remain ventrally among the motor neurons.) Axons that sprout from the young interneurons form the white matter by growing outward along the length of the CNS. These events occur in both the spinal cord and the brain.

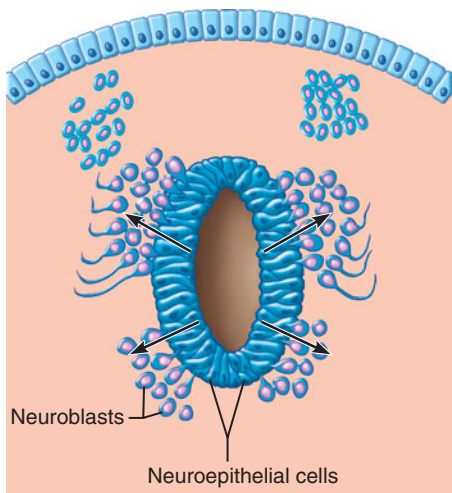
Most of the events described so far take place in the second month of development, but neurons continue to form rapidly until about the sixth month. At that time, neuron formation slows markedly, although it may continue at a reduced rate into childhood. Just before neuron formation slows, the early neuroglial cells differentiate into astrocytes and oligodendrocytes. As the division of its cells slows, the neuroepithelium differentiates into the layer of ependymal cells.

Sensory neurons arise not from the neural tube but from the neural crest (**Figure 12.16c**). This explains why the cell bodies of sensory neurons lie *outside* the CNS. Like motor neurons and interneurons, sensory neurons stop dividing during the fetal period.

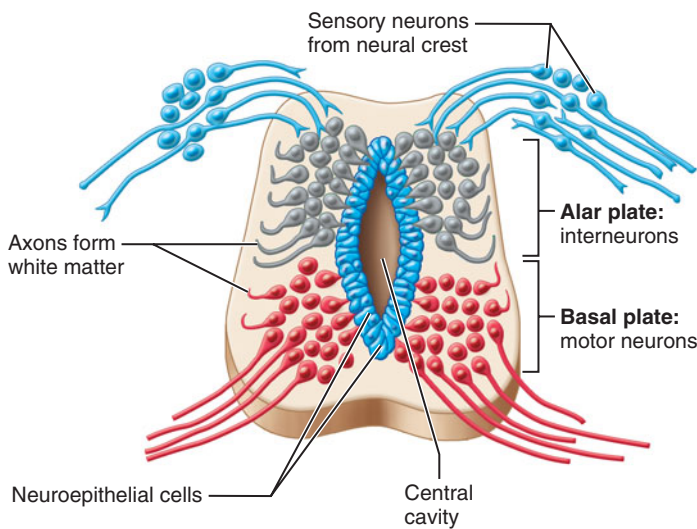
Neuroscientists are actively investigating how forming neurons meet and form synapses with one another. As the growing axons elongate at *growth cones*, they are attracted by chemical signals such as *neurotrophins* (nu-ro-tro'finz) released from other neurons and astrocytes. At the same time, the receiving dendrites send out thin, wiggling extensions to reach the approaching axons and form synapses. Which synaptic connections are made, and which persist, are determined by two factors: (1) the amount of neurotrophin initially received by an axon and (2) the degree to which a synapse is used after being established. Neurons that make “bad” connections are signaled to die via apoptosis (programmed cell



(a) 28 days.
Neural tube and neural crest form from invaginating ectoderm.



(b) Week 5.
Neuroepithelial cells of the neural tube divide and migrate externally to become neuroblasts and neuroglia.



(c) Week 6.
Neural crest cells form the sensory neurons.

Dorsal neuroblasts form the alar plate (future interneurons). Long axons extending from the interneurons form the white matter.

Ventral neuroblasts form the basal plate (future motor neurons).

FIGURE 12.16 Development of the nervous system in weeks 5 and 6 of the embryonic period.

death). Of the many neurons formed during the embryonic period, about one-half die before birth. This initial overproduction of neurons ensures that all necessary neural connections will be made and that mistaken connections will be eliminated.

As mentioned previously, fully differentiated neurons do not divide. Furthermore, in the postnatal period there is no obvious replacement of dead neurons by any neural stem cells. For this reason, such stem cells traditionally were thought not to exist. This is called the *no-new-neurons doctrine*. However, the no-new-neurons doctrine was overturned by the discovery of neural stem cells in adult humans. Some dividing cells in the subependymal zone have been shown to form new neurons in two regions of the adult brain—the hip-

pocampus and the olfactory bulb (see Chapter 13). Perhaps such stem cells can someday be induced to form new neurons and new neural networks in people with brain injuries or degenerative brain diseases.

check your understanding

19. What type of neurons forms from neuroblasts in the basal plate?
20. How does the development of sensory neurons explain why their cell bodies are located outside the CNS?

