

CHAPTER 24

COMMUNICATION I:

NERVOUS AND SENSORY SYSTEMS

Outline

Neurons: The Basic Functional Units of the Nervous System

Neuron Structure: The Key to Function

Neuron Communication

Resting Membrane Potential

Mechanism of Neuron Action

Transmission of the Action Potential

Invertebrate Nervous Systems

Vertebrate Nervous Systems

The Spinal Cord

Spinal Nerves

The Brain

Cranial Nerves

The Autonomic Nervous System

Sensory Reception

Invertebrate Sensory Receptors

Baroreceptors

Chemoreceptors

Georeceptors

Hygroreceptors

Phonoreceptors

Photoreceptors

Proprioceptors

Tactile Receptors

Thermoreceptors

Vertebrate Sensory Receptors

Lateral-Line System and Electrical Sensing

Lateral-Line System and Mechanoreception

Hearing and Equilibrium in Air

Hearing and Equilibrium in Water

Skin Sensors of Damaging Stimuli

Skin Sensors of Heat and Cold

Skin Sensors of Mechanical Stimuli

Sonar

Smell

Taste

Vision

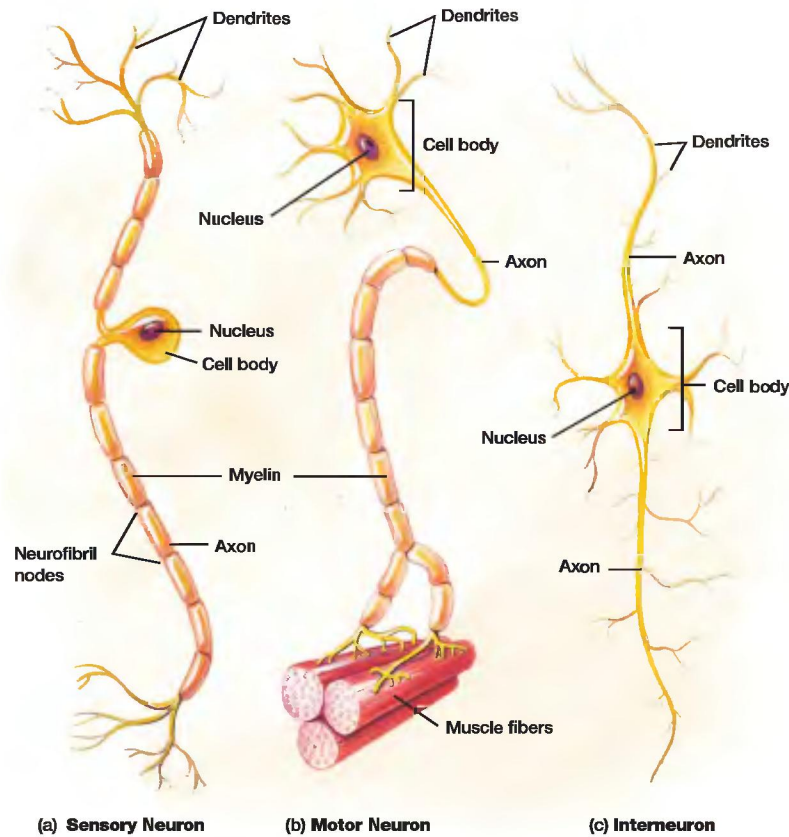
Concepts

1. The nervous system helps to communicate, integrate, and coordinate the functions of the various organs and organ systems in the animal body.
2. Information flow through the nervous system has three main steps: (1) the collection of information from outside and inside the body (sensory activities), (2) the processing of this information in the nervous system, and (3) the initiation of appropriate responses.
3. Information is transmitted between neurons directly (electrically) or by means of chemicals called neurotransmitters.
4. The evolution of the nervous system in invertebrates has led to the elaboration of organized nerve cords and the centralization of responses in the anterior portion of the animal.
5. The vertebrate nervous system consists of the central nervous system, made up of the brain and spinal cord, and the peripheral nervous system, composed of the nerves in the rest of the body.
6. Nervous systems evolved through the gradual layering of additional nervous tissue over reflex pathways of more ancient origin.
7. Sensory receptors or organs permit an animal to detect changes in its body, as well as in objects and events in the world around it. Sensory receptors collect information that is then passed to the nervous system, which determines, evaluates, and initiates an appropriate response.
8. Sensory receptors initiate nerve impulses by opening channels in sensory neuron plasma membranes, depolarizing the membranes, and causing a generator potential. Receptors differ in the nature of the environmental stimulus that triggers an eventual nerve impulse.
9. Many kinds of receptors have evolved among invertebrates and vertebrates, and each receptor is sensitive to a specific type of stimulus.
10. The nature of its sensory receptors gives each animal species a unique perception of its body and environment.

