39

Neural Control: Neurons

OUTLINE

I. Information flow through the nervous system
II. Organization of the vertebrate nervous system
III. Structure of the neuron
  A. Dendrites
  B. The axon
IV. Nerves and ganglia
V. Transmission of a neural impulse
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VI. Integration
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VIII. Reflex action

LEARNING OBJECTIVES

After you have read this chapter you should be able to:

1. Trace the flow of information through the nervous system.
2. Describe the principal divisions of the vertebrate nervous system.
3. Compare the functions of neurons and neuroglia.
4. Draw a diagram of a neuron, giving the name and function of each structure.
5. Describe the structure of a nerve and of a ganglion.
6. Explain how the resting potential of a neuron is maintained.
7. Contrast local changes in potential with an action potential.
8. Describe the effects of calcium imbalance, local anesthetics, and such agents as DDT on neuron excitability.
9. Describe synaptic transmission, and explain how it regulates the direction of neural transmission.
10. List the neurotransmitters described in the chapter, and give an example of where each is secreted.
11. Draw diagrams to illustrate convergence, divergence, facilitation, and reverberating circuits.
12. Define and describe the process of neural integration.
13. Draw a reflex pathway consisting of three neurons, label each structure, and indicate the direction of information flow; relate reflex action to the processes of reception, transmission, integration, and actual response.

Vibrations from approaching footsteps provoke an earthworm to retreat quickly into its burrow. When a crayfish is hungry, it seeks out and devours a wiggling worm. A child learns to look both ways before crossing a busy street, and a college student learns the principles of biology or calculus. All of these activities, and countless others, are made possible by the nervous system. In complex animals the endocrine system works with the nervous system in regulating many behaviors and physiological processes. The endocrine system generally provides a relatively slow and long-lasting regulation, whereas the nervous system permits a very rapid response.

Changes within the body or in the outside world that can be detected by an organism are termed **stimuli.** The ability of an organism to survive and to maintain homeostasis depends largely upon how effectively it can respond to stimuli in its internal or external environment.

Information Flow Through the Nervous System

The nervous system is bombarded with thousands of stimuli each day. It receives information, transmits messages, sorts and interprets incoming data, and then sends the proper messages so that the responses will be coordinated and homeostatic. Even the simplest response to a stimulus generally requires a sequence of information flow through the nervous system that includes reception, transmission of impulses to the brain or spinal cord, integration, transmission of impulses from the brain or spinal cord, and response by an effector—usually a muscle or gland.

Imagine that you are very hungry and an obliging friend sets a delicious steak dinner before you. You cannot lift the first forkful to your mouth until **reception, transmission, integration,** and **response** by an effector have taken place (Fig. 39-1). First, you must detect the food—the stimulus. At least two types of **receptors** (your eyes and your olfactory epithelium) receive the information. Second, these messages must be sent to your brain, informing you that they have received a stimulus. **Afferent (sensory) neurons** transmit this information in the form of neural impulses *from* the sense organs *to* the brain.

When a decision to eat the food has been made, **efferent (motor) neurons** transmit the message from the brain to the appropriate effector cells—in this case, certain muscle fibers in your arm and hand. The last process in this sequence is the actual contraction of the muscle fibers necessary to carry out the response. Now, finally, you spear the food with the fork and lift it into your mouth.

Organization of the Vertebrate Nervous System

In vertebrates the **central nervous system (CNS)** consists of a complex brain that is continuous with a single, dorsal, tubular nerve cord (spinal cord). The central nervous system integrates all incoming information and determines appropriate responses. Within the CNS, afferent neurons **synapse,** that is, make functional connections with **association neurons,** also called **interneurons.** Each association neuron may synapse with many other association neurons. At these synapses incoming neural messages are sorted out and interpreted.

The **peripheral nervous system (PNS)** consists of the sensory receptors and the nerves lying outside the brain and spinal cord. Twelve pairs of cranial nerves (ten in fish and amphibians) and several pairs of spinal nerves (31 pairs in humans) link the CNS with various parts of the body. Afferent neurons in these nerves continually inform the CNS about stimuli that impinge upon the body. Efferent neurons then transmit the impulses from the CNS to appropriate effector cells—muscles and glands—which make the adjustments necessary to preserve homeostasis.

For convenience, the PNS can be subdivided into somatic and autonomic systems. The **somatic system** consists of the receptors and nerves concerned with stimuli in the outside world. The **autonomic system** consists of the receptors and nerves operating to regulate the internal environment. In the autonomic system there are two types of efferent nerves: sympathetic and parasympathetic. These divisions of the vertebrate nervous system are discussed in Chapter 40.

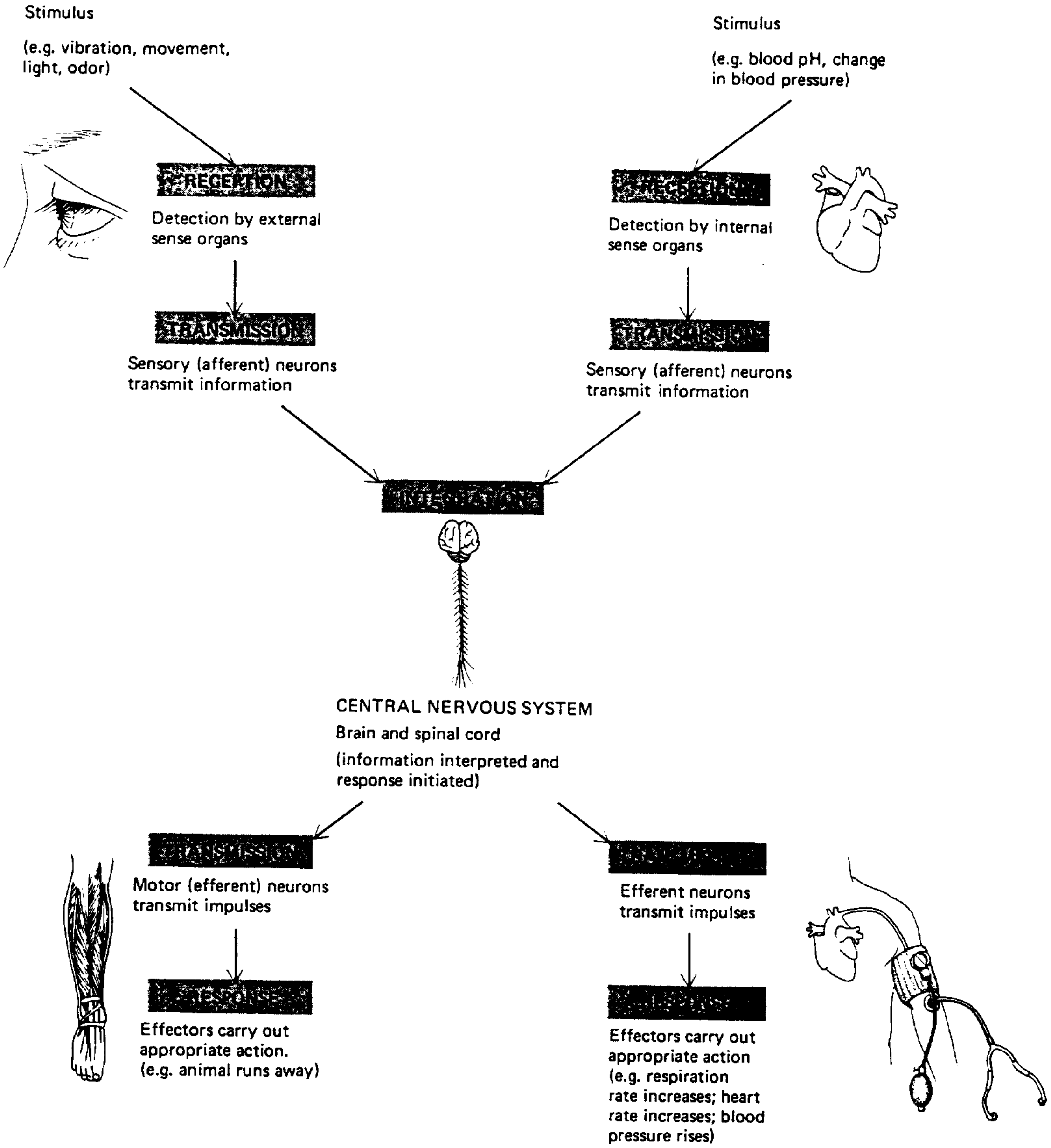


Figure 39–1 Flow of information through the nervous system.

Structure of the Neuron

The **neuron,** or nerve cell, is the structural and functional unit of the nervous system. The specialized supporting cells of nervous tissue are called **neuroglia.** A typical **multipolar neuron** consists of a **cell body,** which has bushy cytoplasmic extensions called **dendrites,** and a single, long cytoplasmic extension, the **axon** (Fig. 39–2). Other types of neurons are illustrated in Figure 39–3.

The cell body contains the nucleus and many of the other organelles as well as the bulk of the cytoplasm. It is concerned with the metabolic maintenance and growth of the neuron. The cell body contains **Nissl substance,** which consists of deeply staining regions of cytoplasm rich in rough endoplasmic reticulum and free ribosomes. This is the site of protein synthesis. Microtubules and microfilaments are distributed throughout the cytoplasm. The microtubules help to maintain the shape of the neuron, especially of the dendrites and axon, and play a role in transporting materials through the axon. The short microfilaments, composed of actin, are also thought to function in transporting materials.

DENDRITES

Dendrites are highly branched extensions of the cytoplasm that project from the cell body. Dendrites and the surface of the cell body are specialized to receive stimuli.

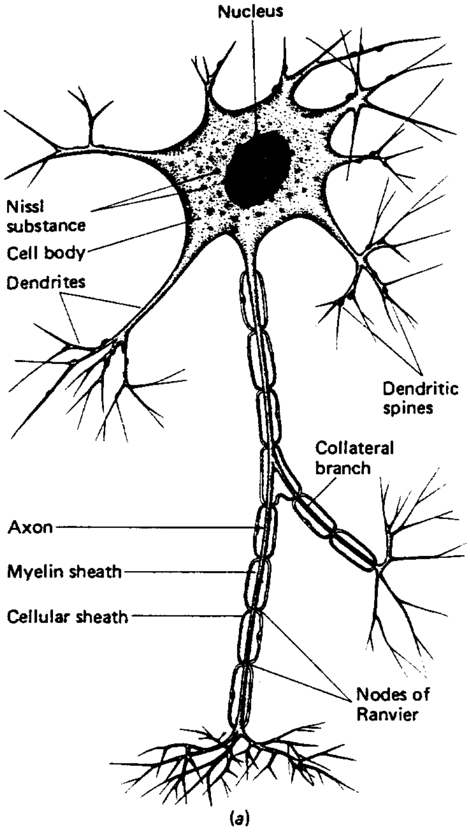
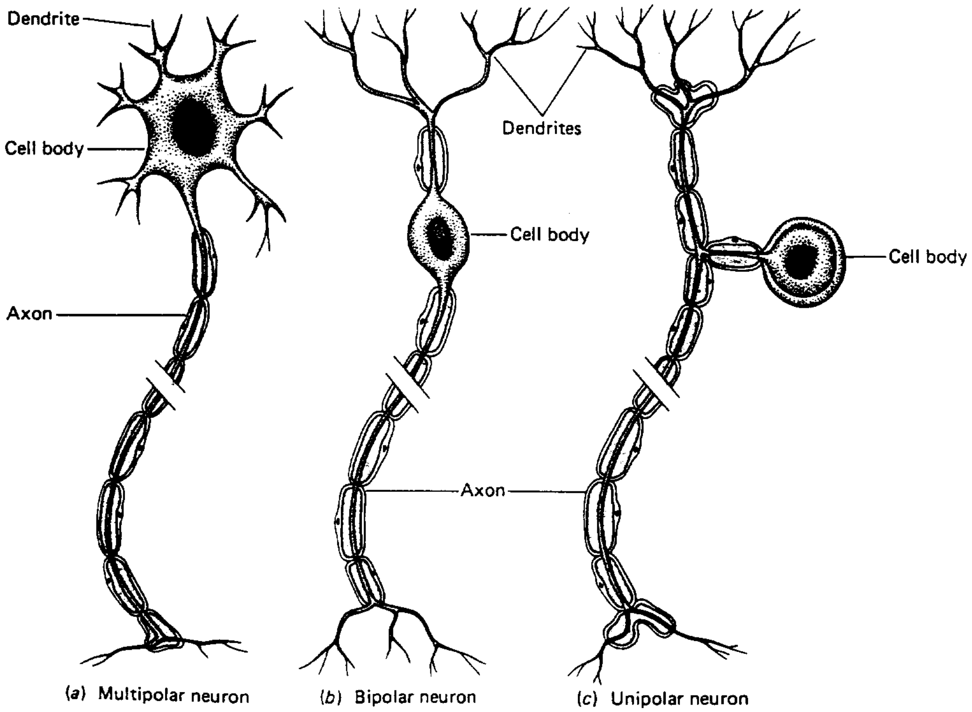


Figure 39–2 A multipolar neuron consists of a cell body, numerous dendrites, and a single, long axon. (*a*) Structure of a multipolar neuron. The axon of this neuron is myelinated, and therefore the myelin sheath is shown as well as the cellular sheath. (*b*) Photomicrograph of nerve tissue showing two multipolar neurons.



(a) Multipolar neuron (b) Bipolar neuron (c) Unipolar neuron

Figure 39–3 Types of neurons classified according to the number of extensions. (*a*) A multipolar neuron. This type of neuron has many short dendrites and one long axon. Motor neurons are of this type. (*b*) A bipolar neuron. A bipolar neuron has one axon and one dendrite. This type of neuron is found in the retina of the eye, in the olfactory nerve, and in the nerves coming from the inner ear. (*c*) A unipolar neuron has a short process that divides into two long processes. The distal process may be called either a dendrite or an axon. Since it functions like a dendrite, it is called a dendrite here. Sensory neurons are unipolar.

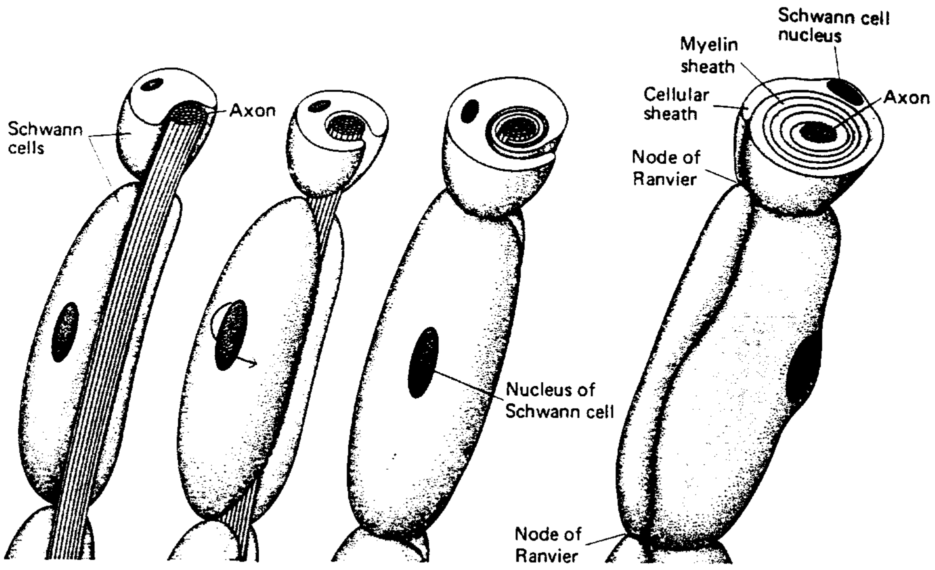


Figure 39–4 Formation of the myelin sheath around the axon of a peripheral neuron. A Schwann cell wraps its cell membrane around the axon many times to form the insulating myelin sheath. The rest of the Schwann cell remains outside the myelin sheath, forming the cellular sheath.

Their surfaces are dotted with thousands of tiny **dendritic spines,** which are the sites of specialized junctions with other neurons.

THE AXON

The axon arises from a thickened area of the cell body, the **axon hillock.** It transmits neural impulses from the cell body to another neuron or effector cell. Although microscopic in diameter, the axon may be very long. A sensory cell located in the toe of a giraffe may be barely 0.1 mm in diameter but spans a distance of several meters before ending in the spinal cord. Perhaps because of its impressive length, the axon is sometimes referred to as a **nerve fiber.**

At its distal end the axon branches extensively. At the ends of these branches are tiny enlargements called **synaptic knobs.** These knobs release a substance (a neurotransmitter) that transmits messages from one neuron to another. Branches called **collaterals** may arise along the length of the axon, permitting extensive interconnections among neurons.

Axons of peripheral neurons are enveloped by a **cellular sheath,** or **neurilemma,** composed of supporting cells called **Schwann cells.** The cellular sheath is important in regeneration of injured nerves (see Focus on Regeneration of an Injured Neuron). In forming the cellular sheath, Schwann cells line up along the axon and wrap themselves around it. On some axons the Schwann cells produce an insulating inner sheath called the **myelin sheath.** This covering forms when the Schwann cell membrane becomes wrapped around the axon several times (Figs. 39–4 and 39–5). Myelin is a white, lipid-rich substance that makes up the cell membrane of the Schwann cell. This fatty material is an excellent electrical insulator and speeds the conduction of nerve impulses (see under Saltatory Conduction, later in chapter). Between adjacent Schwann cells there are gaps called **nodes of Ranvier.** At these points, which are from 50 to 1500 μm apart, the axon is not insulated with myelin. Almost all axons more than 2 μm in diameter are myelinated, that is, possess myelin sheaths. Those with a smaller diameter are generally unmyelinated.

Axons within the CNS have no neurilemma. Their myelin sheaths are formed by another type of neuroglial cells (oligondendrocytes) rather than by Schwann cells. Certain areas of the brain and spinal cord are composed principally of myelinated axons. The myelin imparts a whitish color to these areas, so that they are referred to as white matter.

When myelin is destroyed, nerve function is impaired. **Multiple sclerosis** is a neurological disease in which patches of myelin deteriorate at irregular intervals along neurons in the CNS. The myelin is replaced by a type of scar tissue, and the affected neurons are not able to conduct impulses. This leads to impaired neural function, including loss of coordination, tremor, and paralysis of affected body parts.

Figure 39–5 Electron micrograph of a section through a single myelinated axon. *AX,* axon; *MS,* myelin sheath; *SC,* Schwann cell; *N,* nucleus of Schwann cell. (Courtesy of Dr. Lyle C. Dearden.)

Nerves and Ganglia

The nerves observed in gross anatomical dissection consist of hundreds or even thousands of axons wrapped in connective tissue (Fig. 39–6). A nerve can be compared to a telephone cable. The individual axons correspond to the wires that run through the cable, and the sheaths and connective tissue coverings correspond to the insulation. Within the CNS, bundles of axons are referred to as **tracts** or **pathways,** rather than nerves. The cell bodies of neurons are usually grouped together in masses called **ganglia.**

Transmission of a Neural Impulse

Once a receptor has been stimulated, the neural message must be transmitted to the CNS and then back to appropriate effector cells. Information must be conducted through a sequence of neurons. Transmission of a nerve impulse down the length of a neuron is an electrochemical process that depends upon changes in ion distribution. Transmission from one neuron to another across a synapse is generally a chemical phenomenon involving the secretion of neurotransmitter by the axon and the action of chemoreceptors in the dendrite.

THE RESTING POTENTIAL

In a **resting neuron**—one not transmitting an impulse—the inner surface of the plasma membrane is negatively charged compared with the interstitial fluid surrounding it (Fig. 39–7). The resting neuron is said to be **electrically polarized,** that is, oppositely charged along the inside of the membrane compared with the interstitial fluid outside. When electric charges are separated in this way, they have the potential of doing work should they be permitted to come together. The difference in electric potential on the two sides of the membrane may be expressed in millivolts (mV). (A millivolt is a thousandth of a volt and is a unit for measuring electrical potential.)