For answers, see Appendix B.

RELATED CLINICAL TERMS

NEUROBLASTOMA (nu"ro-blas-to'mah) (*oma* = tumor) A malignant tumor in children arising from cells that have retained a neuroblast-like structure. These blastomas sometimes originate in the brain, but most are of neural crest origin in the PNS.

NEUROLOGIST (nu-rol'o-jist) A medical specialist in the study of the nervous system and its disorders.

NEUROPATHY (nu-rop'ah-the) Any disease of the nervous tissue, but particularly a degenerative disease of nerves.

NEUROTOXIN (nu"ro-tok'sin) Substance that is poisonous or destructive to nervous tissue; examples are botulism and tetanus toxins.

RABIES (*rabies* = madness) A viral infection of the nervous system transferred to humans by the bites of—or other contact with—infected mammals such as dogs, bats, raccoons, foxes, and skunks. Once it enters the body, the virus is transported through peripheral nerve axons to the CNS, where it causes inflammation of the brain, resulting in delirium and death. Because of extensive vaccination of dogs and careful medical treatment of animal bites, human rabies is now very rare in the United States, but it kills about 40,000 people a year worldwide. A vaccine- and antibody-based treatment is effective if given before symptoms appear.

CHAPTER SUMMARY

Functional Organization of the Nervous System (pp. 348–351)

Functions of the Nervous System (p. 348)

1. The nervous system controls most of the other organ systems in the body. Its chief functions are to monitor, integrate, and respond to information in the environment.

Basic Divisions of the Nervous System (pp. 348–351)

2. The central nervous system consists of the spinal cord and brain. The peripheral nervous system is external to the CNS and consists of nerves and ganglia.
3. The nervous system receives sensory inputs and dictates motor outputs. Sensory (afferent) signals are carried from sensory receptors through the PNS into the CNS. Motor (efferent) signals are carried away from the CNS and through the PNS to the effectors, which are muscles and glands. As shown in Figure 12.3 and Table 12.1, the types of sensory inputs and motor outputs are further categorized as somatic (outer body) and visceral (mainly inner body), and general (widespread) and special (localized).
4. Proprioception refers to a series of senses that monitor the degree of stretch in muscles, tendons, and joint capsules. Proprioception thus senses the positions and movements of our body parts.

Nervous Tissue (pp. 351–359)

The Neuron (pp. 351–356)

5. Neurons are long-lived, nondividing cells. Each has a cell body and cell processes. The processes are an axon and dendrites.
6. The neuron cell body has a nucleus containing a dark nucleolus near its center. Its cytoplasm contains supportive neurofibrils and chromatophilic (Nissl) bodies, which are concentrations of rough endoplasmic reticulum and free ribosomes. The chromatophilic bodies in the cell body manufacture proteins and membranes for the entire neuron, thereby continuously maintaining and renewing the contents of the cell, including the processes. Except for those found in ganglia, all neuron cell bodies are in the CNS.
7. Most neurons have a number of branched dendrites, receptive sites that conduct signals from other neurons toward the neuron cell body.
8. Most neurons have one axon, which generates and conducts nerve impulses away from the neuron cell body. Impulses begin at the initial segment of the axon, arising from the cone-shaped axon hillock. Impulses end at the knoblike axon terminals, which participate in synapses and release neurotransmitter molecules.
9. A synapse is a functional junction between neurons. Synapses may be electrical (gap junctions) or, more commonly, chemical. The two main categories of synapses are axodendritic and axosomatic.

10. At synapses, information is transferred from a presynaptic neuron to a postsynaptic neuron. Synaptic vesicles in the presynaptic cell fuse with the presynaptic membrane and empty neurotransmitter molecules into the synaptic cleft. Taken up by the postsynaptic membrane, this neurotransmitter influences ability to generate a nerve impulse in the postsynaptic neuron.
11. Anatomically, neurons are classified by the number of processes issuing from their cell body as multipolar, bipolar, or unipolar.
12. Functionally, neurons are classified according to the direction in which they conduct impulses. Sensory neurons conduct impulses toward the CNS, motor neurons conduct away from the CNS, and interneurons lie in the CNS between sensory and motor neurons.