The two forms of communication in an animal that integrate body functions to maintain homeostasis are: (1) neurons, which transmit electrical signals that report information or initiate a quick response in a specific tissue; and (2) hormones, which are slower, chemical signals that initiate a widespread, prolonged response, often in a variety of tissues. This chapter focuses on the function of the neuron, the anatomical organization of the nervous system in animals, and the ways in which the senses collect information and transmit it

This chapter contains evolutionary concepts, which are set off in this font.

370 PART THREE Form and Function: A Comparative Perspective

**FIGURE 24.1**

Types of Vertebrate Neurons. (a) Sensory neurons transmit information from the environment to the central nervous system. (b) Motor neurons transmit information from the central nervous system to muscles or glands, and tend to have short dendrites and long axons. (c) Interneurons connect other neurons, permitting integration of information.

along nerves to the central nervous system. To conclude the study of communication, chapter 25 examines how hormones affect long-term changes in an animal's body.

NEURONS: THE BASIC FUNCTIONAL UNITS OF THE NERVOUS SYSTEM

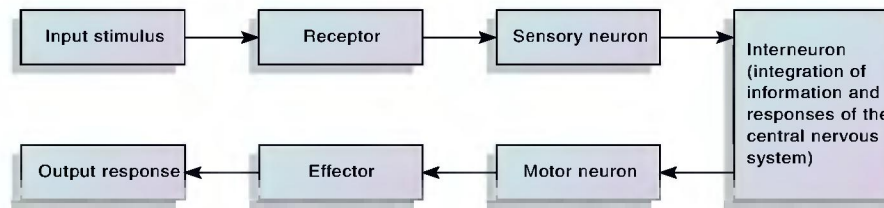
The functional unit of the nervous system is a highly specialized cell called the **neuron** (Gr. “nerve”). Neurons are specialized to produce signals that can be communicated over short to relatively long distances, from one part of an animal's body to another. Neurons have two important properties: (1) excitability, the ability to respond to stimuli; and (2) conductivity, the ability to conduct a signal.

The three functional types of neurons are sensory neurons, interneurons, and motor neurons. **Sensory (receptor or afferent) neurons** either act as receptors of stimuli themselves or are activated by receptors (figure 24.1a). Changes in the internal or external environments stimulate sensory neurons, which respond by

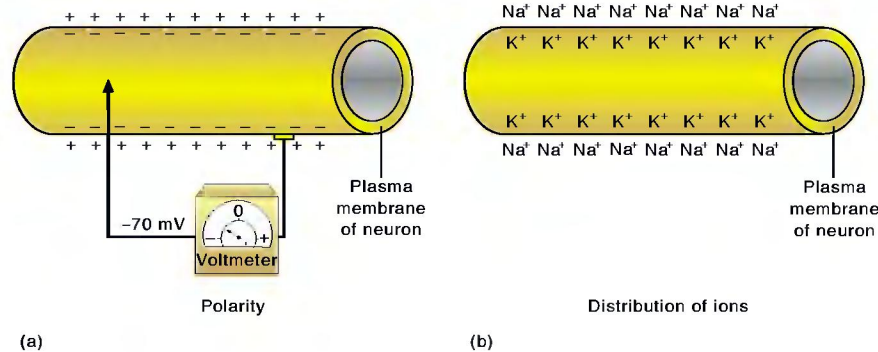
sending signals to the major integrating centers where information is processed. **Interneurons** (figure 24.1c) comprise the integrating centers and receive signals from the sensory neurons and transmit them to motor neurons. **Motor (effector or efferent) neurons** (figure 24.1b) send the processed information via a signal to the body's effectors (e.g., muscles), causing them to contract, or to glands, causing them to secrete. Figure 24.2 summarizes the flow of information in the nervous system.

NEURON STRUCTURE: THE KEY TO FUNCTION

Most neurons contain three principal parts: a cell body, dendrites, and an axon (see figure 24.1). The **cell body** has a large, central nucleus. The motor neuron in figure 24.1b has many short, thread-like branches called **dendrites** (Gr. *dendron*, tree), which are actually extensions of the cell body and conduct signals toward the cell body. The **axon** is a relatively long, cylindrical process that conducts signals (information) away from the cell body.

**FIGURE 24.2**

Generalized Pathway for the Flow of Information within the Nervous System. An input stimulus initiates impulses within some sensory structure (the receptor); the impulses are then transferred via sensory neurons to interneurons. After response selection, nerve impulses are generated and transferred along motor neurons to an effector (e.g., a muscle or gland), which elicits the appropriate output response.

**FIGURE 24.3**

Resting Membrane Potential. (a) A voltmeter measures the difference in electrical potential between two electrodes. When one microelectrode is placed inside a neuron at rest, and one is placed outside, the electrical potential inside the cell is -70 mV relative to the outside. (b) In a neuron at rest, sodium is more concentrated outside and potassium is more concentrated inside the cell. A neuron in this resting condition is said to be polarized.