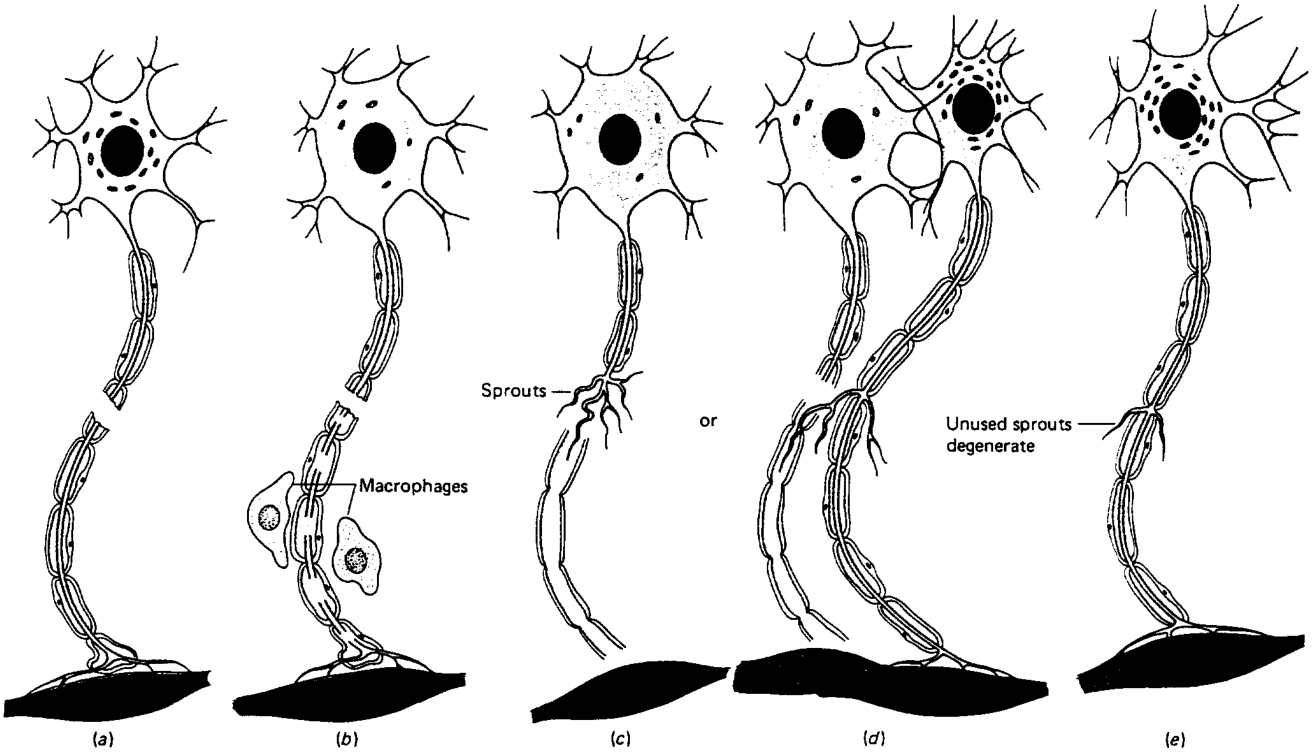
The **resting potential** of a neuron is about 70 mV. By convention this is expressed as −70 mV because the inner surface of the plasma membrane is negatively charged relative to the interstitial fluid. The resting membrane can be measured by placing one electrode, insulated except at the tip, inside the cell and a second electrode on the outside surface. The two electrodes are connected with a suitable recording instrument such as a galvanometer, which measures current by electro-

FOCUS ON

Regeneration of an Injured Neuron

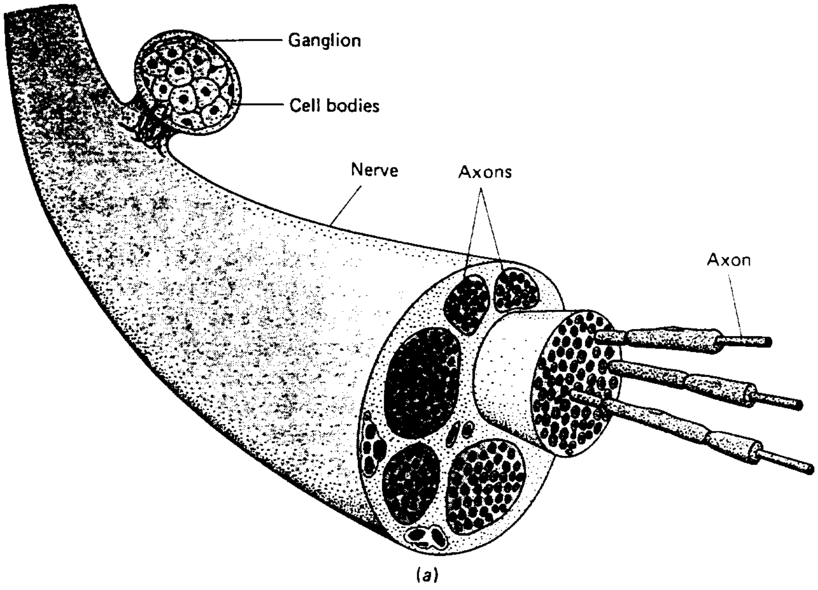
When an axon is separated from its cell body by a cut, it soon degenerates. A hollow tube of Schwann cells remains, but myelin eventually disappears. As long as the cell body of the neuron has not been injured, however, it is capable of regenerating a new axon. Sprouting begins within a few days following cutting (see accompanying figure). The growing axon enters the old sheath tube and proceeds along it to its final destination. Axons can grow in the absence of sheaths if some conduit is provided for them. They can, for example, be made to grow within sections of blood vessels or extremely fine plastic tubes. The length of time required for regeneration depends on how far the nerve has to grow and may require as long as 2 years. When cuts occur within the spinal cord or brain, regeneration, if if occurs at all, is very feeble. It is thought that growth of new sprouts in the CNS is prevented by scar tissue formed by neuroglial cells at the site of injury.

It is remarkable that (if not blocked by scar tissue or other barrier) each regenerating axon of a cut peripheral nerve finds its way back to its former point of termination, whether this be a specific connection in the central nervous system or a specific muscle or sense organ in the periphery. If, during the early stages of development of an amphibian, an extra limb bud is transplanted next to the normally developing limb, both will grow to maturity. The extra limb then moves synchronously with the normal one. Anatomical examination reveals that the nerve that innervates the normal limb sends out branches to the extra one. Clearly, the extra limb exerts some stimulating influence on the growing nerves to produce more branches, and some directive influence as well.



Regeneration of an injured neuron. (*a*) A neuron is severed. (*b*) The part of the axon that has been separated from its nucleus degenerates. Its myelin sheath also degenerates, and macrophages phagocytize the debris. The cell body enlarges and the Nissl substance breaks down, a sign of increased protein synthesis. (*c*) The tip of the severed axon begins to sprout, and one or more sprouts may find their way into the empty cellular sheath, which has remained intact. The sprout grows slowly and becomes myelinated. (*d*) Sometimes an adjacent undamaged neuron may send a collateral sprout into the cellular sheath of the damaged neuron. (*e*) Eventually the neuron may regenerate completely, so that function is fully restored. Unused sprouts degenerate.

magnetic action. If both electrodes are placed on the outside surface of the neuron, no potential difference between them is registered; all points on the outside are at equal potential.



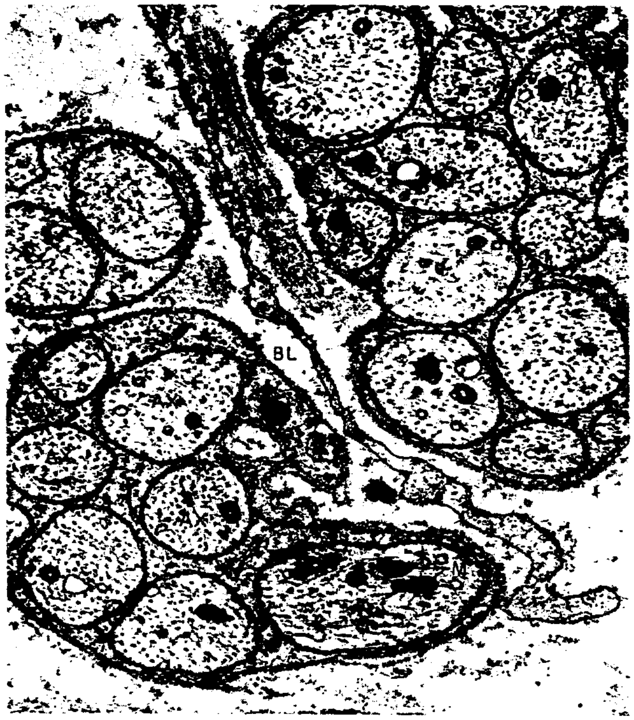


Figure 39–6 A nerve consists of bundles of axons held together by connective tissue. The cell bodies belonging to these axons are grouped together in a ganglion. (*a*) Structure of a nerve and a ganglion. (*b*) Electron micrograph showing cross section through a portion of the sciatic nerve (approximately ×30,000). The axons shown here are unmyelinated. *AX*, axon; *M*, mitochondria; *CO*, collagen fibers; *BL*, basal lamina. (Courtesy of Dr. Lyle C. Dearden.)

What is responsible for the resting potential? It results from the presence of a slight excess of *negative* ions *inside* the plasma membrane and a slight excess of *positive* ions *outside* the plasma membrane. This imbalance in ion distribution is brought about by several factors. The plasma membrane of the neuron has very efficient sodium pumps that actively transport sodium out of the cell against a concentration and an electrochemical gradient. The sodium pump requires energy and uses ATP derived from metabolic processes within the nerve cell. The same pumps may also actively transport potassium ions into the cell. About three sodium ions are pumped out of the neuron for every two potassium ions that are pumped in. Thus, more positive ions are pumped out than in.

The neuron membrane is much more permeable to potassium than to sodium. For this reason, sodium cannot easily diffuse back into the resting neuron, but potassium ions are able to diffuse out. Potassium ions leak out through the membrane along a concentration gradient until the positive charge outside the membrane reaches a level that repels the outflow of additional positively charged potassium ions. A steady state is reached when the potassium outflow equals the inward flow of sodium ions. At this point the resting potential is about −70 mV.

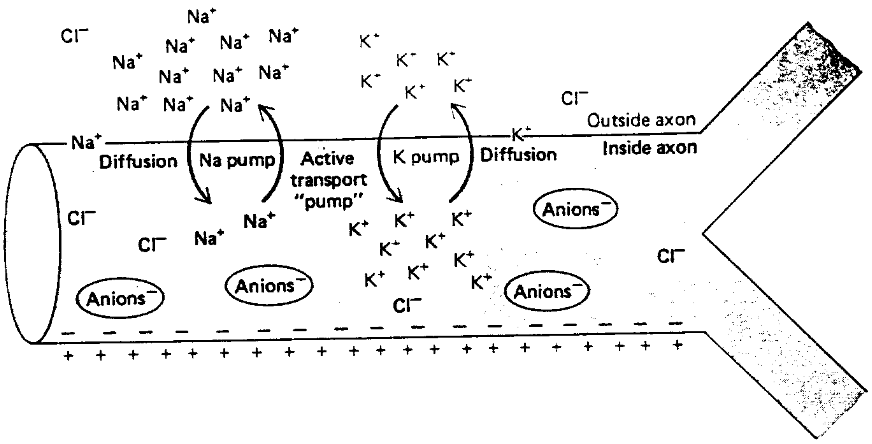


Figure 39–7 Segment of an axon of a resting (nonconducting) neuron. Sodium is actively pumped out of the cell, and potassium is pumped in. Sodium is unable to diffuse back to any extent, but potassium does diffuse out along its concentration gradient. Because of the unequal distribution of ions, the inside of the axon is negatively charged compared with the outer tissue fluid. The presence of negatively charged proteins and other large anions in the cell contributes to this polarity.

Contributing to the overall ionic situation are large numbers of negatively charged proteins and organic phosphates within the neuron that are too big to diffuse out. The plasma membrane is permeable to negatively charged chloride ions, but because of the positively charged ions that accumulate outside the membrane, chloride ions are attracted to the outside and tend to accumulate there.

The resting potential is due mainly to the outward diffusion of potassium ions along their concentration gradient. The conditions for this diffusion, however, are set by the action of the sodium–potassium pumps. The active transport of ions by these pumps is a form of cellular work, and so requires energy.

LOCAL CHANGES IN POTENTIAL

An electrical, chemical, or mechanical stimulus may alter the resting potential by increasing the permeability of the plasma membrane to sodium, or by making the neuron more negative relative to the interstitial fluid. Such local responses in the membrane potential are called **postsynaptic potentials.** When they occur in receptor cells, they are called *receptor potentials.*

Neurophysiologists think that the neuronal membrane contains specific sodium gates. Apparently, these gates lead into channels through the membrane that are formed by proteins. **Excitatory stimuli** open sodium gates, permitting sodium ions to rush into the cell. This passage of positive sodium ions into the cell depolarizes the membrane, that is, causes the membrane potential to become less negative for a brief moment. **Inhibitory stimuli** may hyperpolarize the membrane, that is, increase the resting potential. This occurs because of an increase in permeability of the membrane to potassium, which permits potassium ions to flow out of the neuron. With additional positively charged potassium ions outside the membrane, the neuron becomes more negative relative to the outside than when it was at rest.

Local changes in potential can cause a flow of electric current. The greater the change in potential, the greater the flow of current. Such a local current flow can function as a signal only over a very short distance, because it fades out within a few millimeters of its point of origin. As we will see, however, postsynaptic potentials can be added together, resulting in action potentials.

THE ACTION POTENTIAL

The membrane of a neuron can depolarize as much as 15 mV (which changes the resting potential to about −55 mV) without initiating an impulse. When the extent of depolarization reaches about −55 mV, a critical point called the **threshold level** or firing level is reached. At this point the resulting depolarization is self-propagating; that is, it spreads down the axon as a wave of depolarization without fading. This wave of depolarization is called a **nerve impulse** or **action potential** (Fig. 39–8).

When threshold level is reached, an almost explosive action occurs as the action potential is produced. The neuron membrane quickly reaches zero potential and even overshoots to about +35 mV so that there is a momentary reversal in

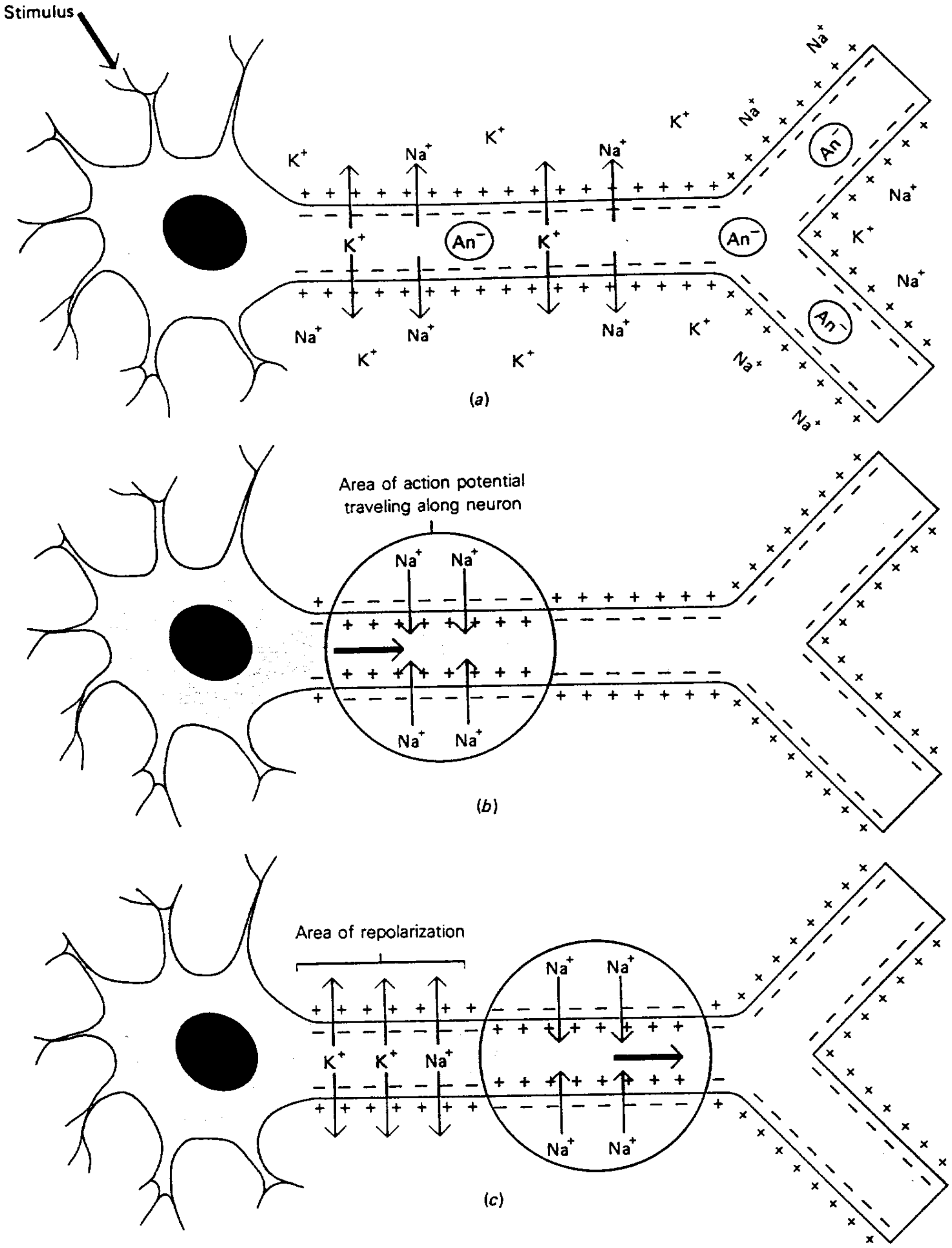


Figure 39–8 Transmission of an impulse along an axon. (*a*) The dendrites (or cell body) of a neuron are stimulated sufficiently to depolarize the membrane to firing level. The axon shown is still in the resting state, and has a resting potential. (*b*), (*c*) An impulse is transmitted as a wave of depolarization that travels down the axon. At the region of depolarization, sodium ions diffuse into the cell. As the impulse passes along from one region to another, polarity is quickly reestablished. Potassium ions flow outward until the resting potential is restored. Sodium is slowly pumped back out of the axon so that resting conditions are reestablished.

polarity. The sharp rise and fall of the action potential is referred to as a **spike.** Figure 39–9 illustrates an action potential.

The action potential is an electric current of sufficient strength to induce collapse of the resting potential in the adjacent area of the membrane. The impulse moves along the axon at a constant velocity and amplitude for each type of neuron. The neuron is said to obey an **all-or-none law** since there are no variations in intensity of the action potential: Either the neuron fires completely, or it does not fire at all.

As the wave of depolarization moves along the axon, the normal polarized state is quickly reestablished behind it. By the time the action potential moves a few millimeters along the axon, the membrane over which it has just passed begins to repolarize. The sodium gates close, so that the membrane becomes impermeable to sodium. Potassium gates in the membrane then open, permitting potassium to leave. The accumulation of potassium ions outside the membrane results in repolarization.

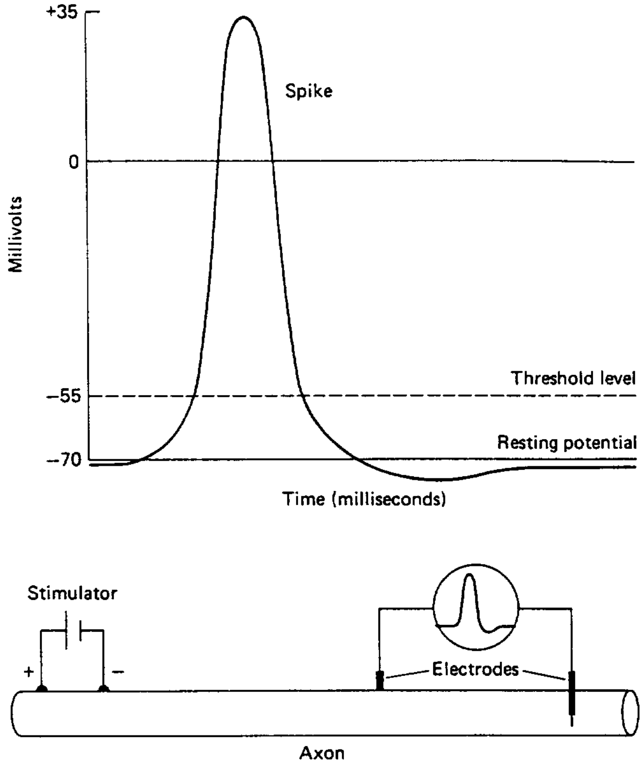


Figure 39–9 An action potential recorded with one electrode inside the cell and one just outside the plasma membrane. When the axon depolarizes to about −55 mV, an action potential is generated.

Repolarization occurs very rapidly, but redistribution of sodium and potassium ions back to the resting condition requires more time. Resting conditions are reestablished when the sodium pump actively transports excess sodium out of the neuron.

During the millisecond or so during which it is depolarized, the axon membrane is in an **absolute refractory period,** when it cannot transmit an action potential no matter how great a stimulus is applied. Then, for two or three additional milliseconds, while the resting conditions are being reestablished, the axon is said to be in a **relative refractory period.** During this time another potential can be generated if the stimulus is stronger than the normal threshold stimulus. Even with the limits imposed by their refractory periods, neurons can transmit several hundred impulses per second!

The electrical and chemical processes involved in the transmission of a nerve impulse are similar in many ways to those involved in muscle contraction. Compared with a contracting muscle, however, a transmitting nerve expends little energy; the heat produced by one gram of nerve stimulated for one minute is equivalent to the energy liberated by the oxidation of 10^{-6} grams of glycogen. This means that if a nerve contained only 1% glycogen to serve as fuel, it could be stimulated continuously for a week or more without exhausting the supply. Nerve fibers are practically incapable of being fatigued as long as an adequate supply of oxygen is available. Whatever "mental fatigue" may be, it is not due to the exhaustion of the energy supply of nerve fibers!