Supporting Cells (pp. 256–259)

13. Non-nervous supporting cells called neuroglia, or glial cells, act to support, protect, nourish, and insulate neurons.
14. Neuroglial cells in the CNS include star-shaped astrocytes, phagocytic microglia, ependymal cells that line the central cavity, and myelin-forming oligodendrocytes. Schwann cells and satellite cells are the neuroglial cells in the PNS.
15. Thick axons are myelinated. Myelin speeds up impulse conduction along these axons.
16. The myelin sheath is a coat of supporting-cell membranes wrapped in layers around the axon. This sheath is formed by Schwann cells in the PNS and by oligodendrocytes in the CNS. The sheath has gaps called nodes of Ranvier. Unmyelinated axons are surrounded by supporting cells, but they are not wrapped by layers of membrane.

Gross Anatomy of the Nervous System:

An Overview (pp. 359–360)

Nerves (pp. 359–360)

17. A nerve is a bundle of axons in the PNS. Each axon is enclosed by an endoneurium; each fascicle of axons is wrapped by a perineurium; and the whole nerve is surrounded by the epineurium. Because they contain more than one kind of tissue, nerves are organs.

Gray and White Matter of the CNS (p. 360)

18. Throughout most of the CNS, the inner gray matter (in which neuron cell bodies are located) is surrounded by outer white matter (which consists of fiber tracts). The extreme center of the spinal cord and brain is a hollow central cavity.

Neuronal Integration (pp. 360–364)

Integration Between the PNS and CNS (pp. 360–361)

19. The nerves of the PNS carry sensory and motor information between the periphery of the body and the CNS. The gray matter of the CNS links neurons of the PNS with interneurons of the CNS. The white matter of the CNS carries information from one part of the CNS to another.

Reflex Arcs (pp. 361–363)

20. Reflexes are rapid, automatic responses to stimuli. They can be either somatic or visceral.
21. Reflexes are mediated by chains of neurons called reflex arcs. The minimum number of elements in a reflex arc is *five*: a receptor, a sensory neuron, an integration center, a motor neuron, and an effector.
22. A few fast reflexes for maintaining balance have only two neurons (sensory and motor). These are monosynaptic stretch reflexes.
23. Most reflexes in humans are polysynaptic. The simplest of these, such as withdrawal reflexes, have three neurons: a sensory neuron, an interneuron, and a motor neuron.

Neuronal Circuits (pp. 362–363)

24. The interneurons of the CNS form complex neuronal circuits. These circuits may be converging, diverging, or reverberating. Input is processed serially or by parallel processing.

Simplified Design of the Nervous System (pp. 363–365)

25. Simple reflex arcs reflect the structural plan of the entire nervous system. Sensory signals are processed by neuronal circuits in the CNS to produce a reflexive response, conscious sensation, and nonreflexive motor actions.

Disorders of Nervous Tissue (pp. 365–367)

Multiple Sclerosis (pp. 365–366)

26. Multiple sclerosis is an autoimmune disease in which myelin in the CNS is destroyed, leading to neuronal dysfunction. It is characterized by periods of relapses and remissions. Common symptoms include visual disturbances, muscle weakness, fatigue, and depression.

Neuronal Regeneration (pp. 366–367)

27. After injury, effective axonal regeneration may occur in the PNS but not in the CNS.

Nervous Tissue Throughout Life (pp. 367–369)

Embryonic Development of Nervous Tissue (pp. 367–369)

28. The brain and spinal cord develop from the embryonic neural tube, which begins as a layer of dividing neuroepithelial cells. These cells migrate externally to become the neuroblasts of the dorsal *alar plate* (future interneurons), ventral *basal plate* (future motor neurons and some interneurons), and neuroglia. Neuroblasts of the neural crest, external to the neural tube, become the sensory neurons. Neuroblasts sprout axons, which grow toward their targets.

REVIEW QUESTIONS

Multiple Choice/Matching Questions

For answers, see Appendix B.

- Which of the following structures is *not* part of the central nervous system? (a) the brain (b) a nerve (c) the spinal cord (d) a tract
- Match the names of the cells in column B with the function they perform, shown in column A.