The neurons of hydras and sea anemones do not have a sheath covering the axon of the neuron. Other invertebrates and all vertebrates have sheathed neurons. When present, the laminated lipid sheath is called **myelin**. In some neurons, a **neurolemmocyte** (formerly known as a Schwann cell) wraps the myelin sheath in layers. In these neurons, gaps called **neurofibril nodes** (formerly **nodes of Ranvier**) segment the myelin sheath at regular intervals. The neurolemmocyte also assists in the regeneration of injured myelinated neurons.

The nervous system receives data (input stimulus), integrates it, and effects a change (output response) in the animal's physiology. In a given neuron, the dendrites are the receptors, the cell body is the integrator, and the ends of the axon are the effectors.

NEURON COMMUNICATION

The language (signal) of a neuron is the nerve impulse or action potential. The key to this nerve impulse is the neuron's plasma membrane and its properties. Changes in membrane permeability and the subsequent movement of ions produce a nerve impulse that travels along the plasma membrane of the dendrites, cell body, and axon of each neuron.

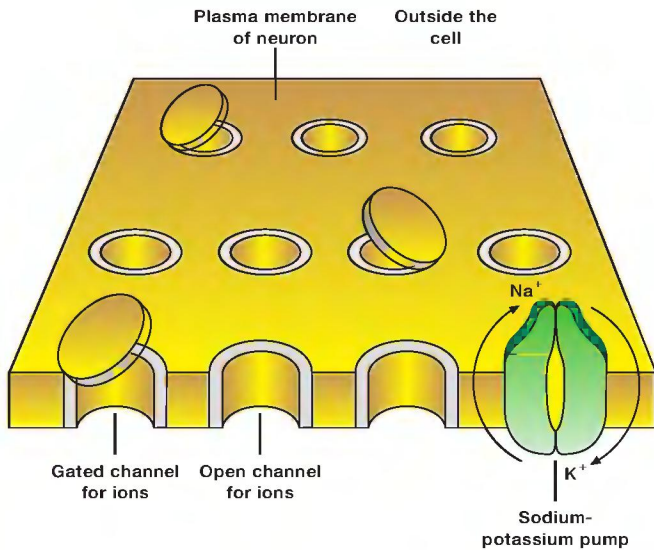
RESTING MEMBRANE POTENTIAL

A "resting" neuron is not conducting a nerve impulse. The plasma membrane of a resting neuron is polarized; the fluid on the inner side of the membrane is negatively charged with respect to the positively charged fluid outside the membrane (figure 24.3). The difference in electrical charge between the inside and the outside of the membrane at any given point is due to the relative numbers of positive and negative ions in the fluids on either side of the membrane, and to the permeability of the plasma membrane to these ions. The difference in charge is called the **resting membrane potential**. All cells have such a resting potential, but neurons and muscle cells are specialized to transmit and recycle it rapidly.

The resting potential is measured in millivolts (mV). A millivolt is 1/1,000 of a volt. Normally, the resting membrane potential is about -70 mV, due to the unequal distribution of various electrically charged ions. Sodium (Na^+) ions are more highly concentrated in the fluid outside the plasma membrane, and potassium (K^+) and negative protein ions are more highly concentrated inside.

The Na^+ and K^+ ions constantly diffuse through ion channels in the plasma membrane, moving from regions of higher concentrations to regions of lower concentrations. (There are also

372 PART THREE Form and Function: A Comparative Perspective

**FIGURE 24.4**

Ion Channels and the Sodium-Potassium Pump. These mechanisms maintain a balance between the sodium ions and potassium ions on both sides of the membrane and create a membrane potential. Some channels are always open, but others open or close by the position of gates, which are proteins that change shape to block or clear the channel. Whether a gate opens or closes a channel depends on the membrane potential. Such gates are said to be voltage regulated. Some of these membrane channels are specific for sodium ions, and others are specific for potassium ions.

larger Cl^- ions and huge negative protein ions, which cannot move easily from the inside of the neuron to the outside.) However, the concentrations of Na^+ and K^+ ions on the two sides of the membrane remain constant due to the action of the **sodium-potassium ATPase pump**, which is powered by ATP (figure 24.4). The pump actively moves Na^+ ions to the outside of the cell and K^+ ions to the inside of the cell. Because it moves three Na^+ molecules out for each two K^+ molecules that it moves in, the pump works to establish the resting potential across the membrane. Both ions leak back across the membrane—down their concentration gradients. K^+ ions, however, move more easily back to the outside, adding to the positive charge there and contributing to the membrane potential of -70 mV.