SALTATORY CONDUCTION

The smooth, progressive impulse transmission just described is characteristic of unmyelinated neurons. In myelinated neurons the myelin insulates the axon except at the nodes of Ranvier, where the membrane makes direct contact with the interstitial fluid. Depolarization skips along the axon from one node of Ranvier to the next (Fig. 39–10). The ion activity at the node depolarizes the next node along the axon. Known as **saltatory conduction,** this type of impulse transmission is more rapid than the continuous type.

Saltatory conduction requires less energy than continuous conduction. Only the nodes depolarize, so fewer sodium and potassium ions are displaced, and the

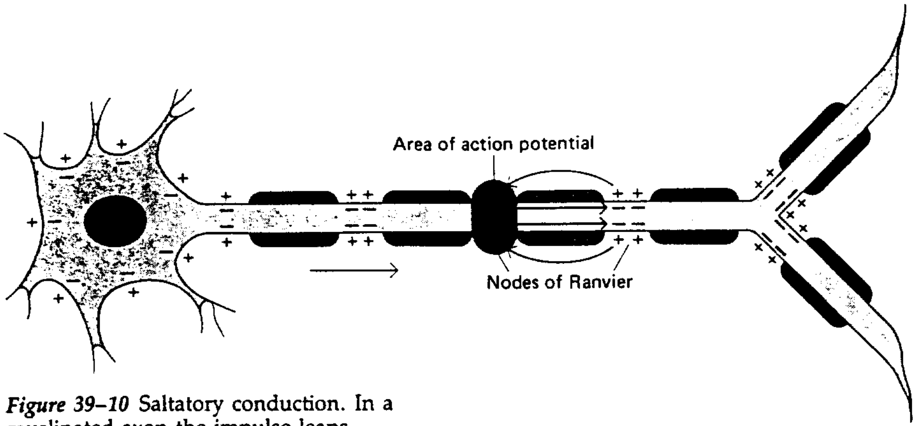


Figure 39–10 Saltatory conduction. In a myelinated axon the impulse leaps along from one node of Ranvier to the next.

cell does not have to work as hard to reestablish resting conditions each time an impulse is transmitted.

SUBSTANCES THAT AFFECT EXCITABILITY

Substances that increase the permeability of the membrane to sodium make the neuron more excitable than normal. Other substances make the neuron less excitable. Calcium balance is essential to normal neural function. When insufficient calcium ions are present, the sodium gates apparently do not close completely between action potentials. Sodium ions then leak into the cell, lowering the resting potential and bringing the neuron closer to firing. The neuron fires more easily—sometimes even spontaneously. As a result, the muscle innervated by the neuron may go into spasm, a condition known as low-calcium tetany. When calcium ions are too numerous, neurons are less excitable and more difficult to fire.

Local anesthetics such as procaine and cocaine are thought to decrease the permeability of the neuron to sodium. Excitability may be so reduced that the neuron cannot propagate an action potential through the anesthesized region. DDT and other chlorinated hydrocarbon biocides interfere with the action of the sodium pump. When nerves are poisoned by these chemicals, they are unable to transmit impulses. Fortunately insects are poisoned by much lower concentrations of DDT than those harmful to humans.

SYNAPTIC TRANSMISSION

A **synapse,** you will recall, is a junction between two neurons. The neurons are generally separated by a tiny gap from 0.002 to 0.02 μm wide (less than a millionth of an inch) called the **synaptic cleft.** A neuron that ends at a specific synapse is referred to as a **presynaptic neuron,** whereas a neuron that begins at a synapse is a **postsynaptic neuron.** A neuron may be postsynaptic with respect to one synapse and presynaptic with respect to another.

Some presynaptic and postsynaptic neurons come very close together (within 2 nm of one another) and form low-resistance gap junctions. Such junctions permit an impulse to be electrically transmitted directly from one cell to another. Electrical synapses of this sort are found in cnidarian nerve nets and in parts of the nervous systems of earthworms, crayfish, and fish.

At most synapses, however, a gap of more than 20 nm separates the two plasma membranes, and the impulse is transmitted by special substances called **neurotransmitters.** When an impulse reaches the synaptic knobs at the end of a presynaptic axon, it stimulates the release of neurotransmitter into the synaptic cleft. This chemical messenger rapidly diffuses across the narrow synaptic cleft and affects the permeability of the membrane of the postsynaptic neuron.

The synaptic knobs continuously synthesize neurotransmitter and store it in little vesicles. Mitochondria in the synaptic knobs provide the ATP required for this synthesis. The enzymes needed are produced in the cell body and move down the axon to the synaptic knobs. Each time an action potential reaches a synaptic knob, calcium ions pass into the cell. This apparently induces several hundred vesicles to fuse with the membrane and to release their contents into the synaptic cleft (Figs. 39–11 and 39–12). After diffusing across the synaptic cleft, the neurotransmitter

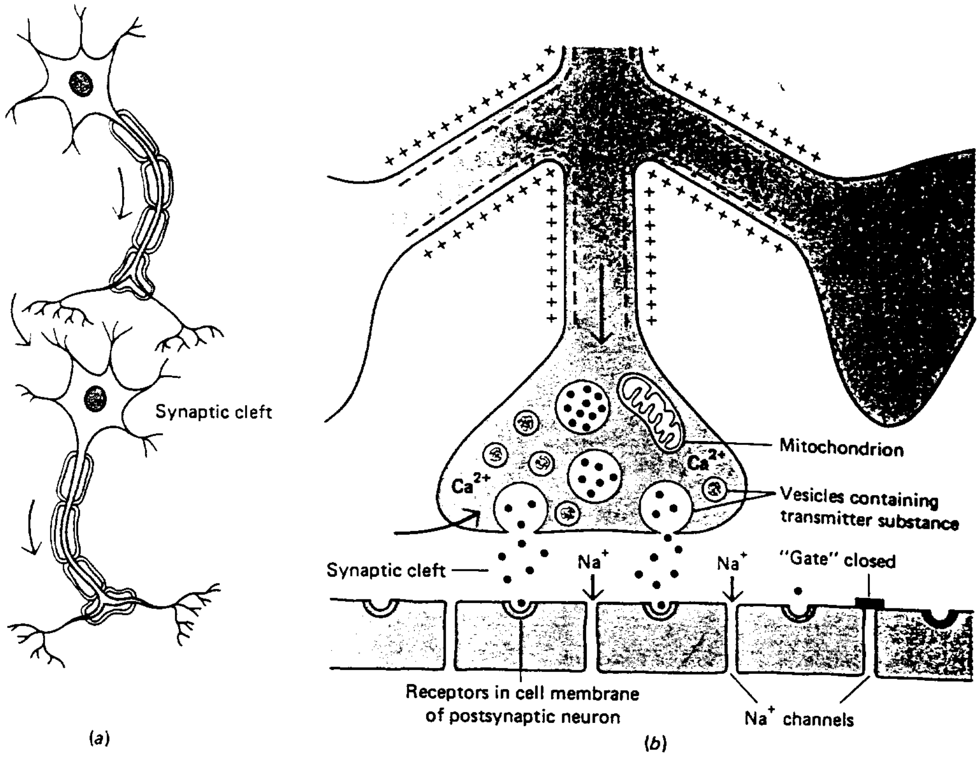


Figure 39–11 Transmission of an impulse between neurons, or from a neuron to an effector. (*a*) In most synapses, the wave of depolarization is unable to jump across the synaptic cleft between the two neurons. (*b*) The problem is solved by the release of neurotransmitter from vesicles within the synaptic knobs of the axon. The neurotransmitter diffuses across the synaptic cleft and may trigger an impulse in the postsynaptic neuron. It is thought that when the neurotransmitter combines with receptors in the membrane of the postsynaptic neuron, sodium gates open, permitting sodium to rush into the axon.

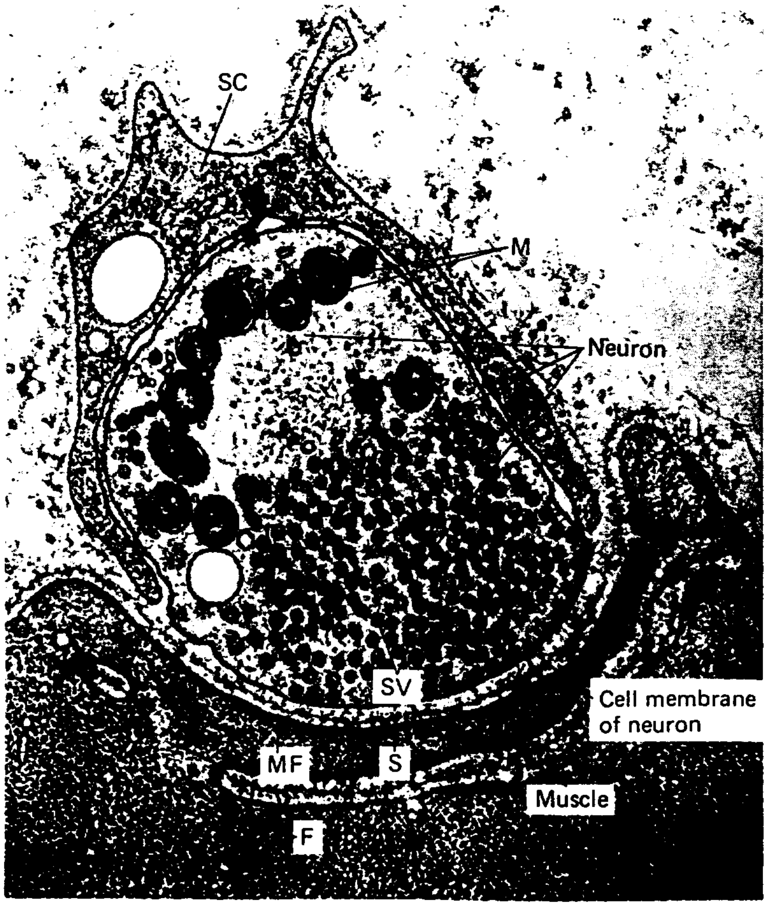


Figure 39–12 Electron micrograph of a synaptic knob filled with synaptic vesicles (approximately ×20,000). This is a motor neuron synapsing with a muscle fiber. *SC*, Schwann cell; *M*, mitochondria; *SV*, synaptic vesicles; *S*, synaptic cleft; *M*, membrane of muscle fiber; *F*, filaments of muscle. (Courtesy of Dr. John Heuser.)

combines with specific receptors on the dendrites or cell bodies of postsynaptic neurons. This opens gates in the membrane, and the resulting redistribution of ions affects the electrical potential of the membrane, either depolarizing or hyperpolarizing it.

In order for repolarization to occur quickly, any excess neurotransmitter must be removed. It is either inactivated by enzymes or reabsorbed into the synaptic vesicles.

Excitatory and Inhibitory Signals

If the effect of a neurotransmitter is to partially depolarize the membrane, the change in potential is called an **excitatory postsynaptic potential,** or **EPSP.** On the other hand, if the effect of the neurotransmitter is to hyperpolarize the postsynaptic membrane, the change in potential is called an **inhibitory postsynaptic potential,** or **IPSP.**

One EPSP by itself is usually too weak to trigger an action potential in the postsynaptic neuron. Its effect is subliminal, that is, below threshold level. However, EPSPs may be added together, a process known as **summation. Temporal summation** occurs when repeated stimuli cause new EPSPs to develop before previous ones have faded. By adding several EPSPs the neuron may be brought to threshold level. In **spatial summation,** several synaptic knobs release transmitter substance at the same time, so that the postsynaptic neuron is stimulated at several points simultaneously. The added effects of this stimulation can also bring the postsynaptic neuron to the critical firing level.

Neurotransmitters

About 30 different substances are now known (or suspected) to be neurotransmitters. Many types of neurons secrete two or even three different types of neurotransmitters. Furthermore, a postsynaptic neuron can have receptors for more than one type of neurotransmitter. Some of its receptors may be excitatory and some inhibitory.

The two neurotransmitters that have been investigated most extensively are acetylcholine and norepinephrine. **Acetylcholine** triggers muscle contraction. It is released not only from motor neurons that innervate skeletal muscle but also by some neurons in the autonomic system and by some neurons in the brain. Cells that release acetylcholine are referred to as **cholinergic neurons.** Acetylcholine has an excitatory effect on skeletal muscle but an inhibitory effect on cardiac muscle. Whether a neurotransmitter excites or inhibits is apparently a property of the postsynaptic receptors with which it combines.

After acetylcholine is released into a synaptic cleft and combines with receptors on the postsynaptic neuron, the remaining molecules must be removed to prevent repeated stimulation of the muscle. The enzyme **cholinesterase** catalyzes the breakdown of acetylcholine into choline and acetate.

Nerve gases and organophosphate biocides inactivate cholinesterase. As a result, the amount of acetylcholine in the synaptic cleft increases with each successive nerve impulse. This causes repetitive stimulation of the muscle fiber and may lead to life-threatening muscle spasms. Should the muscles of the larynx go into spasm, for example, a person may die of asphyxiation.

Norepinephrine is released by sympathetic neurons as well as by many neurons in the brain and spinal cord. Neurons that release norepinephrine are called **adrenergic neurons.** Norepinephrine and the neurotransmitters epinephrine and dopamine belong to a class of compound known as **catecholamines.** After their release from synaptic knobs, catecholamines are removed mainly by re-uptake into the vesicles in the synaptic knobs. Some are inactivated by enzymes such as monoamine oxidase (MAO). Catecholamines affect mood, and many drugs that modify mood do so by altering the levels of these substances in the brain. Other neurotransmitters are listed in Table 39–1.

DIRECTION AND SPEED OF CONDUCTION

In the laboratory it can be demonstrated that an impulse can move in both directions within a single axon. However, in the body an impulse generally stops when it reaches the dendrites, because there is no neurotransmitter present there to con-

TABLE 39–1
Some Neurotransmitters

Substance	*Origin*	*Comments*
Acetylcholine	Myoneural (muscle–nerve) junctions; preganglionic autonomic endings;* postganglionic parasympathetic nerve endings; parts of brain	Inactivated by cholinesterase
Norepinephrine	Postganglionic sympathetic endings; reticular activating system; areas of cerebral cortex, cerebellum, and spinal cord	Reabsorbed by vesicles in synaptic axons knob; inactivated by MAO (monoamine oxidase); norepinephrine level in the brain affects mood
Dopamine	Limbic system; cerebral cortex; basal ganglia; hypothalamus	Thought to affect motor function; may be involved in pathogenesis of schizophrenia;† amount reduced in Parkinson's disease
Serotonin (5-HT, 5-hydroxytryptamine)	Limbic system; hypothalamus; cerebellum; spinal cord	May play a role in sleep; LSD antagonizes serotonin; thought to be inhibitory
Epinephrine	Hypothalamus; thalamus; spinal cord	Identical with the hormone released by the adrenal glands
GABA (γ-Amino-butyric acid)	Spinal cord; cerebral cortex; Purkinje cells in cerebellum	Thought to act as inhibitor in brain and spinal cord
Glycine	Released by neurons mediating inhibition in spinal cord	Acts as an inhibitor
Endorphins and enkephalins	Many parts of CNS	Group of compounds that affect pain perception and other aspects of behavior

*These and other structures listed in this table are discussed in Chapter 40.
†Studies suggest that the brains of schizophrenics have more dopamine receptors than those of nonschizophrenics.

duct it across a synapse. This limitation imposed by the location of the neurotransmitters makes neural transmission unidirectional. Neural pathways thus function as one-way streets, with the usual direction of transmission from the axon of the presynaptic neuron across the synapse to the dendrite or cell body of the postsynaptic neuron.

Compared with the speed of an electric current or the speed of light, the rate of nerve impulse travel is rather slow. Still, some neurons can transmit impulses at a rate of more than 120 meters per second. The rate of conduction of impulses increases as the diameter of the axon increases. Such an increase in diameter decreases the internal electrical resistance along the length of the axon, permitting sodium ions to spread rapidly when they enter the axon. In some invertebrates, giant axons that can transmit impulses very rapidly are employed to conduct danger signals. In vertebrates, the presence of the myelin sheath[1] permits rapid saltatory conduction of impulses along myelinated neurons. The largest, most heavily myelinated neurons conduct impulses most rapidly.

When considering speed of conduction through a sequence of neurons, the number of synapses must be taken into account. Each time an impulse is conducted from one neuron to another, there is a slight synaptic delay (about 0.5 msec). Synaptic delay is due to the time required for the release of transmitter substance, its diffusion, its binding to postsynaptic membrane receptors, and the generation of the action potential in the postsynaptic neuron.

Integration

Neural integration is the process of adding and subtracting incoming signals and determining an appropriate response. Each neuron synapses with hundreds of other neurons. It is the job of the dendrites and cell body of every neuron to inte-

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[1] By separating the nodes, where depolarization is possible, the myelin sheath forces an electric current to flow between a depolarized node and the next as yet undepolarized node. This current immediately produces depolarization of that node. Since current flow is faster than depolarization, the fewer and farther apart the nodes are, the more quickly the nerve impulse is conducted.

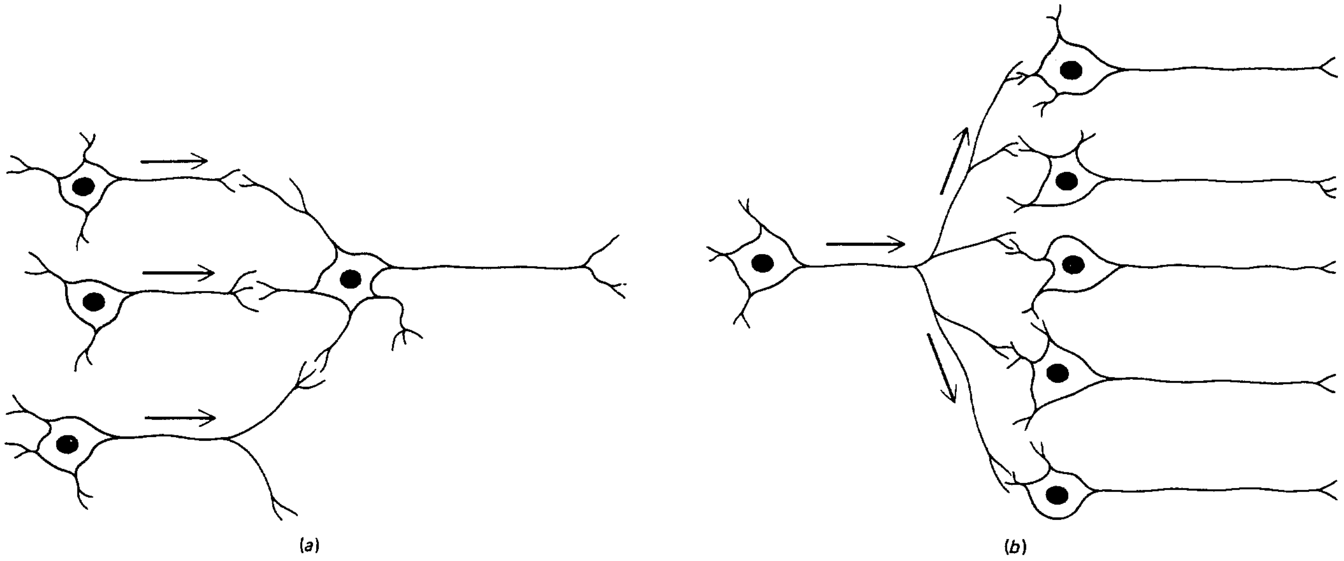


Figure 39–13 Organization of neural circuits. (*a*) Convergence of neural input. Several presynaptic neurons synapse with one postsynaptic neuron. This organization in a neural circuit permits one neuron to receive signals from many sources. (*b*) Divergence of neural output. A single presynaptic neuron synapses with several postsynaptic neurons. This organization allows one neuron to communicate with many others.

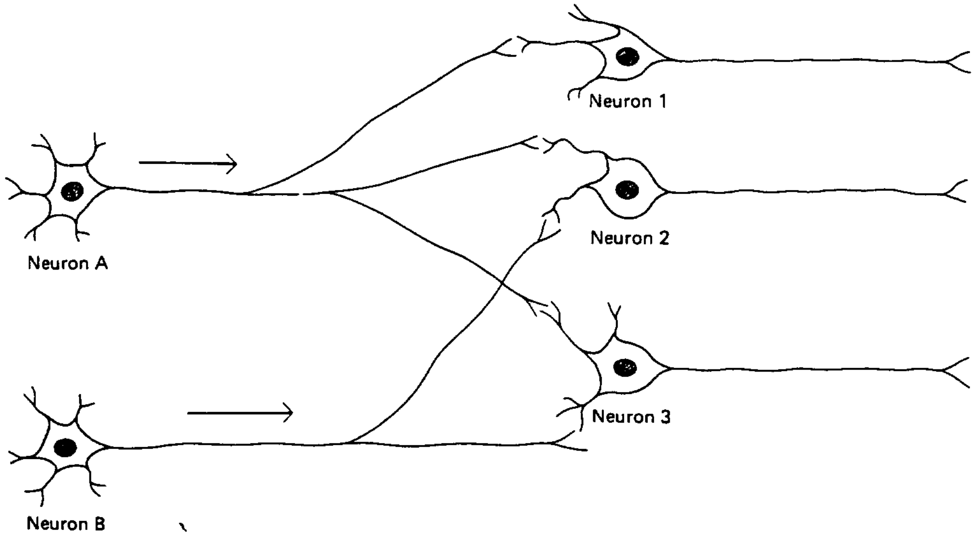
grate the numerous messages that they are continually receiving. Hundreds of EPSPs and IPSPs may be tabulated before an impulse is actually transmitted. When sufficient excitatory neurotransmitter predominates, the neuron is brought to the threshold level and an action potential is generated. Such an arrangement permits the neuron and the entire nervous system far greater flexibility and a wider range of response than would be possible if every EPSP generated an action potential.