Column A

- ____ (1) form myelin in the CNS
- ____ (2) line the central cavity of the brain
- ____ (3) form myelin in the PNS
- ____ (4) CNS phagocytes
- ____ (5) regulate ionic composition of the fluid around neurons in the CNS
- ____ (6) remove neurotransmitters in the CNS

Column B

- (a) astrocytes
- (b) ependymal cells
- (c) microglia
- (d) oligodendrocytes
- (e) satellite cells
- (f) Schwann cells

- Which of the following structures is in the somatic part of the human body? (a) bladder, (b) biceps muscle, (c) lung, (d) stomach.
- Classify the following inputs and outputs as either somatic sensory (SS), visceral sensory (VS), somatic motor (SM), or visceral motor (VM).
 - ____ (1) pain from skin
 - ____ (2) taste
 - ____ (3) efferent innervation of a gland
 - ____ (4) efferent innervation of the gluteus maximus
 - ____ (5) a stomachache
 - ____ (6) a sound one hears
 - ____ (7) efferent innervation of the masseter
- An example of an effector is (a) the eye, (b) a gland, (c) a sensory neuron, (d) a motor neuron.
- Which of the following parts of a neuron occupies the gray matter in the spinal cord? (a) tracts of long axons, (b) motor neuron cell bodies, (c) sensory neuron cell bodies, (d) nerves.
- A ganglion is a collection of (a) neuron cell bodies, (b) axons of motor neurons, (c) interneuron cell bodies, (d) axons of sensory neurons.
- A synapse between an axon terminal and a neuron cell body is classified as (a) axodendritic, (b) axoaxonic, (c) axosomatic, (d) axoneuronic.
- Myelin is most like which of the following cell parts introduced in Chapter 2? (a) the cell nucleus, (b) smooth endoplasmic reticulum, (c) ribosomes, (d) the plasma membrane.

- Match the following parts of the adult nervous system with the embryonic cells that give rise to them: (a) alar plate cells, (b) basal plate cells, (c) neural crest cells.
 - ____ (1) sensory neurons
 - ____ (2) motor neurons
 - ____ (3) dorsal interneurons

- Afferent neurons of the PNS synapse in the CNS with (a) axons in the white matter, (b) neuron cell bodies in the gray matter, (c) neuron cell bodies in the white matter, (d) axons in the gray matter.
- A monosynaptic reflex is an example of (a) a convergent circuit, (b) parallel processing, (c) serial processing, (d) a reverberating circuit.
- Most nerves are composed of (a) afferent neurons only, (b) efferent neurons only, (c) dendrites, (d) axons of afferent and efferent neurons, (e) neuron cell bodies and neuroglia.
- Place the connective tissue coverings surrounding a nerve in order from superficial (1) to deep (3).
 - ____ perineurium ____ epineurium ____ endoneurium

Short Answer Essay Questions

- Define proprioception.
- Sin Young incorrectly classified proprioception as general somatic *motor* because it refers to the innervation of muscles. Actually, proprioception is general somatic *sensory*. Explain why.
- Define interneuron.
- Distinguish gray matter from white matter of the CNS in terms of location and composition.
- Describe the appearance of a cell nucleus of a neuron.
- Describe the differences between neurons and neuroglia in terms of structure, function, and location.
- Distinguish a nerve from a nerve fiber and a neuron.
- Explain why damage to peripheral nerve fibers is often reversible, whereas damage to CNS fibers rarely is.
- Draw a reflex arc in place in the nervous system (recall Figure 12.11). Would the reflex still function if the neurons in the sensory ganglia were destroyed?
- Define axon and dendrite.
- Why are the cell bodies of sensory neurons located outside the CNS?
- Describe the relationship between axons and Schwann cells in myelinated versus unmyelinated nerve fibers.

CRITICAL REASONING & CLINICAL APPLICATION QUESTIONS

1. Two anatomists were arguing about a sensory neuron. One anatomist said its peripheral process is an axon and gave two good reasons, but the other called the peripheral process a dendrite and also gave a good reason. Cite all three reasons given, and state your own opinion.
2. A CT scan and other diagnostic tests indicated that Laressa had developed an oligodendroglioma. Can you deduce from its name what an oligodendroglioma is?
3. The following event received worldwide attention in 1962: A boy playing in a train yard fell under a train, and his right arm was cut off cleanly by the wheels. Surgeons reattached the arm, sewing nerves and vessels back together. The surgery proceeded very well. The arm immediately regained its blood supply, yet the boy could not move the limb or feel anything in it for months. Explain why it took longer to reestablish innervation than circulation.
4. Rochelle developed multiple sclerosis when she was 27. After 8 years she had lost a good portion of her ability to control her skeletal muscles. Explain how this happened.
5. Reflexes can be somatic (as in the knee jerk response) or visceral (as in vomiting). Given that both result in an involuntary motor response, why aren't they both considered visceral motor?
6. A peripheral nerve that is damaged can regenerate after a period of time (6–12 months), such that its function is renewed. Damage to the spinal cord is a permanent injury. Why such different prognoses for these two injuries?



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