MECHANISM OF NEURON ACTION: CHANGING THE RESTING MEMBRANE POTENTIAL INTO THE ACTION POTENTIAL (NERVE IMPULSE)

Changing the resting electrical potential across the plasma membrane is the key factor in the creation and subsequent conduction of a nerve impulse. A stimulus that is strong enough to initiate an impulse is called a threshold stimulus. When such a stimulus is applied to a point along the resting plasma membrane, the

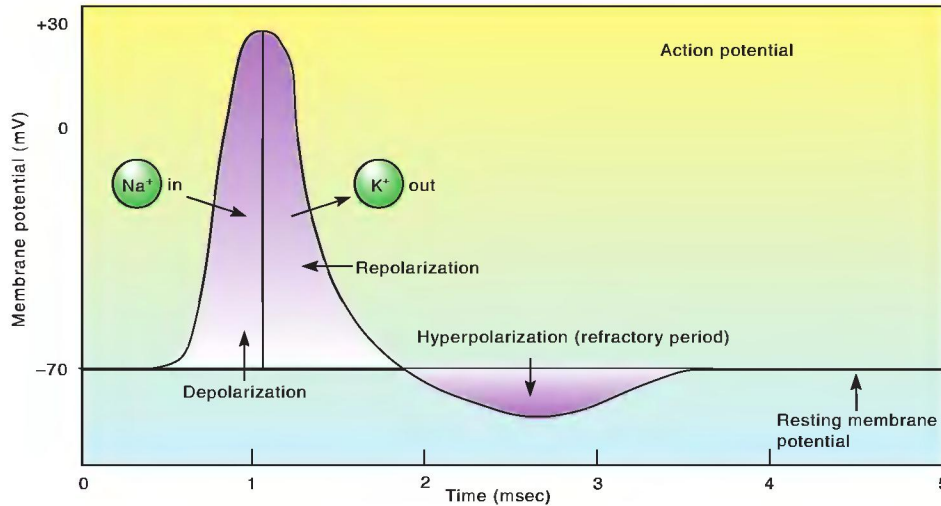
permeability to Na^+ ions increases at that point. The inflow of positively charged Na^+ ions causes the membrane potential to go from -70 mV toward 0. This loss in membrane polarity is called **depolarization** (figure 24.5). When depolarization reaches a certain level, special Na^+ channels (voltage-gated) that are sensitive to changes in membrane potential quickly open, and more Na^+ ions rush to the inside of the neuron. Shortly after the Na^+ ions move into the cell, the Na^+ gates close, but now voltage-gated K^+ channels open, and K^+ ions rapidly diffuse outward. The movement of the K^+ ions out of the cell builds up the positive charge outside the cell again, and the membrane becomes **repolarized**. This series of membrane changes triggers a similar cycle in an adjacent region of the membrane, and the wave of depolarization moves down the axon as an **action potential**. Overall, the transmission of an action potential along the neuron plasma membrane is a wave of depolarization and repolarization.

After each action potential, there is an interval of time when it is more difficult for another action potential to occur because the membrane has become hyperpolarized (more negative than -70 mV) due to the large number of K^+ ions that rushed out. This brief period is called the **refractory period**. During this period, the resting potential is being restored at the part of the membrane where the impulse has just passed. Afterward, the neuron is repolarized and ready to transmit another impulse.

A minimum stimulus (threshold) is necessary to initiate an action potential, but an increase in stimulus intensity does not increase the strength of the action potential. The principle that states that an axon will “fire” at full power or not at all is the **all-or-none law**.

Increasing the axon diameter and/or adding a myelin sheath increases the speed of conduction of a nerve impulse. Axons with a large diameter transmit impulses faster than smaller ones. Large-diameter axons are common among many invertebrates (e.g., crayfishes, earthworms). The largest are those of the squid (*Loligo*), where axon diameter may be over 1 mm, and the axons have a conduction velocity greater than 36 m/second! (The giant squid axons provide a simple, rapid triggering mechanism for quick escape from predators. A single action potential elicits a maximal contraction of the mantle muscle that it innervates. Mantle contraction rapidly expels water, “jetting” the squid away from the predator.) Most vertebrate axons have a diameter of less than 10 μm ; however, some fishes and amphibians have evolved large, unmyelinated axons 50 μm in diameter. These extend from the brain, down the spinal cord, and they activate skeletal muscles for rapid escapes.

Regardless of an axon’s diameter, the myelin sheath greatly increases conduction velocity. The reason for this velocity increase is that myelin is an excellent insulator and effectively stops the movement of ions across it. Action potentials are generated only at the neurofibril nodes. In fact, the action potential “jumps” from one node to the next node. For this reason, conduction along myelinated fibers is known as **saltatory conduction** (*L. saltare*, to jump). It takes less time for an impulse to jump from node to node along a myelinated fiber than to travel smoothly along an unmyelinated fiber. **Myelination allows rapid conduction in small neurons and thus provides for the evolution of**

**FIGURE 24.5**

Action Potential as Recorded on an Oscilloscope During the depolarization phase of the action potential, sodium (Na^+) ions rush to the inside of a neuron. The repolarization phase is characterized by a rapid increase in potassium (K^+) ions on the outside of the neuron. The action potential is sometimes called a “spike” because of its shape on an oscilloscope screen.

nervous systems that do not occupy much space within the animal.