Every neuron acts as an integrator, sorting through the thousands of bits of information continually bombarding it. Since more than 90% of the neurons in the body are located in the brain and spinal cord most neural integration takes place there.

Organization of Neural Circuits

Neurons are organized into specific pathways, or **circuits.** Within a neural circuit many presynaptic neurons may converge upon a single postsynaptic neuron. In **convergence,** the postsynaptic neuron is controlled by signals from two or more presynaptic neurons (Fig. 39–13). An association neuron in the spinal cord, for instance, may receive information from sensory neurons entering the cord, from neurons originating at other levels of the spinal cord, and even from neurons bringing information from the brain. Information from all of these converging neurons must be integrated before an action potential is generated in the association neuron and an appropriate motor neuron is stimulated.

Figure 39–14 Facilitation. Neither neuron *A* nor *B* can itself fire neuron 2 or 3. However, stimulation by either *A* or *B* does depolarize the neuron toward threshold level (if the stimulation is excitatory). This facilitates the postsynaptic neuron so that if the other presynaptic neuron stimulates it, threshold level may be reached and an action potential will be generated.



In **divergence,** a single presynaptic neuron stimulates many postsynaptic neurons (Fig. 39–13). Each presynaptic neuron may synapse with up to 25,000 or more different postsynaptic neurons. In **facilitation,** the neuron is brought close to threshold level by EPSPs from various presynaptic neurons but is not yet at the threshold level. The neuron can be easily excited by a new EPSP. Figure 39–14 illustrates facilitation: Neither neuron *A* nor neuron *B* can by itself fire neuron 2 or 3. However, when either neuron *A* or *B* is fired, neurons 2 and 3 are facilitated. Then when the other presynaptic neuron fires, the postsynaptic neuron receives sufficient neurotransmitter to generate an action potential.

A very important type of neural circuit is the **reverberating circuit.** This is a neural pathway arranged so that a neuron collateral synapses with an association neuron (Fig. 39–15). The association neuron synapses with a neuron in the sequence that can send new impulses again through the circuit. New impulses can be generated again and again until the synapses involved become fatigued (owing to depletion of neurotransmitter), or until they are stopped by some sort of inhibition. Reverberating circuits are thought to be important in rhythmic breathing, in maintaining alertness, and perhaps in short-term memory.

Reflex Action

A **reflex action** is a stereotyped, automatic response to a given stimulus that depends only on the anatomic relationships of the neurons involved. Reflexes are functional units of the nervous system, and many physiological mechanisms depend upon reflex actions. A reflex typically involves part of the body rather than the whole. Constriction of the pupil in response to bright light is an example. Breathing, heart rate, salivation, and regulation of blood pressure and temperature are other examples of reflex actions. A change in body temperature, for instance, acts as a stimulus, causing the temperature-regulating center in the brain to mobilize homeostatic mechanisms that bring body temperature back to normal. Many responses to external stimuli, such as withdrawing from painful stimuli, are also reflex actions.

The simple knee jerk, or patellar reflex, is an example of a very simple type of reflex requiring a chain of only two sets of neurons. Because only one group of synapses is involved, this type of reflex is called a **monosynaptic reflex.** Yet even this simple reflex action requires the sequence of information flow through the nervous system discussed earlier—reception, transmission, integration, and response by an effector. In the knee jerk the receptors are muscle spindles that respond to stretch stimuli when the tendon is tapped suddenly. Afferent neurons transmit the impulses to the spinal cord, where integration takes place at the synapses between afferent and efferent neurons. An efferent neuron then transmits the impulse to the effector cells. The muscle fibers contract, resulting in a sudden straightening of the leg.

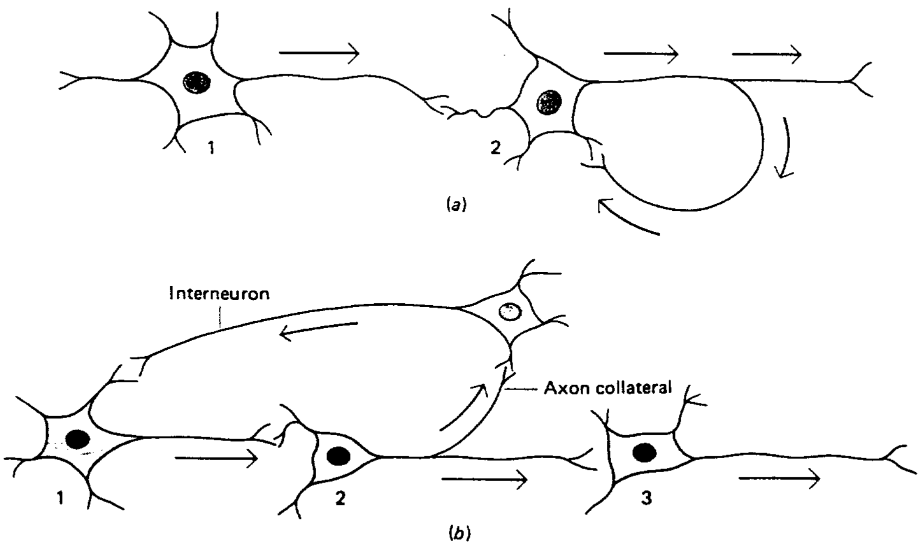


Figure 39–15 Reverberating circuits. (*a*) A simple reverberating circuit in which an axon collateral of the second neuron turns back and synapses with one of its own dendrites so that the neuron continues to stimulate itself. (*b*) In this neural circuit an axon collateral of the second neuron synapses with an interneuron. The interneuron synapses with the first neuron in the sequence. New impulses are triggered again and again in the first neuron, causing reverberation. See text for explanation of factors that can bring a halt to this reverberation.

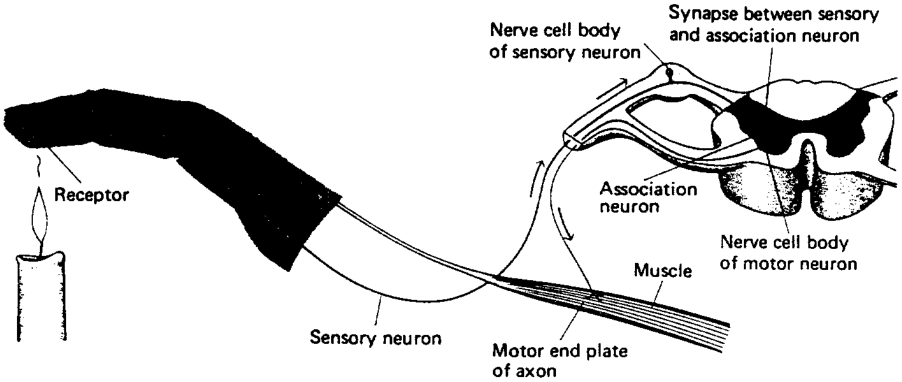


Figure 39–16 A withdrawal reflex is polysynaptic. The one shown here involves a chain of three neurons. A sensory neuron transmits the message from the receptor to the CNS, where it synapses with an association neuron. Then an appropriate motor neuron (shown in color) transmits an impulse to the muscles that move the hand away from the flame (the response).

Withdrawal reflexes are **polysynaptic**, requiring participation of three sets of neurons (Fig. 39–16). For example, an accidental burn on your finger would cause you to jerk your hand away from the painful stimulus even before you became aware of the pain. The pain receptors (dendrites of sensory neurons) in your fingers send messages through afferent neurons to the spinal cord. There each neuron synapses with an association neuron. Integration takes place and impulses are sent via appropriate efferent neurons to muscles in the arm and hand, instructing them to contract, jerking the hand away from the harmful stimulus. At the same time that the association neuron sends a message to the motor neuron, it may also dispatch a message up the neurons in the spinal cord to the brain. Very quickly you become conscious of your plight and can make the decision to hold your hand under cold water. This is not part of the reflex action, however.

That the brain is not essential to many reflex actions can be demonstrated by an experiment often performed in college physiology laboratories. The brain of a frog is destroyed, creating a "spinal" animal. Then a piece of acid-soaked paper is applied to the animal's back. No matter how many times the piece of paper is placed on the skin, one leg will invariably move upward and flick it away. This experiment also demonstrates that reflex actions are stereotyped and automatic. A frog with a brain might make the response two or three times, but eventually would try a different response—perhaps hop away.

Some reflex actions—for example, the pupil reflex—do involve the brain, but only the so-called lower parts, which are functionally similar to the spinal cord and have nothing to do with conscious thought. Some reflex actions can be consciously inhibited or facilitated. An example is the reflex that voids the urinary bladder when it fills with urine. In babies, urination is a reflex action; when the bladder fills with urine and is stretched to a critical point, a sphincter muscle relaxes and urine passes out of the body. In early childhood we learn to facilitate the reflex consciously, stimulating it before bladder pressure reaches a critical level. We also learn to inhibit the reflex consciously if the bladder becomes full at an inconvenient time or place.

Much of the behavior in a relatively simple animal such as a sea star can be explained in terms of reflex actions. The sea star can extend and retract its tube feet and make postural movements associated with ambulation. The extension and retraction of the tube feet are unoriented reflex responses. The apparent coordination of all the tube feet, retracting in unison when a wave washes over the animal, is simply the sum of individual responses to a common stimulus. Numerous aspects of crustacean behavior are primarily reflex responses—the withdrawal of the eye stalk, the opening and closing of the claws, and movements associated with escape, defense, feeding, and copulation.

Although we might, in theory, construct an animal capable of many responses simply out of reflexes, reflexes in complex animals account for only a small part of total behavior. Reflex actions and behavior are discussed further in Chapter 48.

SUMMARY

I. Information flow through the nervous system begins with reception. Information is then transmitted to the CNS via afferent neurons. Integration takes place within the CNS, and appropriate nerve impulses are then transmitted by efferent neurons to the effectors that carry out the response.

II. The vertebrate nervous system is divided into central nervous system (CNS) and peripheral nervous system (PNS).
  - *A.* The CNS consists of brain and spinal cord.
  - *B.* The PNS consists of sensory receptors and nerves; it may be divided into somatic and autonomic systems.

III. The neuron is the structural and functional unit of the nervous system.
  - *A.* A typical multipolar neuron consists of a cell body from which project many branched dendrites and a single, long axon.
  - *B.* The axon is surrounded by a neurilemma. Many axons are also enveloped in a myelin sheath.

IV. A nerve consists of hundreds of axons wrapped in connective tissue; a ganglion is a mass of cell bodies.

V. Transmission of a neural impulse is an electrochemical mechanism.
  - *A.* A neuron that is not transmitting an impulse has a resting potential.
    1. The inner surface of the plasma membrane is negatively charged as compared to the outside.
    2. Sodium–potassium pumps continuously transport sodium ions out of the neuron, and transport potassium ions in.
    3. Potassium ions are able to leak out more readily than sodium ions are able to leak in.
  - *B.* Excitatory stimuli are thought to open sodium gates in the plasma membrane. This permits sodium to enter the cell and depolarize the membrane. Inhibitory stimuli hyperpolarize the membrane.
  - *C.* When the extent of depolarization reaches threshold level, an action potential may be generated.
    1. The action potential is a wave of depolarization that spreads along the axon.
    2. The action potential obeys an all-or-none law.
    3. As the action potential moves down the axon, repolarization occurs very quickly behind it.
  - *D.* Saltatory conduction takes place in myelinated neurons. In this type of transmission, depolarization skips along the axon from one node of Ranvier to the next.
  - *E.* Excitability of a neuron can be affected by calcium concentration and by certain substances such as local anesthetics and biocides.
  - *F.* Synaptic transmission generally depends upon release of a neurotransmitter from vesicles in the synaptic knobs of the presynaptic neuron.
    1. The neurotransmitter diffuses across the synaptic cleft and combines with specific receptors on the postsynaptic neuron.
    2. This may cause an excitatory postsynaptic potential (EPSP) or an inhibitory postsynaptic potential (IPSP).
    3. Temporal or spatial summation may bring the postsynaptic neuron to the threshold level.
  - *G.* The largest, most heavily myelinated neurons conduct impulses most rapidly.

VI. Neural integration is the process of adding and subtracting EPSPs and IPSPs and determining an appropriate response.

VII. Complex neural pathways are possible because of such neuronal associations as convergence, divergence, and facilitation.

VIII. A simple reflex action includes reception of a stimulus, transmission of impulses to the CNS via an afferent neuron, integration within the CNS, transmission of impulses via a motor neuron to an effector, and response by the effector.

POST-TEST

1. Afferent neurons transmit information from the ____________ ____________ to the ____________ ____________ ____________.

2. Functional connections between neurons are called ____________.

3. Changes in the environment that can be detected by an organism are termed ____________.

4. The peripheral nervous system consists of sensory ____________ and ____________.

5. A nerve cell is properly referred to as a ____________; the supporting cells of nervous tissue are called ____________.

6. Dendrites are specialized to ____________ ____________; the axon functions to ____________ from the ____________ ____________ to a ____________.

7. The cellular sheath is important in ________________________.

8. In some peripheral neurons, Schwann cells produce both a ____________ ____________ and a ____________ ____________.

9. A ganglion consists of a mass of ____________ ____________.

10. The ____________ ____________ of a neuron is due mainly to the outward diffusion of potassium ions along their concentration gradient.

11. ____________ stimuli are thought to open sodium gates, thereby permitting sodium to rush into the cell.

12. The passage of sodium ions into the neuron ____________ the cell membrane.

13. A wave of depolarization that travels down the axon is called a nerve impulse or ____________ ____________.

14. Because there is no variation in the intensity of an action potential the neuron is said to obey an

________________________ law.

15. In saltatory conduction, depolarization skips along the axon from ________________.

16. When insufficient calcium ions are present, the ________ ________ is lowered and the neuron fires ________ (*more/less*) easily.

17. When an impulse reaches the synaptic knobs, it stimulates the release of ________.

18. The neurotransmitter that stimulates muscle contraction is ________.

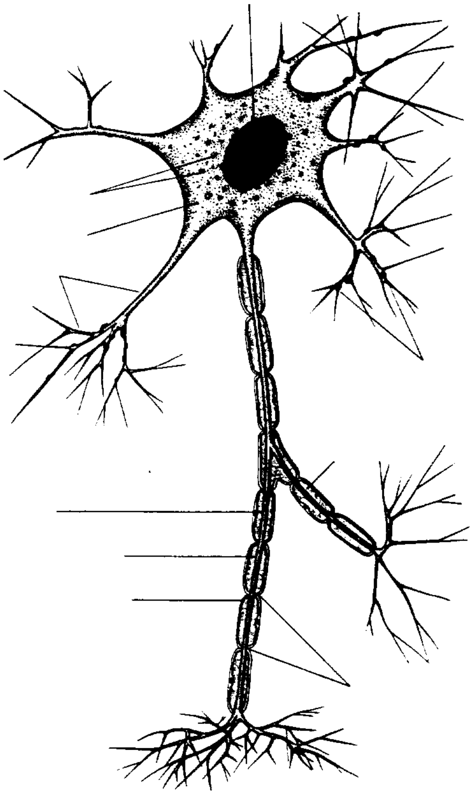
19. Adrenergic neurons release the neurotransmitter ________.

20. In ________, a single presynaptic neuron stimulates many postsynaptic neurons.

21. A stereotyped, automatic response to a given stimulus that depends only on the anatomic relationships of the neurons involved is called a ________ ________.

22. In a typical withdrawal reflex, pain receptors send messages through ________ neurons to the ________ ________, where ________ takes place.

23. Label the following diagram. (Refer to Fig. 39–2(*a*) as necessary.)



REVIEW QUESTIONS

1. Distinguish between a neuron and a nerve.
2. Imagine that a very unfriendly-looking monster suddenly appears before you. What processes must take place within your nervous system before you can make your escape?
3. Contrast the functions of an afferent and efferent neuron.
4. Describe the functions of the following:
   a. myelin
   b. a ganglion
   c. neuroglia
   d. dendrites
   e. axon
5. What is meant by the resting potential of a neuron? How do sodium-potassium pumps contribute to the resting potential?
6. What is an action potential? What is responsible for it?
7. What is the all-or-none law?
8. Contrast saltatory conduction with conduction in an unmyelinated neuron.
9. How is neural function affected by the presence of too much calcium? too little calcium?
10. Describe the functions of the following substances:
    a. acetylcholine
    b. cholinesterase
    c. norepinephrine
11. Contrast convergence and divergence.
12. What is summation? Describe facilitation.
13. Draw a diagram illustrating a withdrawal reflex, and label each neuron involved. Indicate the direction of neural transmission.

40

Neural Control: Nervous Systems

OUTLINE

- *I.* Invertebrate nervous systems
  - *A.* Nerve nets and radial systems
  - *B.* Bilateral nervous systems
- *II.* The vertebrate brain
  - *A.* The hindbrain
  - *B.* The midbrain
  - *C.* The forebrain
- *III.* The human central nervous system
  - *A.* The spinal cord
  - *B.* The brain
    - *1.* The reticular activating system
    - *2.* The limbic system
    - *3.* Brain waves
    - *4.* Sleep
    - *5.* Learning and memory
    - *6.* Effects of environmental experience on the brain
- *IV.* The peripheral nervous system
  - *A.* The cranial nerves
  - *B.* The spinal nerves
  - *C.* The autonomic system
- *V.* Effects of drugs on the nervous system

LEARNING OBJECTIVES

After you have read this chapter you should be able to:

1. Compare nerve nets with bilateral nervous systems.
2. Describe five specific advances characteristic of bilateral nervous systems, and compare them with systems found in radially symmetric animals.
3. Compare the nervous system of a planarian with that of an arthropod, a mollusk, and a vertebrate.
4. Trace the development of the principal parts of the vertebrate brain (e.g., cerebrum, cerebellum, medulla) from the forebrain, midbrain, and hindbrain.
5. Discuss the differences in relative size and function of the principal parts of the brain in fish, amphibians, reptiles, birds, and mammals.
6. Describe the structures that protect the human brain and spinal cord.
7. Describe the spinal cord, and list its principal functions.
8. Describe the three functional areas of the human cerebral cortex and give their functions.
9. Give the functions of the reticular activating system and the limbic system.
10. Identify three main types of brain wave patterns, and relate them to specific types of activity.
11. Contrast REM sleep with non-REM sleep.
12. Review current theories of learning and memory as presented in this chapter.
13. Cite experimental evidence linking environmental stimuli with demonstrable changes in the brain and with learning and motor abilities.
14. Identify the structures and functions of the peripheral nervous system. (At the option of your instructor, list the cranial nerves and give their function.)
15. Describe the functions of the autonomic system and contrast the functions of the sympathetic and parasympathetic systems, giving examples of the effects of these systems on specific organs.
16. Describe the actions and effects of various drugs on mood states.

Even though some organisms do not have a brain, or even nerves, they still must make at least some response to stimuli in order to survive. In a one-celled organism such as an amoeba, the entire cellular surface may be sensitive to stimuli such as light, heat, touch, and certain chemicals. Cytoplasm itself is **irritable,** that is, sensitive to changes in the environment. Thus, information may be conducted throughout the cytoplasm of even a single-celled organism enabling it to respond appropriately, either by moving toward a stimulus or by withdrawing from it. Some protozoa do have specialized receptors, and in ciliates there is a system for coordinating ciliary action. However, in such organisms the range and types of responses are very limited and stereotyped. For varied and sophisticated responses to be possible, an organism must have a complex nervous system.

Invertebrate Nervous Systems

There is no nervous system in the sponge. Whatever responses it makes are at the cellular level. Among other invertebrates there are two main types of nervous systems: nerve nets and bilateral nervous systems.

NERVE NETS AND RADIAL SYSTEMS

The simplest organized nervous system is the **nerve net** found in *Hydra* and other cnidarians (Fig. 40–1). In a nerve net the nerve cells are scattered throughout the body. No central control organ and no definite pathways are present. Sensory cells, specialized to receive stimuli, transmit information to ganglion cells (interneurons), which are the main cells of the nerve net. From the ganglion cells, information is passed on somewhat haphazardly to neurosecretory cells, which apparently send chemical messages to effector cells such as the cnidocytes (stinging cells). Impulses are transmitted in all directions, becoming less intense as they spread from the region of initial stimulation. If the stimulus is strong, the number of neurons of the net receiving the message will be more than if the stimulus is weak.

Since it produces responses that involve the body as a whole, or large parts of it at the same time, such a diffuse pattern of transmission is permissible in a radially symmetric animal with sluggish, slow means of locomotion. Responses in cnidarians are limited to discharge of nematocysts and contractions that permit movement. In some cnidarians several nerve nets are present, some mediating quick responses and some mediating slow responses. These nerve nets may work together to integrate information.