TRANSMISSION OF THE ACTION POTENTIAL BETWEEN CELLS

After an action potential travels along an axon, it reaches the end of a branching axon terminal called the **end bulb**. The **synapse** (Gr. *synapsis*, connection) is the junction between the axon of one neuron and the dendrite of another neuron or effector cell. The space (junction) between the end bulb and the dendrite of the next neuron is the **synaptic cleft**. The neuron carrying the action potential toward a synapse is the presynaptic (“before the synapse”) neuron. It initiates a response in the receptive segment of a postsynaptic (“after the synapse”) neuron leading away from the synapse. The presynaptic cell is always a neuron, but the postsynaptic cell can be a neuron, muscle cell, or gland cell.

Synapses can be electrical or chemical. In an **electrical synapse**, nerve impulses transmit directly from neuron to neuron when positively charged ions move from one neuron to the next. These ions depolarize the postsynaptic membrane, as though the two neurons were electrically coupled. An electrical synapse can rapidly transmit impulses in both directions. Electrical synapses are common in fishes and partially account for their ability to dart swiftly away from a threatening predator.

In a **chemical synapse**, two cells communicate by means of a chemical agent called a **neurotransmitter**, which the presynaptic neuron releases. A neurotransmitter changes the resting potential in the plasma membrane of the receptive segment of the postsynaptic cell, creating an action potential in that cell, which continues the transmission of the impulse.

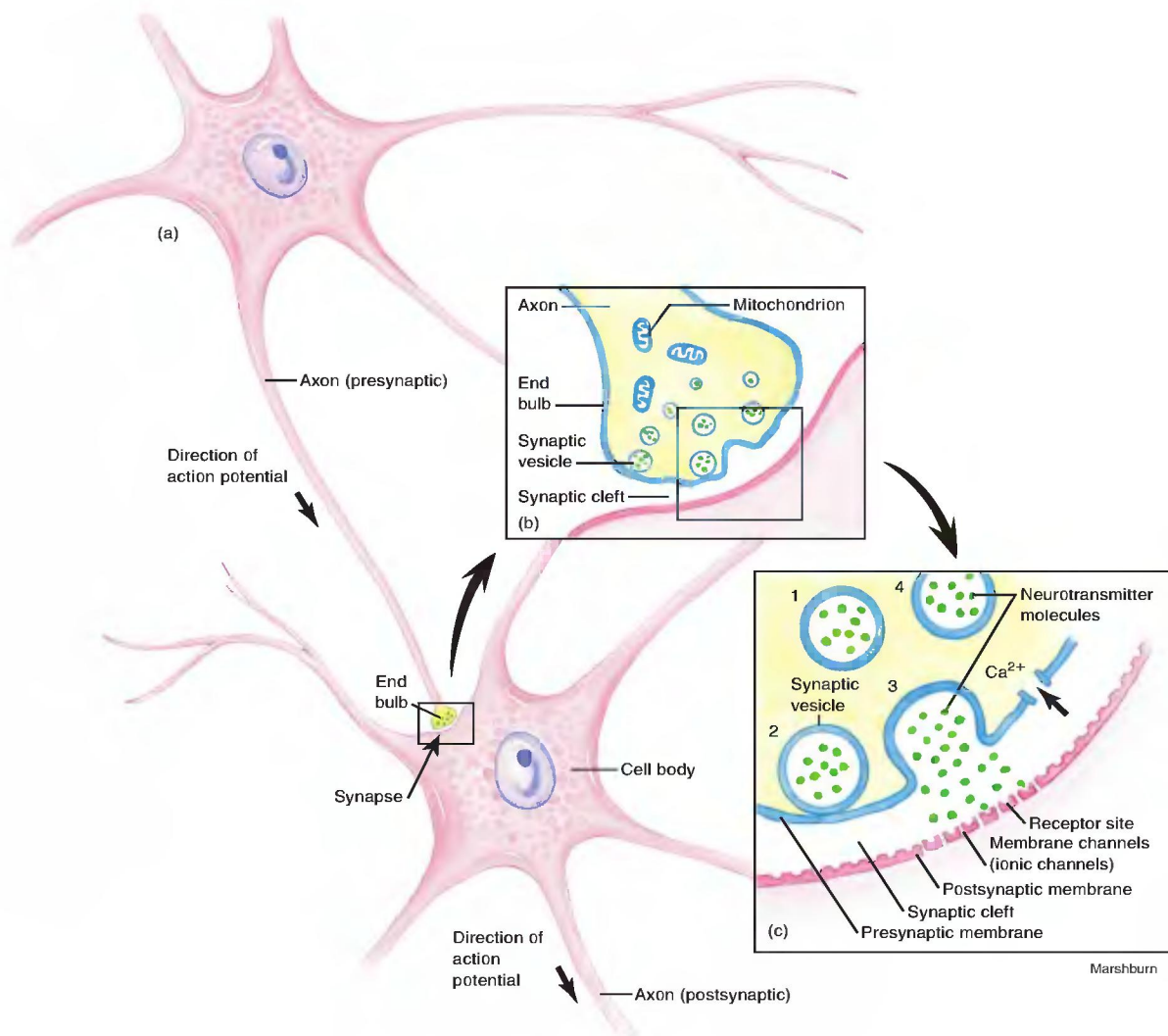
When a nerve impulse reaches an end bulb, it causes storage vesicles (containing the chemical neurotransmitter) to fuse with the plasma membrane. The vesicles release the neurotransmitter by exocytosis into the synaptic cleft (figure 24.6). One common neurotransmitter is the chemical **acetylcholine**; another is **norepinephrine**. (More than 50 other possible transmitters are known.)

When the released neurotransmitter (e.g., acetylcholine) binds with receptor protein sites in the postsynaptic membrane, it causes a depolarization similar to that of the presynaptic cell. As a result, the impulse continues its path to an eventual effector. Once acetylcholine has crossed the synaptic cleft, the enzyme acetylcholinesterase quickly inactivates it. Without this breakdown, acetylcholine would remain and would continually stimulate the postsynaptic cell, leading to a diseased state. You have probably created a similar diseased state at the synapses of the fleas on your dog or cat. The active ingredient in most flea sprays and powders is parathion. It prevents the breakdown of acetylcholine in the fleas, as well as pets and people. However, because fleas are so small, the low dose that immobilizes the fleas does not affect pets or humans.

INVERTEBRATE NERVOUS SYSTEMS

All cells respond to some stimuli and relay information both internally and externally. Thus, even when no real nervous system is present, such as in the protozoa and sponges, coordination and reaction to external and internal stimuli do occur. For example, the regular beating of protozoan cilia (see figure 23.16) or the response of flagellates to varying light intensities requires intracellular coordination. Only animals that have achieved the tissue

374 PART THREE Form and Function: A Comparative Perspective

**FIGURE 24.6**

Chemical Transmission across a Synapse. (a) Pre- and postsynaptic neurons with synaptic end bulb. (b) Enlarged view of the end bulb containing synaptic vesicles. (c) Enlargement of a portion of the end bulb showing exocytosis. The sequence of events in neurotransmitter release is: (1) a synaptic vesicle containing neurotransmitter approaches the plasma membrane; (2) due to the influx of calcium ions, the vesicle fuses with the membrane; (3) exocytosis occurs; and (4) the vesicle reforms and begins to fill with more neurotransmitter.

level of organization (e.g., the diploblastic and triploblastic animals) have true nervous systems, however. This clearly excludes the protozoa and sponges.

Among animals more complex than sponges, five general evolutionary trends in nervous system development are apparent. *The first has been integrated throughout Part Two of this text. More complex animals possess more detailed nervous systems.*

Of all animals, the cnidarians (hydras, jellyfishes, and sea anemones) have the simplest form of nervous organization. These animals have a **nerve net**, a latticework that conducts impulses from one area to another (figure 24.7a). In nerve nets, impulse

conduction by neurons is bidirectional. Cnidarians lack brains and even local clusters of neurons. Instead, a nerve stimulus anywhere on the body initiates a nerve impulse that spreads across the nerve net to other body regions. In jellyfishes, this type of nervous system is involved in slow swimming movements and in keeping the body right-side up. At the cellular level, the neurons function in the way discussed earlier in this chapter.

Echinoderms (e.g., sea stars, sea urchins, sea cucumbers) still have nerve nets, but of increasing complexity. For example, sea stars have three distinct nerve nets. The one that lies just under the skin has a circumoral ring and five sets of nerve cords running out to the animal's arms. Another net serves the muscles