The somewhat more complex nervous system of the echinoderm consists of a circumoral (around the mouth) nerve ring from which a large radial nerve extends into each arm. These nerves coordinate movement of the animal. In asteroids (sea stars), a nerve net mediates the responses of the dermal gills to tactile stimulation.

BILATERAL NERVOUS SYSTEMS

In bilaterally symmetric animals the nervous system is usually more complex than in radially symmetric animals. A bilateral form of symmetry usually reflects a more active way of life, with the need to respond quickly to the environment in a sophisticated manner. The following trends can be identified:

1. Increased number of nerve cells.
2. Concentration of nerve cells to form thick cords or masses of tissue, which become nerves, nerve cords, ganglia, and brain.
3. Specialization of function. For example, transmission of nerve impulses in one direction requires both **afferent** nerves, which conduct impulses toward a central nervous system, and **efferent** nerves, which transmit impulses away from the central nervous system and to the effector cells. Various parts of the central nervous system are usually specialized also to perform specific functions, so that distinct structural and functional regions can be identified.
4. Increased number of association neurons and complexity of synaptic contacts. This permits much greater integration of incoming messages, provides a greater range of responses, and allows far more precision in responses.

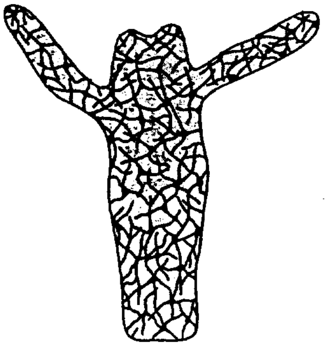


Figure 40–1 The nerve net of *Hydra* and other cnidarians is the simplest organized nervous system. No central control organ and no definite neural pathways are present.

5. Cephalization, or formation of a head. A bilaterally symmetric animal generally moves in a forward direction, so concentration of sense organs at the front end of the body is important for detection of an enemy quickly enough to escape or for seeing or smelling food in time for its capture. Response can be more rapid if these sense organs are linked by short pathways to decision-making nerve cells nearby. Therefore, nerve cells are also usually concentrated in the head region, comprising a definite brain.

In planarian flatworms, there are concentrations of nerve cells in the head region referred to as **cerebral ganglia** (Fig. 40–2). These serve as a primitive "brain" and exert some measure of control over the rest of the nervous system. Two ventral longitudinal nerve cords extend from the ganglia to the posterior end of the body. Transverse nerves connect the brain with the eyespots and anterior end of the body. This arrangement is referred to as a **ladder-type** nervous system.

In annelids and arthropods, there is also typically a pair of ventrally located longitudinal nerve cords (Figs. 40–3 and 40–4). The cell bodies of the nerve cells are massed into pairs of ganglia located in *each* body segment. Afferent and efferent neurons are located in lateral nerves that link the ganglia with muscles and other body structures.

When the earthworm brain is removed, the animal can move almost as well as before, but when it bumps into an obstacle it persists in futile efforts to move forward instead of turning aside. The brain is therefore necessary for adaptive movements; it enables the earthworm to respond appropriately to environmental change.

In complex arthropods, especially in insects, some of the abdominal ganglia move anteriorly in the course of embryonic development and fuse with the thoracic ganglia. In some arthropods the cerebral ganglia are somewhat brainlike in that specific functional regions have been identified in them (Fig. 40–4).

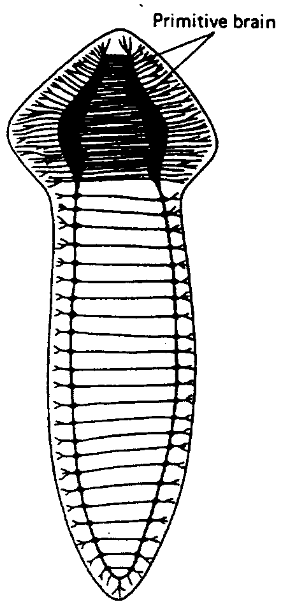
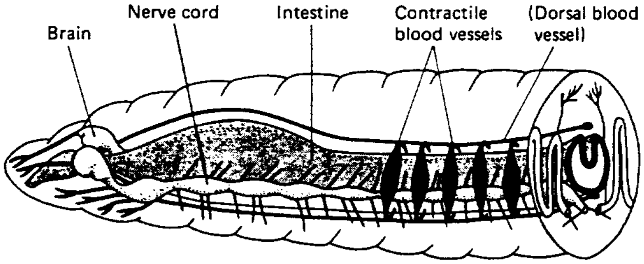
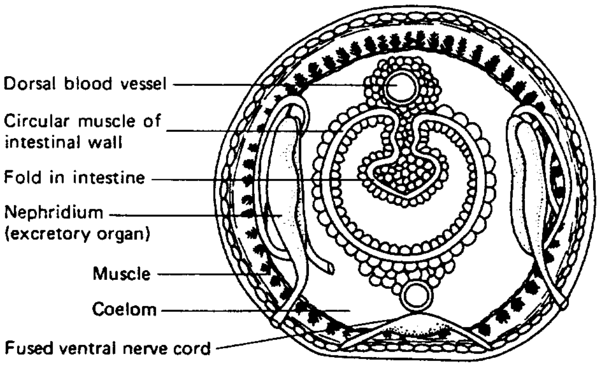


Figure 40–2 Planarian flatworms have a ladder-type nervous system. Cerebral ganglia in the head region serve as a simple brain and, to some extent, control the rest of the nervous system.

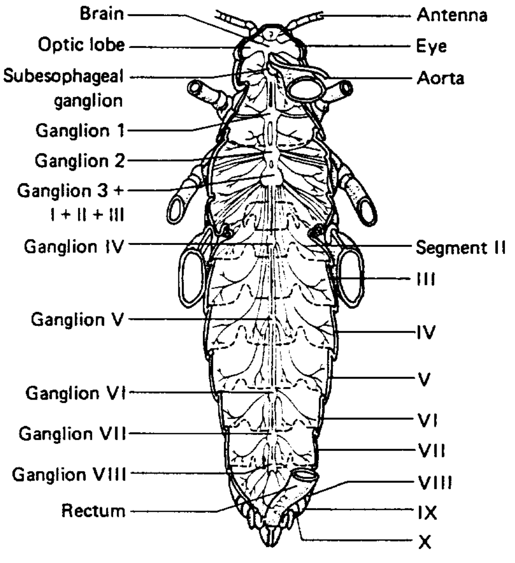


(*a*) Lateral view

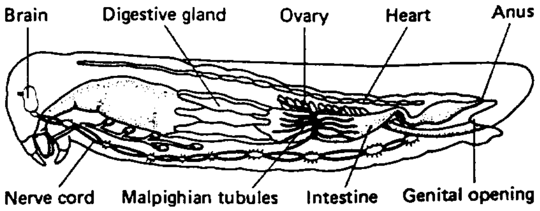


(*b*) Cross section

Figure 40–3 The nervous system of the earthworm is typical of those found in other annelids. The cell bodies of the neurons are located in ganglia found in each body segment. They are connected by the paired ventral longitudinal nerve cords.



(*a*) Ventral view



(*b*) Lateral view

Figure 40–4 In the insect nervous system the cerebral ganglia serve as a simple brain. Two ventral nerve cords are present.

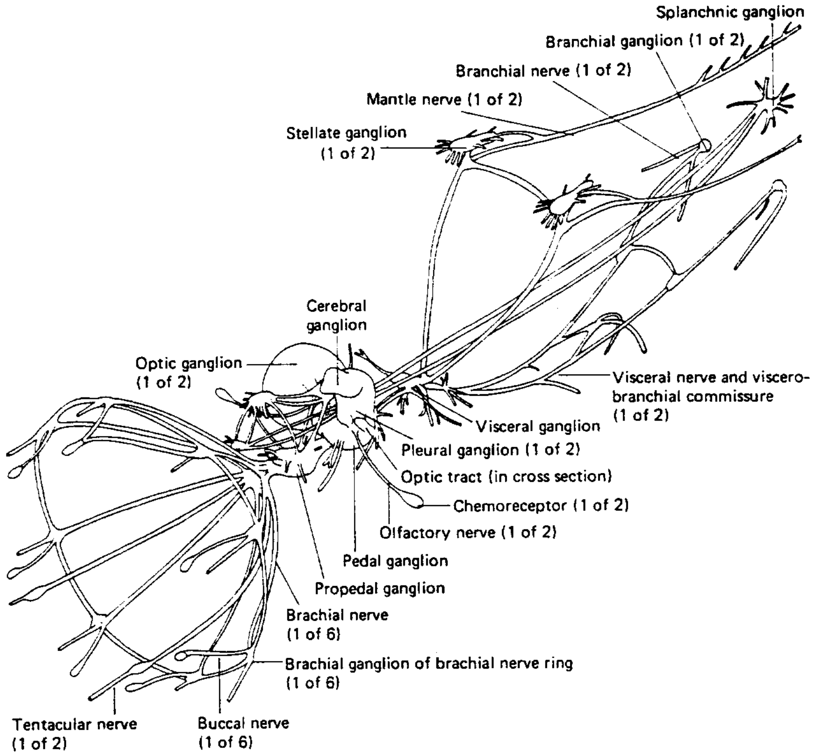


Figure 40–5 The cephalopod nervous system. Several ganglia including the cerebral, optic, and pedal ganglia make up the "brain." These structures contain millions of nerve cell bodies.

In mollusks there are typically at least three pairs of ganglia: **cerebral ganglia,** found dorsal to the esophagus (which serve as a coordinating center for complex reflexes and which also have a motor function); **visceral ganglia,** located among the organs (which control shell opening and closing); and **pedal ganglia,** located in the foot (which control the movement of the foot). The visceral and pedal ganglia are connected to the cerebral ganglia by nerve cords.

In cephalopods, such as the octopus, there is a tendency toward concentration of the nerve cells in a central region (Fig. 40–5). All the ganglia are massed in the **circumesophageal ring,** which contains about 168 million nerve cell bodies. With this complex brain, it is no wonder that the octopus is considered to be among the most intelligent of the invertebrates. Octopuses have considerable learning abilities and can be taught quite complex tasks.

The Vertebrate Brain

In the early embryo the brain and spinal cord differentiate from a single tube of tissue, the **neural tube.** Anteriorly, the tube expands and differentiates into the structures of the brain. Posteriorly, the tube develops into the spinal cord. Brain and spinal cord remain continuous and their cavities communicate. As the brain begins to differentiate, three primary swellings develop in the anterior end of the neural tube. These give rise to the **forebrain, midbrain,** and **hindbrain** (Fig. 40–6). As indicated in Table 40–1, the forebrain further subdivides to form the **telencephalon** and **diencephalon.** The telencephalon gives rise to the cerebrum, and the diencephalon to the thalamus and hypothalamus. The hindbrain subdivides to form the **metencephalon,** which gives rise to the cerebellum and pons, and the **myelencephalon,** which gives rise to the medulla. The medulla, pons, and midbrain make up the **brain stem,** the elongated portion of the brain that looks like a stalk holding up the cerebrum.

At the most posterior part of the brain, the **medulla** is continuous with the spinal cord. Its cavity, the **fourth ventricle,** communicates with the **central canal** of the spinal cord. The fourth ventricle communicates with the **third ventricle** (located within the diencephalon) by means of a channel, the cerebral aqueduct, that runs

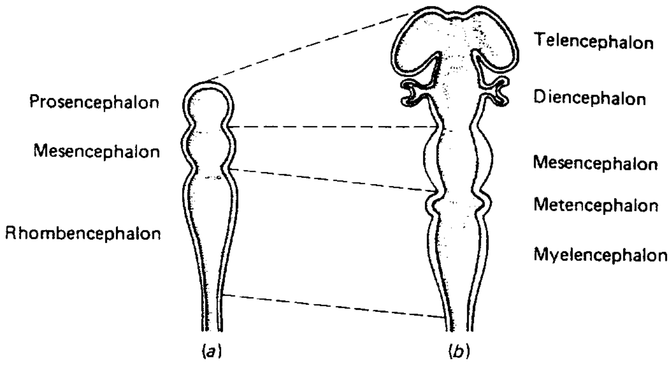


Figure 40–6 Early in the development of the vertebrate embryo, the anterior end of the neural tube differentiates into the forebrain, midbrain, and hindbrain. These primary divisions subdivide and then give rise to specific structures of the adult brain (see Table 40–1).

through the midbrain. The third ventricle in turn is connected with the **lateral** (first and second) **ventricles** within the cerebrum by way of the **interventricular foramen.**

As illustrated in Figure 40–7, all vertebrates from fish to mammals have the same basic brain structure. Certain parts of the brain are specialized to perform specific functions, and some regions, such as the cerebellum and cerebrum, are vastly more complex in the higher vertebrates.

THE HINDBRAIN

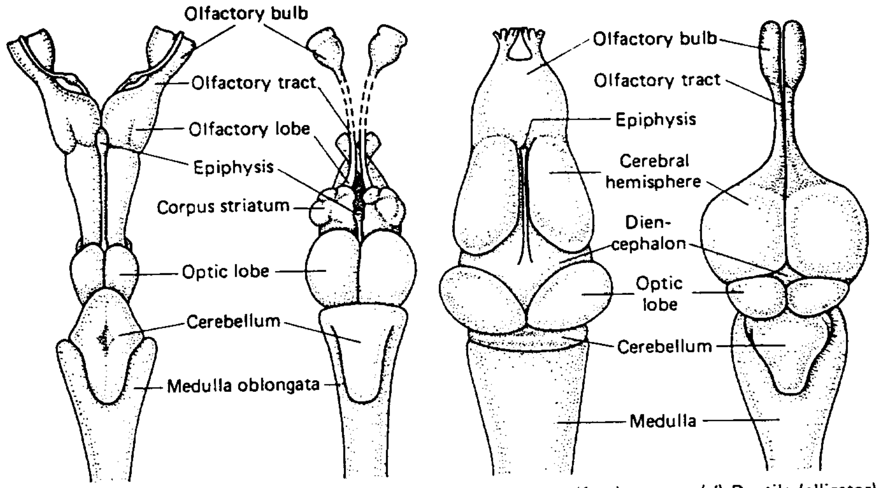
The walls of the medulla are thick and made up largely of nerve tracts that connect the spinal cord with various parts of the brain. In complex vertebrates the medulla contains discrete nuclei that serve as **vital centers** regulating respiration, heart beat, and blood pressure. Other reflex centers in the medulla regulate such activities as swallowing, coughing, and vomiting.

The size and shape of the **cerebellum** vary greatly among the vertebrate classes. Development of the cerebellum in different animals is correlated roughly with the extent and complexity of muscular activity. In some fish, birds, and mammals the cerebellum is highly developed, whereas it tends to be small in cyclostomes, amphibians, and reptiles. The cerebellum coordinates muscle activity and is responsible for muscle tone, posture, and equilibrium. Injury or removal of the cerebellum results not in paralysis but in impairment of muscle coordination. A bird without a cerebellum is unable to fly, and its wings thrash about jerkily. When the human cerebellum is injured by a blow or by disease, muscular movements are uncoordinated. Any activity requiring delicate coordination, such as threading a needle, is very difficult, if not impossible.

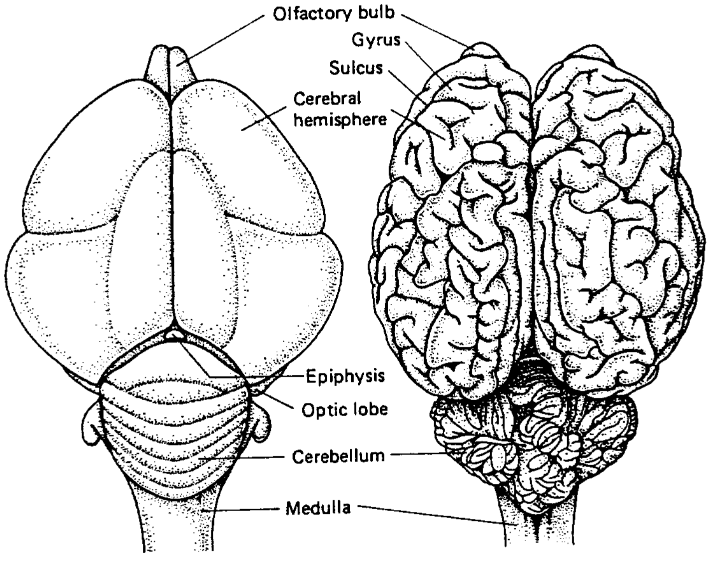
In mammals, a large mass of fibers known as the **pons** connects various parts of the brain. The pons forms a bulge on the anterior surface of the brain stem. The pons contains nuclei that relay impulses from the cerebrum to the cerebellum.

TABLE 40–1
Differentiation of CNS Structures

Early Embryonic Divisions	*Subdivisions*	*Derivatives in Adult*	*Cavity*
Brain			
Forebrain (prosencephalon)	Telencephalon	Cerebrum	Lateral ventricles (first and second ventricles)
	Diencephalon	Thalamus, hypothalamus, epiphysis (pineal body)	Third ventricle
Midbrain (mesencephalon)	Midbrain	Optic lobes in fish and amphibians; superior and inferior colliculi	Cerebral aqueduct
Hindbrain (rhombencephalon)	Metencephalon Myelencephalon	Cerebellum, pons Medulla oblongata	Fourth ventricle
Spinal cord		Spinal cord	Central canal



(*a*) Shark (*b*) Codfish (*c*) Amphibian (frog) (*d*) Reptile (alligator)



(*e*) Bird (goose) (*f*) Mammal (horse)

Figure 40–7 Comparison of the brains of members of six vertebrate classes indicates basic similarities and evolutionary trends. Note that different parts of the brain may be specialized in the various groups. For example, the large olfactory lobes in the shark brain (*a*) are essential to this predator's highly developed sense of smell. During the course of evolution, the cerebrum and cerebellum have become larger and more complex. In the mammal (*f*) the cerebrum is the most prominent part of the brain; the cerebral cortex, the thin outer layer of the cerebrum, is highly convoluted (folded), which greatly increases its surface area.

THE MIDBRAIN

In fish and amphibians the midbrain is the most prominent part of the brain. In these animals the midbrain is the main association area. It receives incoming sensory information, integrates it, and sends decisions to appropriate motor nerves. The dorsal portion of the midbrain is differentiated to some degree in these lower vertebrates. For example, the **optic lobes,** specialized for visual interpretations, are part of the midbrain. In reptiles, birds, and mammals, many of the functions of the optic lobes are assumed by the cerebrum. In mammals, the midbrain consists of the **superior colliculi,** which are centers for visual reflexes such as pupil constriction, and the **inferior colliculi,** which are centers for certain auditory reflexes. The mammalian midbrain also contains the **red nucleus,** a center that integrates information regarding muscle tone and posture.

THE FOREBRAIN

The forebrain consists of the diencephalon and telencephalon. The diencephalon contains the thalamus and hypothalamus (Fig. 40–7). In all vertebrate classes the **thalamus** is a relay center for motor and sensory messages. In mammals all sensory messages (except those from the olfactory receptors) are delivered to the thalamus before being relayed to the sensory areas of the cerebrum.

Below the thalamus, the **hypothalamus** forms the floor of the third ventricle. The hypothalamus is the principal integration center for the regulation of the viscera (internal organs). It provides input to centers in the medulla and spinal cord that regulate activities such as heart rate, respiration, and digestive system function. The hypothalamus also links the nervous and endocrine systems. In fact, the pituitary gland (an important endocrine gland) hangs down from the hypothalamus. **Releasing hormones** produced by the hypothalamus regulate the secretion of several hormones produced by the anterior lobe of the pituitary gland. In reptiles, birds, and mammals, body temperature is controlled by the hypothalamus. The hypothalamus also regulates appetite and water balance, and is involved in emotional and sexual responses.

The telencephalon differentiates to form the cerebrum, and, in most vertebrate groups, the **olfactory bulbs.** The olfactory bulbs are concerned with the chemical sense of smell, the dominant sense in most aquatic and terrestrial vertebrates. In fact, much of brain development in vertebrates appears to be focused upon the integration of olfactory information. In fish and amphibians, the cerebrum is almost entirely devoted to the integration of such incoming sensory information.

Birds are an exception among the vertebrates in that their sense of smell is generally poorly developed. In them, however, a part of the cerebrum called the **corpus striatum** is greatly developed. This structure is thought to control the innate, stereotyped, yet complex action patterns characteristic of birds. Just above the corpus striatum is a region thought to govern learning in birds.

In most vertebrates the cerebrum is divided into right and left hemispheres. Most of the cerebrum is made of **white matter** consisting mainly of axons connecting various parts of the brain. In mammals and most reptiles there is a layer of **gray matter** called the **cerebral cortex** that makes up the outer portion of cerebral tissue. Certain reptiles possess a different type of cortex, not found in lower vertebrates, known as the **neopallium;** it serves as an association area, a region that links sensory and motor functions and is responsible for higher functions such as learning. The neopallium is much more extensive in mammals, making up the bulk of the cerebrum,[1] which becomes the most prominent part of the brain. In mammalian embryonic development, in fact, the cerebrum expands and grows backwards, covering many of the other brain structures.