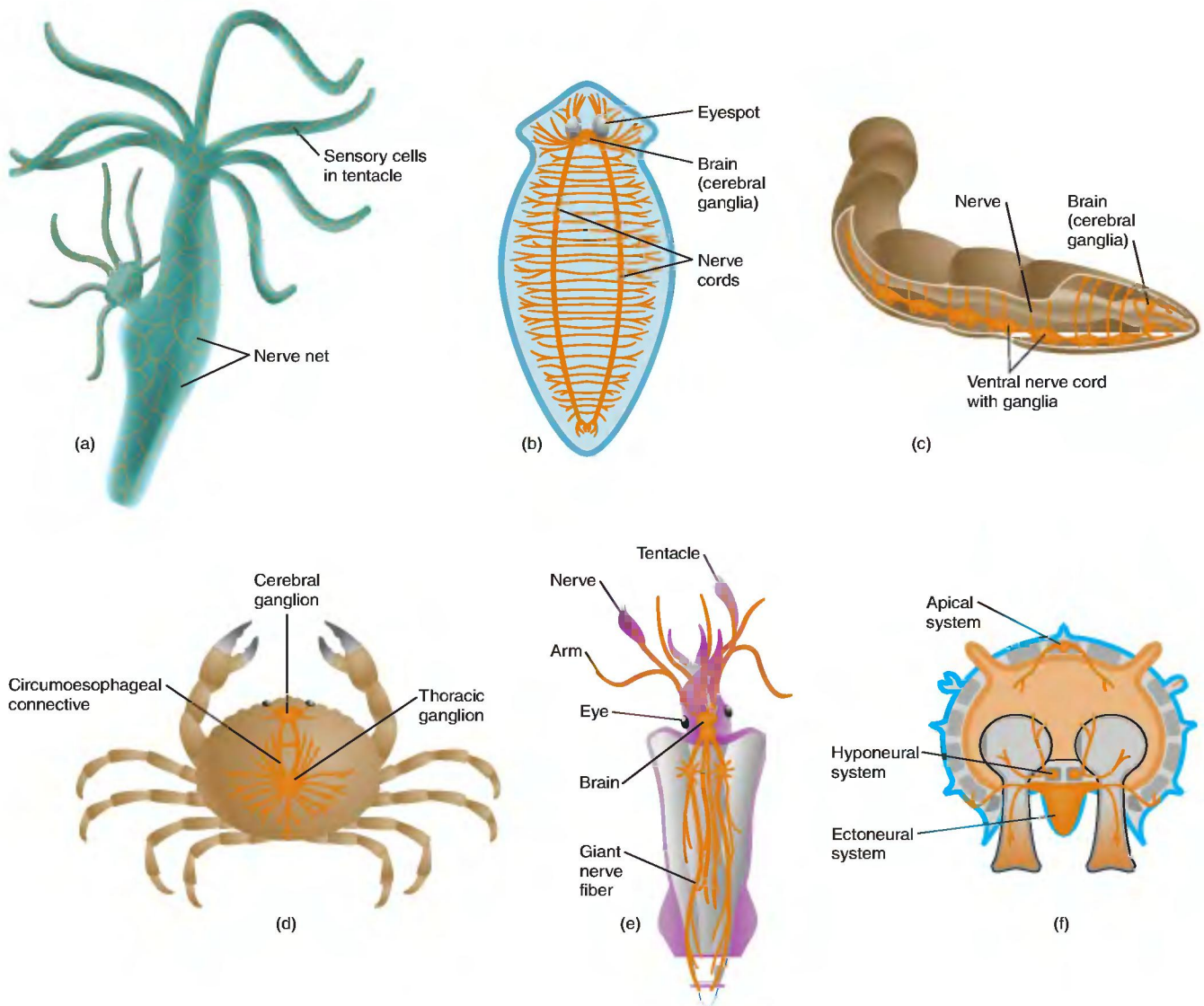


FIGURE 24.7

Some Invertebrate Nervous Systems. (a) The nerve net of *Hydra*, a cnidarian, represents the simplest neural organization. (b) Brain and paired nerve cords of a planarian flatworm. This is the first nervous system showing differentiation into a peripheral nervous system and a central nervous system. (c) Brain, ventral nerve cord, ganglia, and peripheral nerves of the earthworm, an annelid worm. (d) A crustacean, showing the principal ganglia and visceral connective nerves. The most primitive crustaceans have nervous systems similar to those of the platyhelminths, whereas (e) some cephalopods (such as the squid) have brains and behavior as complex as those of fishes. (f) Cross section of a starfish arm. Nerves from the ectoneural system terminate on the surface of the hyponeural system, but the two systems have no contact.

between the skin plates, called ossicles. The third net connects to the tube feet. This degree of nerve net complexity permits locomotion, a variety of useful reflexes, and some degree of “central” coordination. For example, when a sea star is flipped over, it can right itself.

Animals, such as flatworms and roundworms, that move in a forward direction have sense organs concentrated in the body region that first encounters new environmental stimuli. **Thus, the**

second trend in nervous system evolution involves cephalization, which is a concentration of receptors and nervous tissue in the animal’s anterior end. For example, a flatworm’s nervous system contains **ganglia** (sing., ganglion), which are distinct aggregations of nerve cells in the head region. Ganglia function as a primitive “brain” (figure 24.7b). Distinct lateral nerve cords (collections of neurons) on either side of the body carry sensory information from the periphery to the head ganglia and carry

376 PART THREE Form and Function: A Comparative Perspective

motor impulses from the head ganglia back to muscles, allowing the animal to react to environmental stimuli.