In mammals the cerebrum is responsible for many of the functions that are performed by other parts of the brain in lower vertebrates. In particular, it has many complex association functions lacking in reptiles, amphibians, and fish. In small or simple mammals, the cerebral cortex may be smooth. However, in large, complex mammals, the surface area is greatly expanded by numerous folds called **convolutions,** or **gyri.** The furrows between them are called **sulci** when shallow and **fissures** when deep.

The Human Central Nervous System

As in other vertebrates, the human central nervous system (CNS) consists of the brain and spinal cord (Fig. 40–8). These soft, fragile organs are carefully protected. Both are encased in bone and wrapped in three layers of connective tissue collectively termed the **meninges.** The three meningeal layers are the tough, outer **dura mater,** the middle **arachnoid,** and the thin, vascular **pia mater** that adheres closely to the tissue of the brain and spinal cord (Fig. 40–9). **Meningitis** is a disease in which these coverings become infected and inflamed.

Between the arachnoid and the pia mater is the **subarachnoid space,** which contains **cerebrospinal fluid.** This shock-absorbing fluid cushions the brain and spinal cord and prevents them from bouncing against the bones of the vertebrae or skull with every movement. Cerebrospinal fluid also circulates through the ventricles of the brain. It is produced by special networks of capillaries called the **choroid plexuses** that project from the pia mater into the ventricles. After circulating through the CNS, cerebrospinal fluid is reabsorbed into the blood.

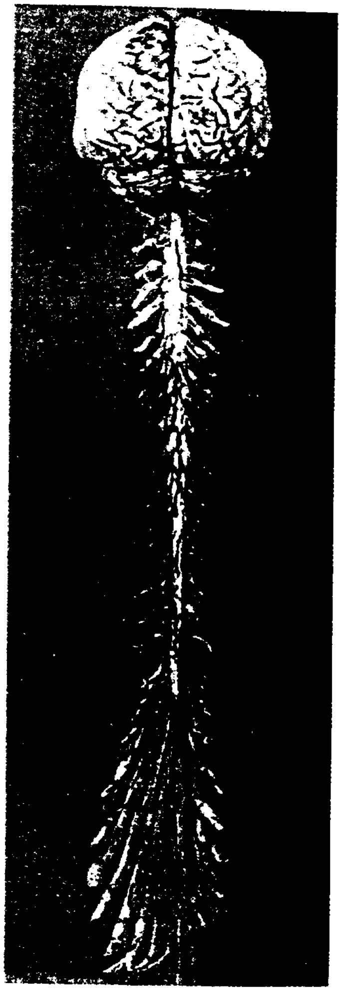


Figure 40–8 Photograph of human brain and spinal cord. The roots of the spinal nerves are still attached. Note the group of nerves that extend caudally from the lower region of the cord. Because they resemble a horse's tail they are referred to as the cauda equina. These nerves have been left undisturbed on the right but have been fanned out on the left. (Dissection by Dr. M. C. E. Hutchinson, Department of Anatomy, Guy's Hospital Medical School, London, England. From Williams and Warwick (eds.): *Gray's Anatomy.*)

THE SPINAL CORD

The tubular **spinal cord** extends from the base of the brain to the level of the second lumbar vertebra. It has two main functions: (1) to transmit impulses to and from the brain and (2) to control many reflex activities. A cross section through the spinal

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[1] In humans about 90% of the cerebral cortex is neopallium and consists of six distinct cell layers.

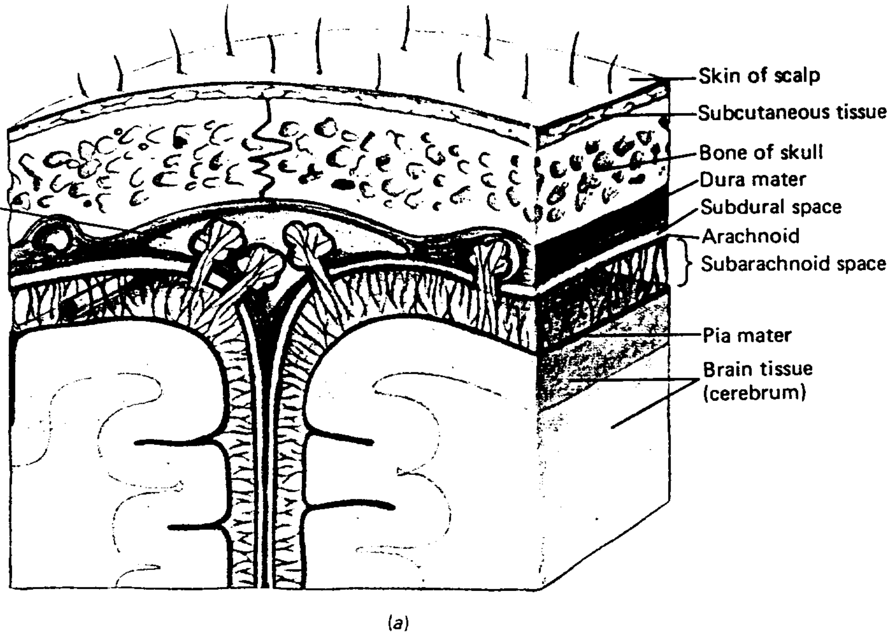
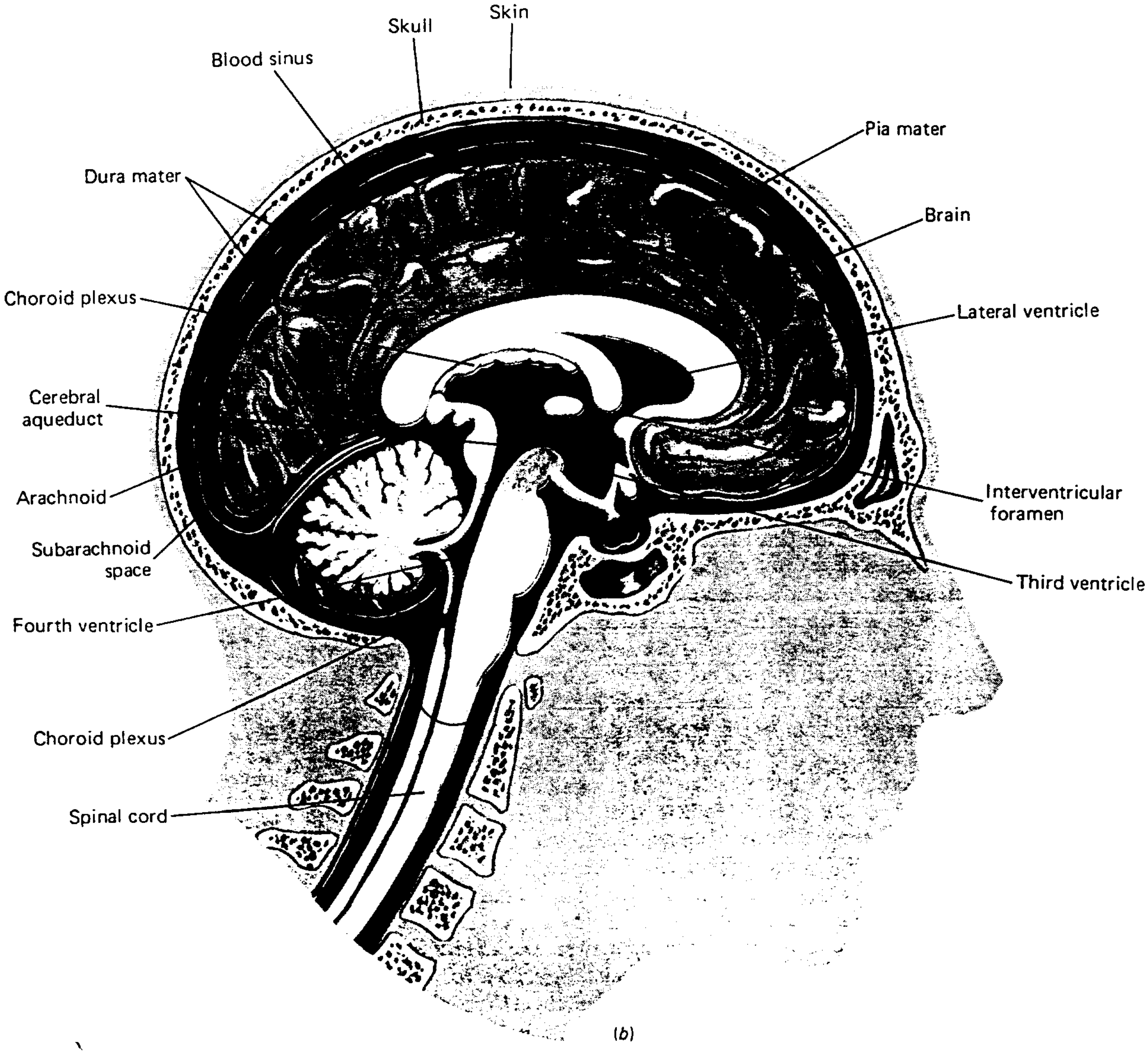
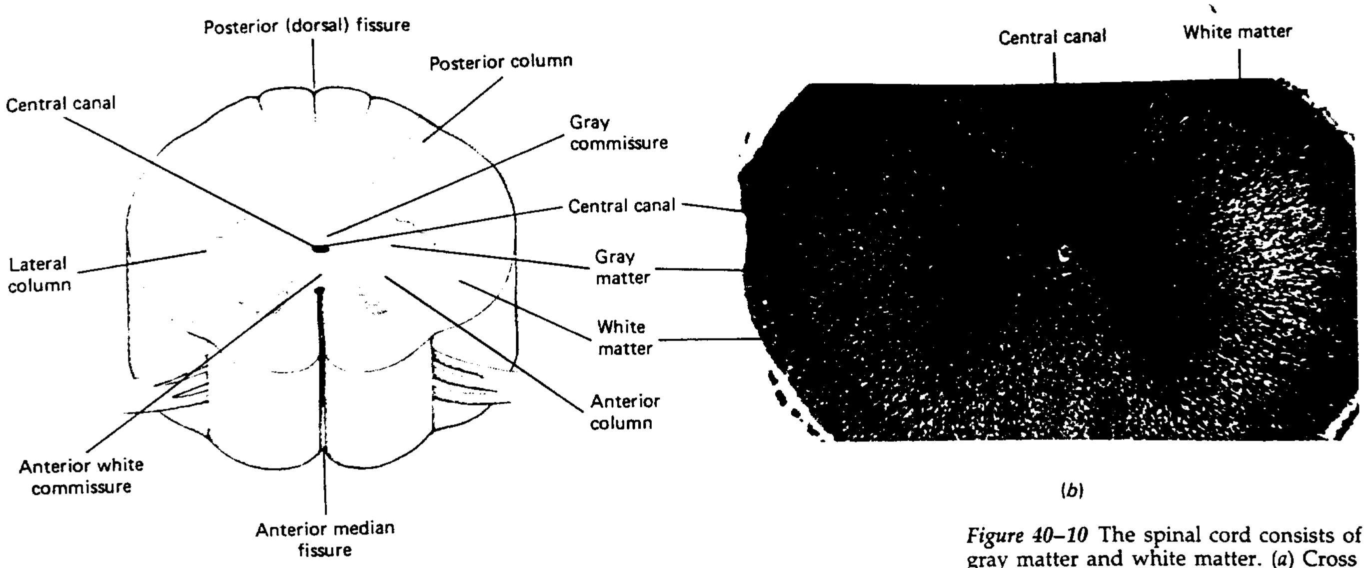


Figure 40–9 The brain is well protected by several coverings and by the cerebrospinal fluid. (*a*) The protective coverings of the brain. Note the large sinus shown between two layers of the dura mater. Blood leaving the brain flows into such sinuses and then circulates to the large jugular veins in the neck. (*b*) Circulation of the cerebrospinal fluid in the brain and spinal cord. This cushioning fluid is produced by the choroid plexuses in the walls of the ventricles. The fluid circulates throughout the ventricles and subarachnoid space. It is continuously produced and continuously reabsorbed into the blood of the dural sinuses.





(a)

(b)

Figure 40–10 The spinal cord consists of gray matter and white matter. (*a*) Cross section through the spinal cord. (*b*) Photomicrograph of a cross section through the spinal cord (approximately ×25).

cord reveals a small **central canal** surrounded by an area of gray matter shaped somewhat like the letter H (Fig. 40–10). Outside the gray matter, the spinal cord consists of white matter. The gray matter is composed of large masses of cell bodies, dendrites, and unmyelinated axons, as well as glial cells and blood vessels. The gray matter is subdivided into sections called **columns.** The white matter consists of myelinated axons arranged in bundles called **tracts,** or **pathways.** Long **ascending tracts** conduct impulses up the cord to the brain. For example, the **spinothalamic tracts,** located in the anterior and lateral columns of the white matter, conduct pain and temperature information from sensory neurons in the skin. The **pyramidal tracts** are descending tracts that convey impulses from the cerebrum to spinal motor nerves at various levels in the cord.

THE BRAIN

The structure and functions of the main parts of the human brain are summarized in Table 40–2. The human brain is illustrated in Figures 40–11 and 40–12. In humans, as in other mammals, the cerebral cortex is functionally divided into three areas: (1) the **sensory areas,** which receive incoming sensory information; (2) the **motor areas,** which control voluntary movement; and (3) the **association areas,** which link the sensory and motor areas and are responsible for thought, learning, language, memory, judgment, and personality.

Experimental evidence has established that there is a considerable amount of localization of function in the cortex. By surgically removing particular regions of the cortex from experimental animals, it has been possible to localize many functions exactly. Functions have also been localized by observing the paralysis or loss of sensation in a patient with a brain injury or tumor and then examining the brain after death to determine the location of the injury. During operations on the brain, surgeons have electrically stimulated small regions and observed which muscles contracted. Since brain surgery can be carried on under local anesthesia, a patient can be asked what sensations are felt when a particular region is stimulated. Curiously, the brain itself has no nerve endings for pain, so that stimulation of the cortex is not painful. Brain activity can be studied by measuring and recording the electrical potentials or "brain waves" given off by various parts of the brain when active.

By combining the data obtained in several ways, investigators have been able to map the human brain, locating the areas responsible for different functions. The posterior **occipital lobes** contain the visual centers. Stimulation of these areas, even by a blow on the back of the head, causes the sensation of light; their removal causes blindness. The centers for hearing are located in the lateral **temporal lobes** of the brain above the ear; stimulation by a blow causes a sensation of noise. Although removal of both auditory areas causes deafness, removal of one does not cause

TABLE 40–2
Divisions of the Human Brain

Division	*Description*	*Functions*
Medulla	Most inferior portion of the brain stem; continuous with spinal cord. Its white matter consists of nerve tracts passing between spinal cord and various parts of the brain; its gray matter consists of nuclei. Its cavity is the fourth ventricle.	Contains vital centers (within its reticular formation) that regulate heartbeat, respiration and blood pressure; contains reflex centers that control swallowing, coughing, sneezing, and vomiting; relays messages to other parts of the brain
Pons	Consists mainly of nerve tracts passing between the medulla and other parts of the brain; forms a bulge on anterior surface of brain stem; contains a respiratory center	Serves as a link to connect and integrate various parts of the brain; helps regulate respiration
Midbrain	Just superior to the pons; contains red nucleus; cavity is the cerebral aqueduct; posteriorly consists of superior and inferior colliculi	Superior colliculi mediate visual reflexes; inferior colliculi mediate auditory reflexes. Red nucleus integrates information regarding muscle tone and posture.
Diencephalon		
Thalamus	Located on each side of the third ventricle; consists of two masses of gray matter partly covered by white matter; contains many important nuclei	Main relay center conducting information between spinal cord and cerebrum. Incoming messages are sorted and partially interpreted within thalamic nuclei before being relayed to appropriate centers in the cerebrum.
Hypothalamus	Forms ventral floor of third ventricle; contains many nuclei. Optic chiasms mark crossing of the optic nerves. The pituitary stalk connects pituitary gland to hypothalamus.	Contains centers for control of body temperature, appetite, and fluid balance; secretes releasing hormones that regulate pituitary gland; helps control autonomic functions; involved in some emotional and sexual responses
Cerebellum	Second largest part of the brain; consists of two lateral cerebellar hemispheres; superior to the fourth ventricle	Responsible for smooth, coordinated movement; maintains posture and muscle tone; helps maintain equilibrium
Cerebrum	Largest, most prominent part of brain. Longitudinal fissure divides cerebrum into right and left hemispheres, each containing a lateral ventricle and each divided into six lobes: frontal, parietal, occipital, temporal, limbic, and insular.	Center of intellect, memory, language, and consciousness; receives and interprets sensory information from all of the organs; controls motor functions
Cerebral cortex	Convoluted, outer layer of gray matter, functionally divided into three areas:	
	Motor areas	Control voluntary movement and certain types of involuntary movement
	Sensory areas	Receive incoming sensory information from eyes, ears, touch and pressure receptors, and other sense organs. Sensory association areas interpret sensory information.
	Association areas	Responsible for thought, learning, language, judgment, and personality; store memories; connect sensory and motor areas
White matter	Consists of association fibers that interconnect neurons within the same hemisphere; fibers that interconnect the two hemispheres (e.g., corpus callosum), and fibers that are part of ascending and descending tracts. Basal ganglia are located within the white matter.	Link various areas of the brain

deafness in one ear but rather produces a decrease in the auditory acuity of both ears.

A fissure called the **central sulcus** crosses the top of each hemisphere from medial to lateral edge. This partially separates the **primary motor areas** in the **frontal lobes** controlling the skeletal muscles from the **parietal lobes** just behind the furrow. The parietal lobes are responsible for the sensations of heat, cold, touch, and pressure that result from stimulation of sense organs in the skin. In both motor and sensory areas there is a further specialization along the furrow from the top of the brain to the side. Neurons at the top of the cortex control the muscles of the

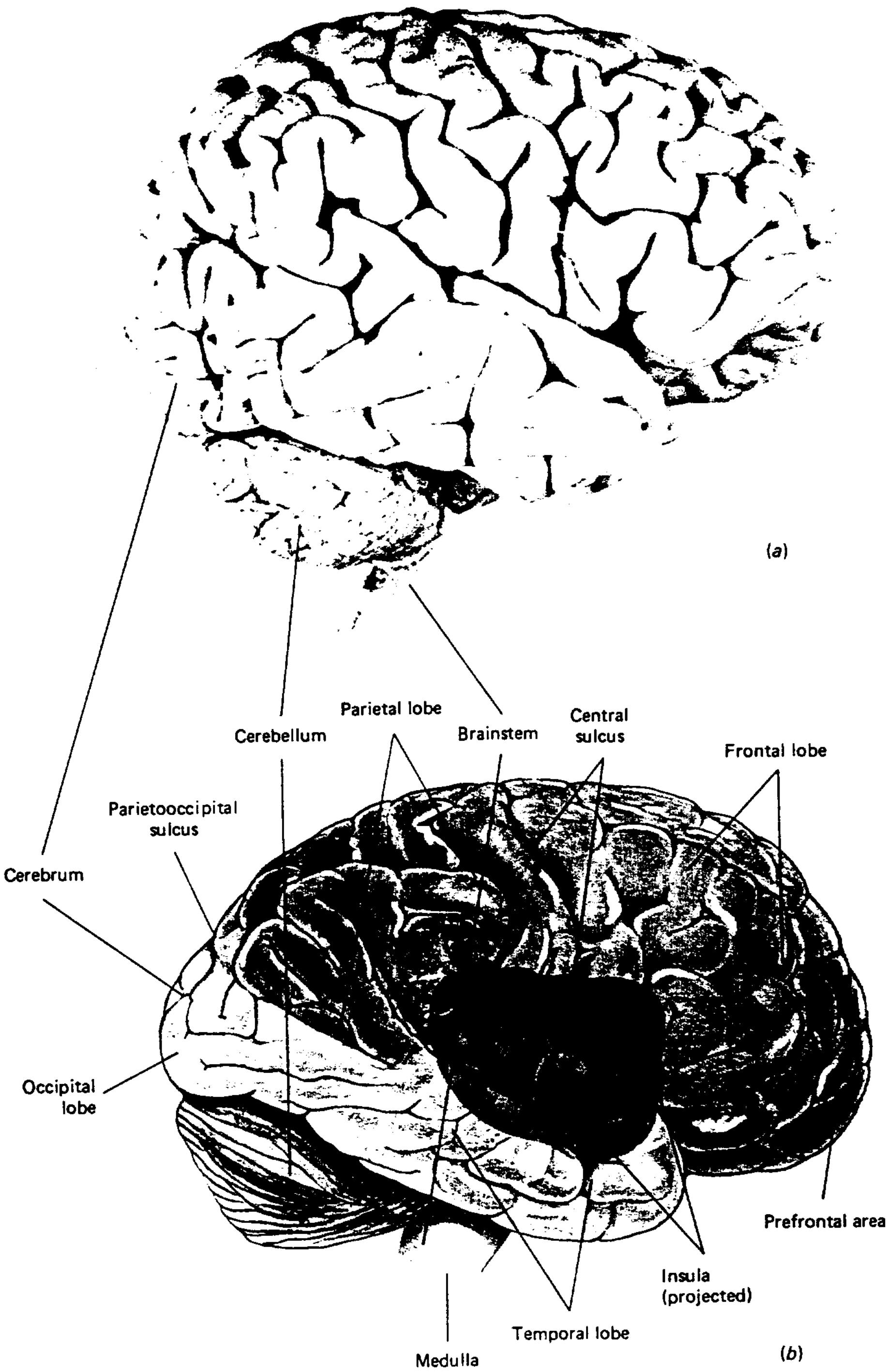


Figure 40–11 Structure of the human brain. (*a*) Photograph of the human brain, lateral view. Note that the cerebrum covers the diencephalon and part of the brain stem. (*b*) Lateral view of the human brain showing the lobes of the cerebrum. Part of the brain has been made transparent so that the underlying insular lobe can be located. ((*a*), from Williams and Warwick (eds.): *Gray's Anatomy*.)

feet; the neurons next in line control those of the shank, thigh, abdomen, and so on; and the neurons farthest around to the side control the muscles of the face.

The size of the motor area in the brain for any given part of the body is proportional not to the amount of muscle but to the elaborateness and intricacies of movement involved. Predictably, there are large areas for the control of the hands and face (Fig. 40–13). There is a similar relationship between the parts of the sensory area and the region of the skin from which it receives impulses. In connections between the body and the brain, not only is there a crossing of the fibers, so that one side of the brain controls the opposite side of the body, but a further "reversal" makes the uppermost part of the cortex control the lower extremities of the body.

When all the areas of known function are plotted, they cover almost all of the rat's cortex, a large part of the dog's, a moderate amount of the monkey's, but only a small part of the total surface of the human cortex (Fig. 40–14). The remaining

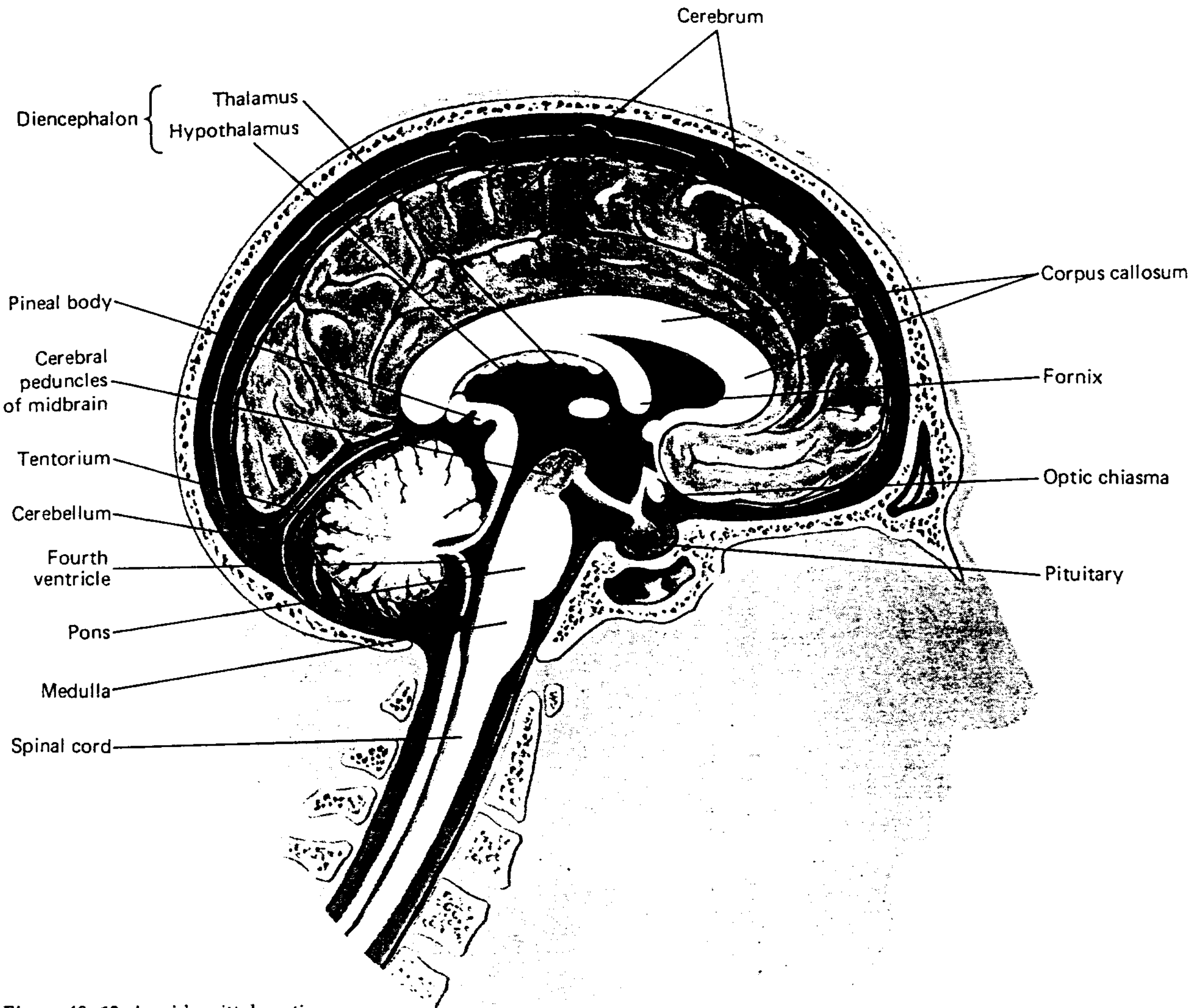


Figure 40–12 A midsagittal section through the brain. Note that in this type of section half of the brain is cut away so that structures normally covered by the cerebrum are exposed.

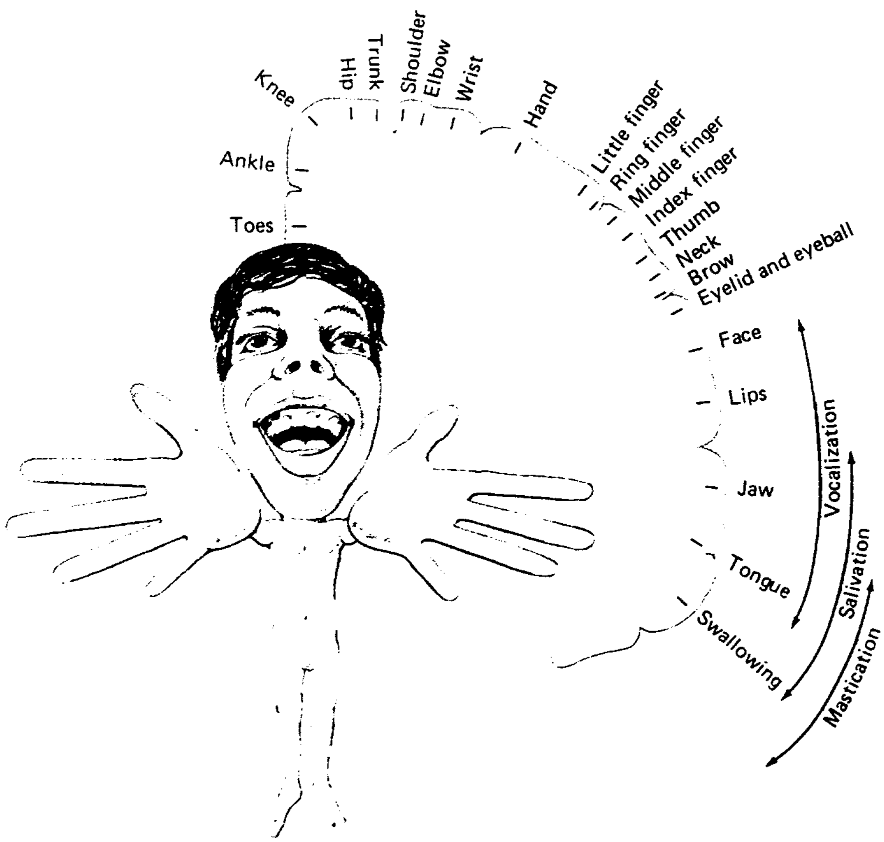


Figure 40–13 A cross section through the primary motor area (precentral gyrus) showing which area of cerebral cortex controls each body part. The figure (known as a motor homunculus) shown here is proportioned to reflect the amount of cerebral cortex devoted to control each body part. Note that more cortical tissue is devoted to controlling those body structures capable of skilled, complex movement.

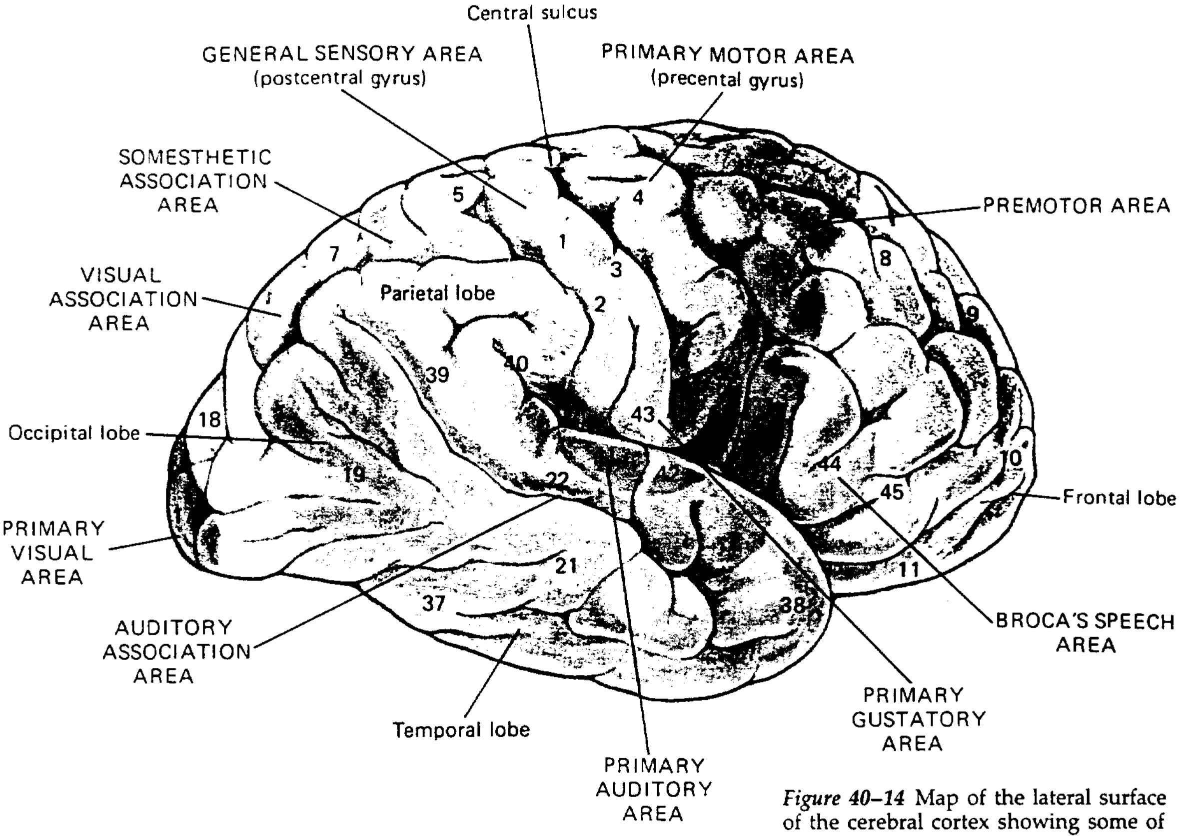


Figure 40–14 Map of the lateral surface of the cerebral cortex showing some of the functional areas. Areas *4*, *6*, and *8* are motor areas; areas *1*, *2*, *3*, *17*, *41*, *42*, and *43* are primary sensory areas; and areas *9*, *10*, *11*, *18*, *19*, *22*, *38*, *39*, and *40* are association areas.

cortical areas are the regions responsible for the higher intellectual faculties of memory, reasoning, learning, imagination and personality; these are the association areas. In some way, the association regions integrate all the diverse impulses constantly reaching the brain into a meaningful unit, so that the proper response is made. When disease or accident destroys the functioning of one or more association areas, **aphasia** may result, a condition in which the ability to recognize certain kinds of symbols is lost. The names of objects may be forgotten, for example, although their functions are remembered and understood.

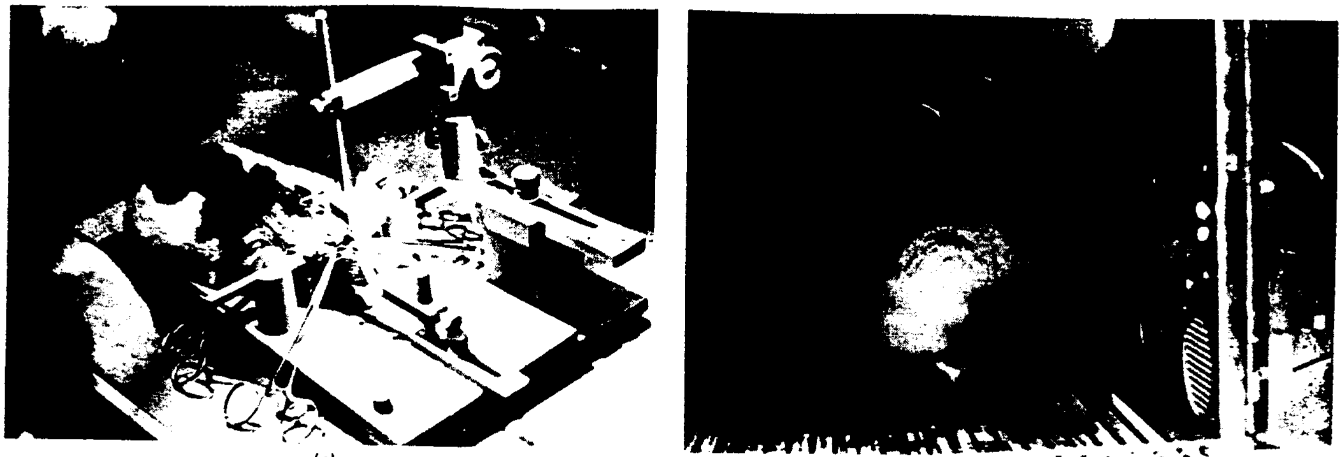
The Reticular Activating System

The **reticular activating system (RAS)** is a complex neural pathway within the brain stem and thalamus. It receives messages from neurons in the spinal cord and from many other parts of the nervous system and communicates with the cerebral cortex by complex neural circuits. The RAS is responsible for maintaining wakefulness. When the RAS is very active and sending many messages into the cerebrum, a state of mental and physical alertness is noted. When RAS activity slows, however, sleepiness results. If the RAS is severely damaged, a deep, permanent coma may result.

The Limbic System

The **limbic system,** another action system of the brain, consists of certain structures of the cerebrum and diencephalon. This system affects the emotional aspects of behavior, sexual behavior, biological rhythms, autonomic responses, and motivation, including feelings of pleasure and punishment. Stimulation of certain areas of the limbic system in an experimental animal results in increased general activity, and may cause fighting behavior or extreme rage.

When an electrode is implanted in the so-called reward center of the limbic system, a rat will press a lever that stimulates this area as many as 15,000 times per hour (Fig. 40–15). Stimulation of this area is apparently so rewarding that an animal will forego food and drink and may continue to press the lever until it drops from exhaustion. When an electrode is implanted in the punishment center of the limbic system, an experimental animal quickly learns to press a lever to *avoid* stimulation. The reward and punishment centers are thought to be important in influencing motivation and behavior.



(a) (b)

Figure 40–15 Electrodes can be implanted in the pleasure center of a rat's brain as shown in (*a*), so that when the rat depresses a lever, a stimulating electric current is delivered directly to the pleasure center, as seen in (*b*).

Brain Waves

Metabolism is invariably accompanied by electrical changes, and the electrical activity of the brain can be recorded by a device known as an **electroencephalograph.** To obtain a recording, called an **electroencephalogram** or **EEG,** electrodes are taped to different parts of the scalp and the activity of the underlying parts of the cortex is measured. The electroencephalograph shows that the brain is continuously active. As seen on the EEG, the most regular manifestations of activity, called **alpha waves,** come mainly from the visual areas in the occipital lobes when the person being tested is resting quietly with eyes closed. These waves occur rhythmically at the rate of 9 or 10 per second and have a potential of about 45 mV (Fig. 40–16).

When the eyes are opened, alpha waves disappear and are replaced by more rapid, irregular waves. That the latter are produced by objects seen can be demonstrated by presenting to the eyes some regular stimulus, such as a light blinking at regular intervals; brain waves with a similar rhythm will appear. As you are reading this biology text your brain should be emitting **beta waves,** which have a fast-frequency rhythm most characteristic of heightened mental activity such as information processing. During sleep, brain waves become slower and larger as the person falls into deeper unconsciousness; these slow, large waves associated with normal sleep are called **delta waves.** The dreams of a sleeping person are mirrored in flurries of irregular waves.

Certain brain diseases alter the character of the waves. Epileptics, for exam-

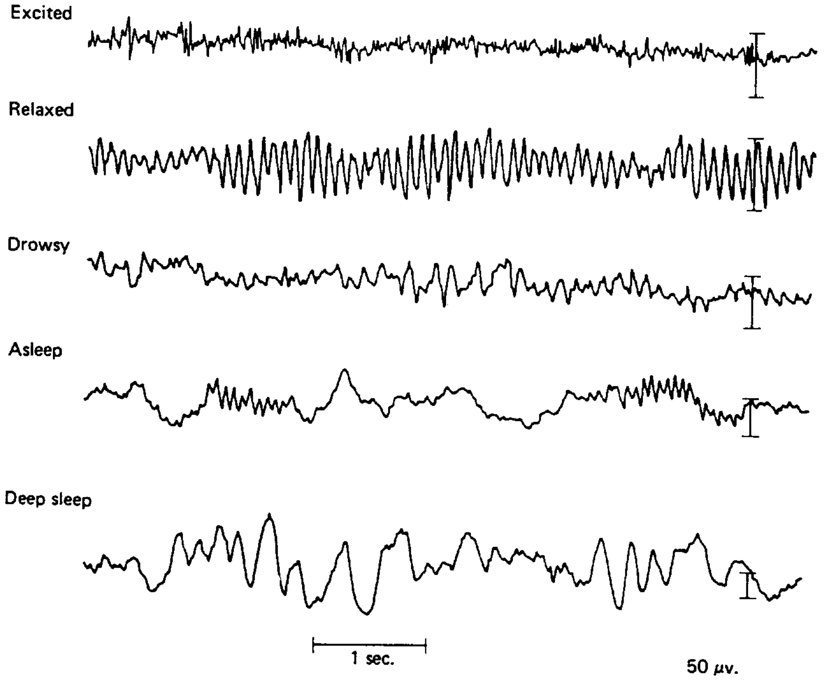


Figure 40–16 Electroencephalograms made while the subject was excited, relaxed, and in various stages of sleep. Recordings made during excitement show brain waves that are rapid and of small amplitude, whereas in sleep the waves are much slower and of greater amplitude. The regular waves characteristic of the relaxed state are called alpha waves. (From Jasper: In Penfield and Erickson: *Epilepsy and Cerebral Localization*)

ple, exhibit a distinctive, readily recognizable wave pattern, and even people who have never had an epileptic attack, but might under certain conditions, show similar abnormalities. The location of brain tumors or the sites of brain damage caused by a blow to the head, for instance, can sometimes be determined by noting the part of the brain showing abnormal waves.

Sleep

Sleep is a state of unconsciousness during which there is decreased electrical activity of the cerebral cortex, and from which a person can be aroused by external stimuli. When signals from the RAS slow down so that the cerebral cortex is deprived of activating input, a person may lapse into sleep. For this reason, we find it easy to go to sleep, even when we are not particularly tired, if there is nothing interesting to occupy the mind. But although we tend to be wakeful in the presence of attention-holding stimuli, there is a limit beyond which sleep is inevitable.

There are thought to be sleep centers in the brain stem. When stimulated, their neurons release the neurotransmitter **serotonin** (5-hydroxytryptamine, or 5HT). Serotonin is thought to inhibit signals passing through the RAS, thus inducing sleep.

Two main stages of sleep are recognized: non-REM and REM. The letters REM are an acronym for rapid eye movements. During **non-REM** sleep, sometimes called normal sleep, metabolic rate decreases, breathing slows, and blood pressure decreases. Delta waves, thought to be generated spontaneously by the cerebral cortex when it is not driven by impulses from other parts of the brain, are characteristic of non-REM sleep.

Every 90 minutes or so, a sleeping person enters the **REM** stage for a time. During this stage, which accounts for about one fourth of total sleep time, the eyes move rapidly about beneath the closed but fluttering lids. Brain waves change to a desynchronized pattern of beta waves. Sleep researchers claim that everyone dreams during REM sleep. Dreams may result from release of norepinephrine within the RAS, which generates stimulating impulses that are fed into the cerebral cortex.

Why sleep is necessary is not understood. Apparently only higher vertebrates with fairly well-developed cerebral cortices sleep. When a person stays awake for unusually long periods, fatigue and irritability result, and even routine tasks cannot be performed well. Perhaps certain waste products accumulate within the nervous system, and sleep gives the nervous system opportunity to dispose of them. When deprived of sleep for several days, a person becomes disoriented and may eventually exhibit psychotic symptoms.