These lateral nerve cords reveal that flatworms also exhibit the third trend in nervous system evolution: bilateral symmetry. Bilateral symmetry (a body plan with roughly equivalent right and left halves) could have led to paired neurons, muscles, sensory structures, and brain centers. This pairing facilitates coordinated movements, such as climbing, crawling, flying, or walking.

In other invertebrates, such as crustaceans, segmented worms, and arthropods, the organization of the nervous system shows further advances. In these invertebrates, axons join into nerve cords, and in addition to a small, centralized brain, smaller peripheral ganglia help coordinate outlying regions of the animal's body. Ganglia can occur in each body segment or can be scattered throughout the body close to the organs they regulate (figure 24.7 c,d,e). Regardless of the arrangement, these ganglia represent the fourth evolutionary trend. The more complex an animal, the more interneurons it has. Because interneurons in ganglia do much of the integrating that takes place in nervous systems, the more interneurons, the more complex behavior patterns an animal can perform.

In echinoderms, such as starfishes, the nervous system is divided into several parts (figure 24.7f). The ectoneural system retains a primitive epidermal position and combines sensory and motor functions. A radial nerve extends down the lower surface of each arm. A deeper hyponeural system has a motor function, and the apical system may have some sensory functions.

The fifth trend in the evolution of invertebrate nervous systems is a consequence of the increasing number of interneurons. The brain contains the largest number of neurons, and the more complex the animal, and the more complicated its behavior, the more neurons (especially interneurons) are concentrated in an anterior brain and bilaterally organized ganglia. Vertebrate brains are an excellent example of this trend.

VERTEBRATE NERVOUS SYSTEMS

The basic organization of the nervous system is similar in all vertebrates. Bilateral symmetry, a notochord, and a tubular nerve cord characterize the evolution of vertebrate nervous systems.

The notochord is a rod of mesodermally derived tissue encased in a firm sheath that lies ventral to the neural tube. It first appeared in marine chordates and is present in all vertebrate embryos, but is greatly reduced or absent in adults. During embryological development in most vertebrate species, vertebrae serially arranged into a vertebral column replace the notochord. This vertebral column led to the development of strong muscles, allowing vertebrates to become fast-moving, predatory animals. Some of the other bones developed into powerful jaws, which facilitated the predatory nature of these animals.

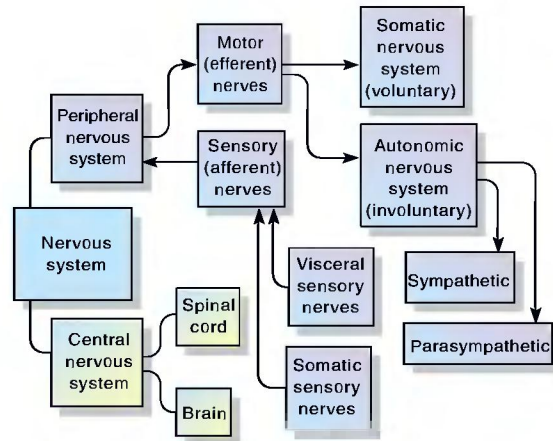


FIGURE 24.8

The Basic Organization of the Nervous System Is Similar in All Vertebrates. This flowchart shows the divisions and nerves of the vertebrate nervous system. Arrows indicate the directional flow of nerve impulses (information).

A related character in vertebrate evolution was the development of a single, tubular nerve cord above the notochord. During early evolution, the nerve cord underwent expansion, regional modification, and specialization into a spinal cord and brain. Over time, the anterior end thickened variably with nervous tissue and functionally divided into the hindbrain, midbrain, and forebrain. In the sensory world of the fast-moving and powerful vertebrates, the anterior sensory receptors became more complex and bilaterally symmetrical. For example, paired structures, such as eyes and ears, developed to better gather information from the outside environment.

The nervous system of vertebrates has two main divisions (figure 24.8). The **central nervous system** is composed of the brain and spinal cord and is the site of information processing. The **peripheral nervous system** is composed of all the nerves of the body outside the brain and spinal cord. These nerves are commonly divided into two groups: **sensory (afferent) nerves**, which transmit information to the central nervous system; and **motor (efferent) nerves**, which carry commands away from the central nervous system. The motor nerves divide into the **voluntary (somatic) nervous system**, which relays commands to skeletal muscles, and the **involuntary (visceral or autonomic) nervous system**, which stimulates other muscles (smooth and cardiac) and glands of the body. The nerves of the autonomic nervous system divide into **sympathetic** and **parasympathetic** systems.

Nervous system pathways are composed of individual neuronal axons bundled like the strands of a telephone cable. In the central nervous system, these bundles of nerve fibers are called **tracts**. In the peripheral nervous system, they are called **nerves**. The cell bodies from which the axons extend often cluster into groups. These groups are called **nuclei** if they are in the central nervous system and **ganglia** if they are part of the peripheral nervous system.