Not only is normal non-REM sleep required, but REM sleep is apparently also essential. In sleep deprivation experiments performed with human volunteers, lack of REM sleep makes subjects anxious and irritable. After such experiments, when the subjects are permitted to sleep normally again, they go through a period when they spend more time than usual in the REM stage. Many types of drugs alter sleep patterns and affect the amount of REM sleep. For example, sleeping pills may increase the total sleeping time, but decrease the time in REM sleep. When a person stops taking such a drug, several weeks may be required before normal sleep patterns are reestablished.

Learning and Memory

Learning is a relatively long-lasting adaptive change in behavior resulting from experience. It is a modification of behavior that cannot be accounted for by sensory adaptation, central excitatory states, biological rhythms, motivational states, or maturation. Laboratory experiments have shown that members of every animal phylum can learn, and field observations indicate that learning is important for a wide variety of natural situations. Even some unicellular organisms that completely lack a nervous system are capable of some simple types of learning.

Learning involves the storage of information in the nervous system and its retrieval on demand. Many recent studies have attempted to discover the physical and chemical basis of memory and learning. Somewhere in the nervous system there must be stored a more-or-less permanent record of what has been learned that can be recalled on future occasions. This record has been termed the memory trace, or **engram**.

Electrical stimulation of the cerebral cortex of a patient undergoing brain surgery can cause vivid recollection of long-forgotten events. From this it had been inferred that the items of memory, the engrams, were filed away in specific parts of the brain. Some years ago, however, Karl Lashley investigated the retention of maze learning in rats by removing portions of the cortex after the rats had learned to solve various problems. Lashley's results indicated that the extent of the memory removed by the operation was a function of how much of the cortex was removed and not of what specific part of the cortex was removed. Lashley concluded that engrams were not sorted out at specific cortical sites but were in some way present throughout its substance. He speculated that memory might be a system of impulses in reverberating circuits (Chapter 39).

Just how the brain stores information and retrieves the memory on command is still the subject of speculation. According to current theory there are several levels of memory. **Short-term memory** involves recalling information for only a few moments. When you look up a telephone number in a directory, for example, you generally remember it just long enough to dial it. Should the line be busy and you turn your attention to another task before returning to try again, you would probably have to look up the number again. Short-term memory may depend upon circuits that continue to reverberate for several minutes until they fatigue, or until new signals that interfere with the old are received.

When a decision is made to store information in **long-term memory,** the brain apparently rehearses the material and then stores it in association with similar memories. Some investigators think that changes take place in the presynaptic knobs or postsynaptic neurons, which permanently facilitate the transmission of impulses within a newly formed neural circuit. Perhaps specific neurons become more sensitive to neurotransmitter. According to this theory, each time a memory is stored, a new neural pathway is facilitated. Such a facilitated circuit is the engram. Several other theories have been proposed involving glial cells, RNA, or protein as memory molecules, or rhythms of firing.

Several minutes are required for a memory to become consolidated in the long-term memory bank. Should a person suffer a brain concussion (or undergo electroshock therapy), memory of what happened immediately before the blow (or delivery of the shock) may be lost. The limbic system is important in processing stored information. When the hippocampus (part of the limbic system located on the lower inner margin of each cerebral hemisphere) is removed, a person can recall information stored in the past but loses the ability to convert new short-term memories to long-term memories. No new information can be stored.

Retrieval of information stored in the long-term memory is of considerable interest—especially to students. Some investigators think that once information is deposited in the long-term memory bank, it remains within the brain permanently. When you seem to forget something, the problem may be that you have actually forgotten the search routine that would permit you to retrieve that item for conscious use.

Effects of Environmental Experience on the Brain

Environmental experience can cause physical as well as chemical changes in brain structure. In one series of studies, a group of rats was provided with an enriched environment, while another group was placed in a deprived environment. Rats in the enriched environment were provided with toys, rat and human interaction, and opportunity to learn. Those in the deprived environment, while given sufficient food, water, and shelter, were deprived of intellectual stimulation and social interaction.

After several weeks rats from each group were killed and their brains were studied. Those exposed to enriched environments exhibited large cell bodies, greater numbers of glial cells, increased numbers of synaptic contacts, and biochemical changes. Some investigators reported that the cerebral cortex actually became thicker and heavier. Animals reared in a complex environment may also be able to process and remember information more quickly than those reared in a deprived environment.

Early environmental stimulation can also promote development of motor areas in the brain. For example, rats encouraged to exercise show increased cerebellar development. Such studies linking the development of the brain with environmental experience support the concept that early stimulation is important for the neural, motor, and intellectual development of children, as well.

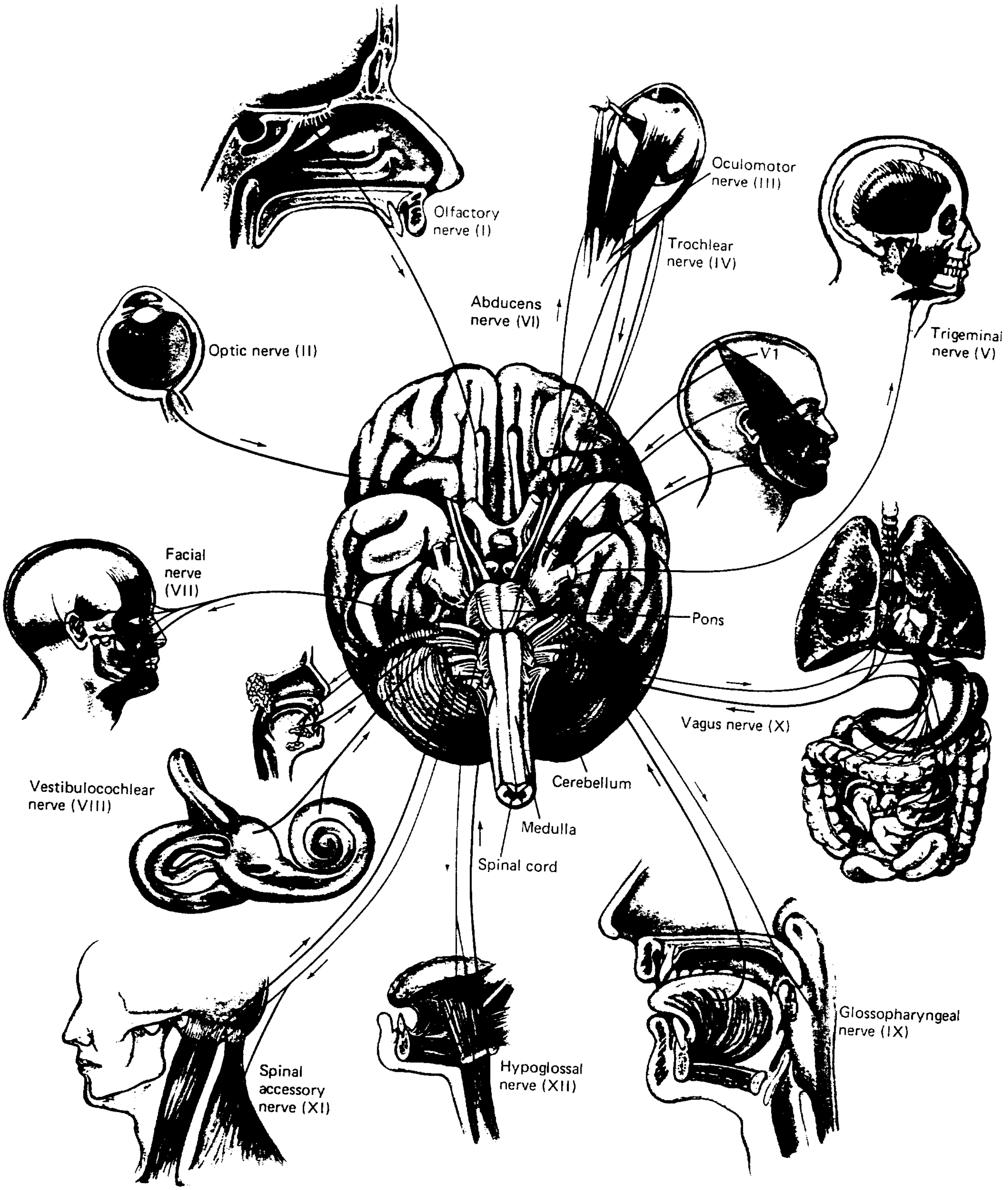


Figure 40–17 Ventral (basal) view of the human brain showing emergence of the cranial nerves. (Black indicates sensory fibers; color indicates motor fibers.)

The Peripheral Nervous System

The **peripheral nervous system (PNS)** consists of the sensory receptors, the nerves that link them with the CNS, and the nerves that link the CNS with the effectors.

THE CRANIAL NERVES

Twelve pairs of **cranial nerves** originate in various parts of the brain and innervate the sense organs, muscles, and glands of the head, as well as many of the internal organs (Fig. 40–17). The same 12 pairs, innervating homologous structures, are

TABLE 40–3
The Cranial Nerves of Mammals

Number	*Name*	*Origin of Sensory Fibers*	*Effector Innervated by Motor Fibers*
I	Olfactory	Olfactory epithelium of nose (smell)	None
II	Optic	Retina of eye (vision)	None
III	Oculomotor	Proprioceptors* of eyeball muscles (muscle sense)	Muscles that move eyeball (with IV and VI); muscles that change shape of lens; muscles that constrict pupil
IV	Trochlear	Proprioceptors of eyeball muscles	Other muscles that move eyeball
V	Trigeminal	Teeth and skin of face	Some of muscles used in chewing
VI	Abducens	Proprioceptors of eyeball muscles	Other muscles that move eyeball
VII	Facial	Taste buds of anterior part of tongue	Muscles used for facial expression; submaxillary and sublingual salivary glands
VIII	Auditory (vestibulocochlear)	Cochlea (hearing) and semicircular canals (senses of movement, balance, and rotation)	None
IX	Glossopharyngeal	Taste buds of posterior third of tongue, lining of pharynx	Parotid salivary gland; muscles of pharynx used in swallowing
X	Vagus	Nerve endings in many of the internal organs: lungs, stomach, aorta, larynx	Parasympathetic fibers to heart, stomach, small intestine, larynx, esophagus, and other organs
XI	Spinal accessory	Muscles of shoulder	Muscles of shoulder
XII	Hypoglossal	Muscles of tongue	Muscles of tongue

*Proprioceptors are receptors located in muscles, tendons, or joints that provide information about body position and movement.

found in all reptiles, birds, and mammals. Fish and amphibia have only the first 10 pairs. Some cranial nerves consist only of sensory neurons (nerves I, II, and VIII), some are composed mainly of motor neurons (nerves III, IV, VI, XI, and XII), and the others are mixed nerves, containing both sensory and motor neurons. The names of the cranial nerves and the structures they innervate are given in Table 40–3. For example, cranial nerve X, the vagus nerve (which forms part of the autonomic system), innervates the internal organs of the chest and upper abdomen.

THE SPINAL NERVES

In human beings, 31 symmetric pairs of **spinal nerves** emerge from the spinal cord (Fig. 40–18). All the spinal nerves are mixed nerves, containing both motor and sensory neurons. Each nerve innervates the receptors and effectors of one region of the body. Each spinal nerve has two **roots,** points of attachment with the cord. All of the sensory neurons enter the cord through the **dorsal root;** all motor fibers leave the cord through the **ventral root** (Fig. 40–19). Just before the dorsal root joins the spinal cord, it is marked by a swelling called the **spinal ganglion,** or **dorsal root**

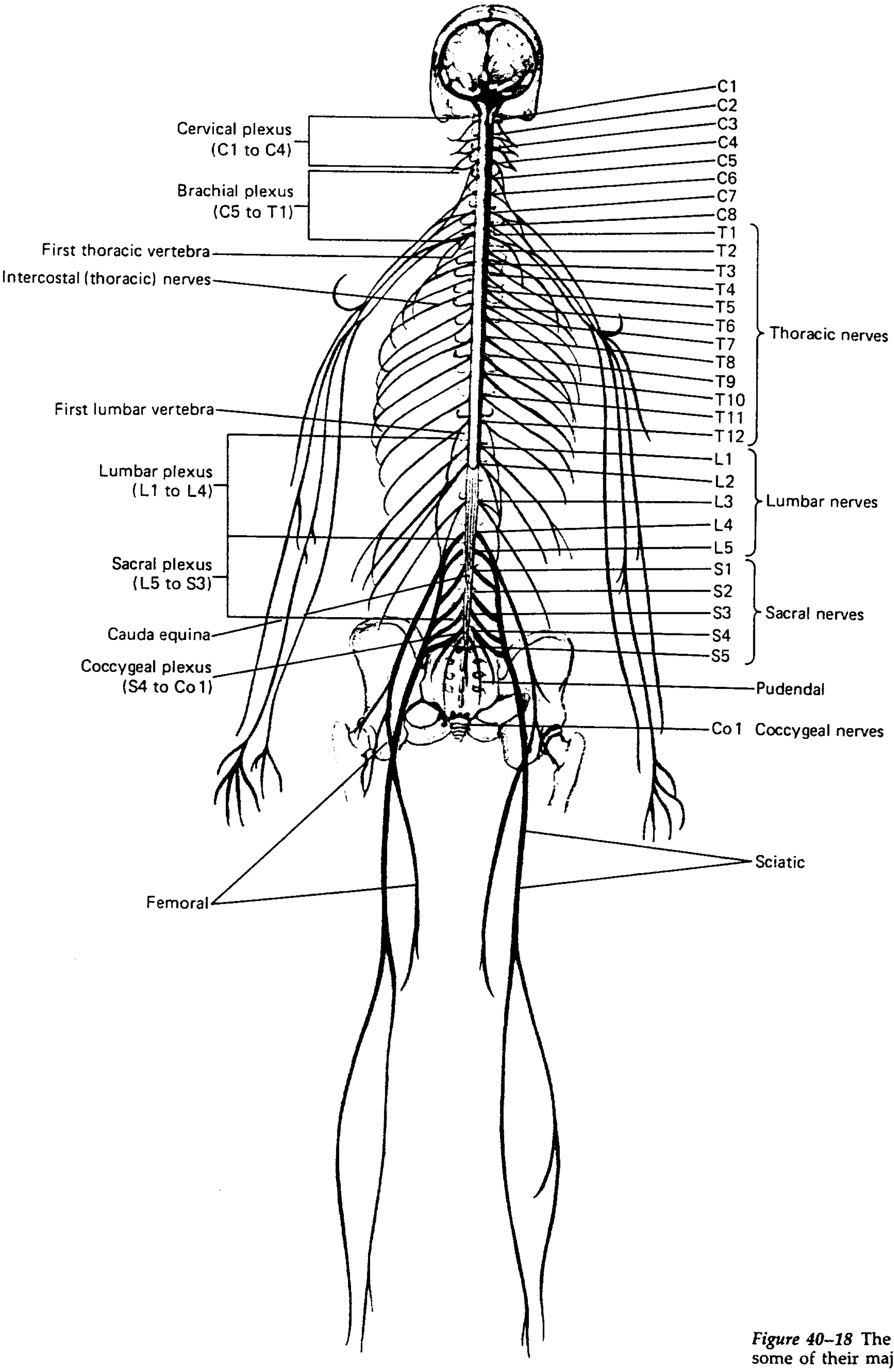


Figure 40–18 The spinal nerves and some of their major branches and plexuses.

ganglion, which consists of the cell bodies of the sensory neurons. Cell bodies of the motor neurons are located within the gray matter of the cord. Dorsal and ventral roots unite, forming the spinal nerve.

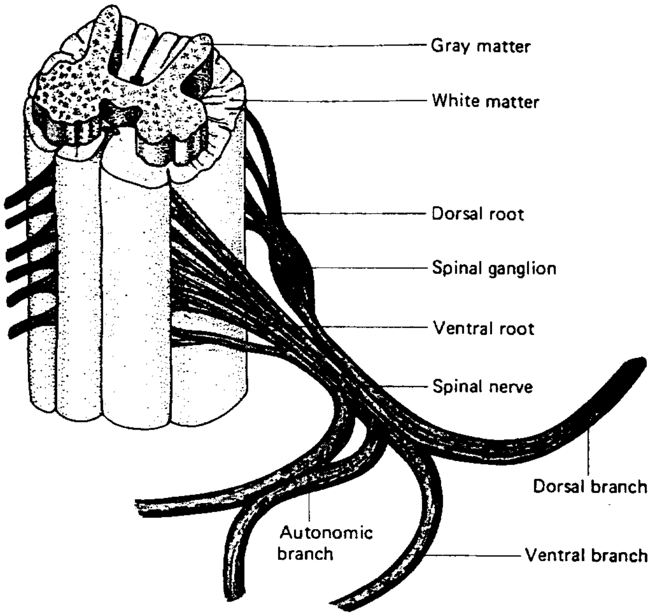
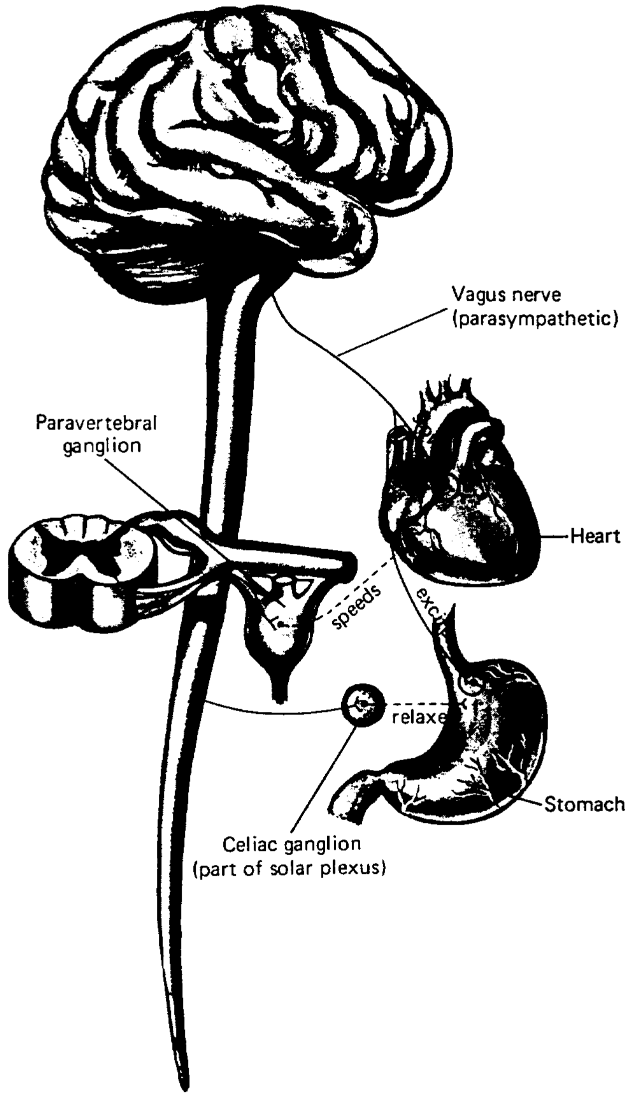


Figure 40–19 Dorsal and ventral roots emerge from the spinal cord and join to form a spinal nerve. The spinal nerve divides into several branches. (Black indicates sensory fibers; color indicates motor fibers.)

Figure 40–20 Dual innervation of the heart and stomach by sympathetic and parasympathetic nerves. (Sympathetic nerves are shown in color; postganglionic fibers are shown as dotted lines.)



If the dorsal root is severed, the part of the body innervated by that nerve suffers complete loss of sensation without paralysis of muscles. If the ventral root is cut, there is complete paralysis of muscles innervated by that nerve, but the senses of touch, pressure, temperature, pain, and kinesthesis (muscle sense) are not impaired.

Beyond the junction of the dorsal and ventral roots, each spinal nerve divides into branches. The dorsal branch serves the skin and muscles of the back. The ventral branch serves the skin and muscles of the sides and ventral part of the body. The autonomic branch innervates the viscera. The ventral branches of several spinal nerves form tangled networks called **plexuses** (Fig. 40–18). Within a plexus, the fibers of a spinal nerve may separate and then regroup with fibers that originated in other nerves. Thus, nerves emerging from a plexus consist of neurons that originated in several different spinal nerves. Among the principal plexuses are the cervical plexus, the brachial plexus, the lumbar plexus, and the sacral plexus.

THE AUTONOMIC SYSTEM

The **autonomic system** helps to maintain a steady state within the internal environment of the body. For example, it helps to maintain a constant body temperature and to regulate the rate of the heartbeat. Receptors within the viscera relay information through afferent nerves to the CNS, and the impulses are transmitted along efferent neurons to the appropriate muscles and glands.

The efferent portion of the autonomic system is subdivided into sympathetic and parasympathetic systems. Many organs are innervated by both (Figs. 40–20 and 40–21). In general, the **sympathetic system** mobilizes energy and enables the body to respond to stress (Table 40–4). Its nerves speed the heart's rate and force of

Figure 40–21 Sympathetic and parasympathetic nervous systems. For clarity, peripheral and visceral nerves of the sympathetic system are shown on separate sides of the cord. Complex as it appears, this diagram has been greatly simplified. (Colored lines represent sympathetic nerves, black lines represent parasympathetic nerves, and dotted lines represent postganglionic nerves.) See Table 40–5 for specific action of the nerves.

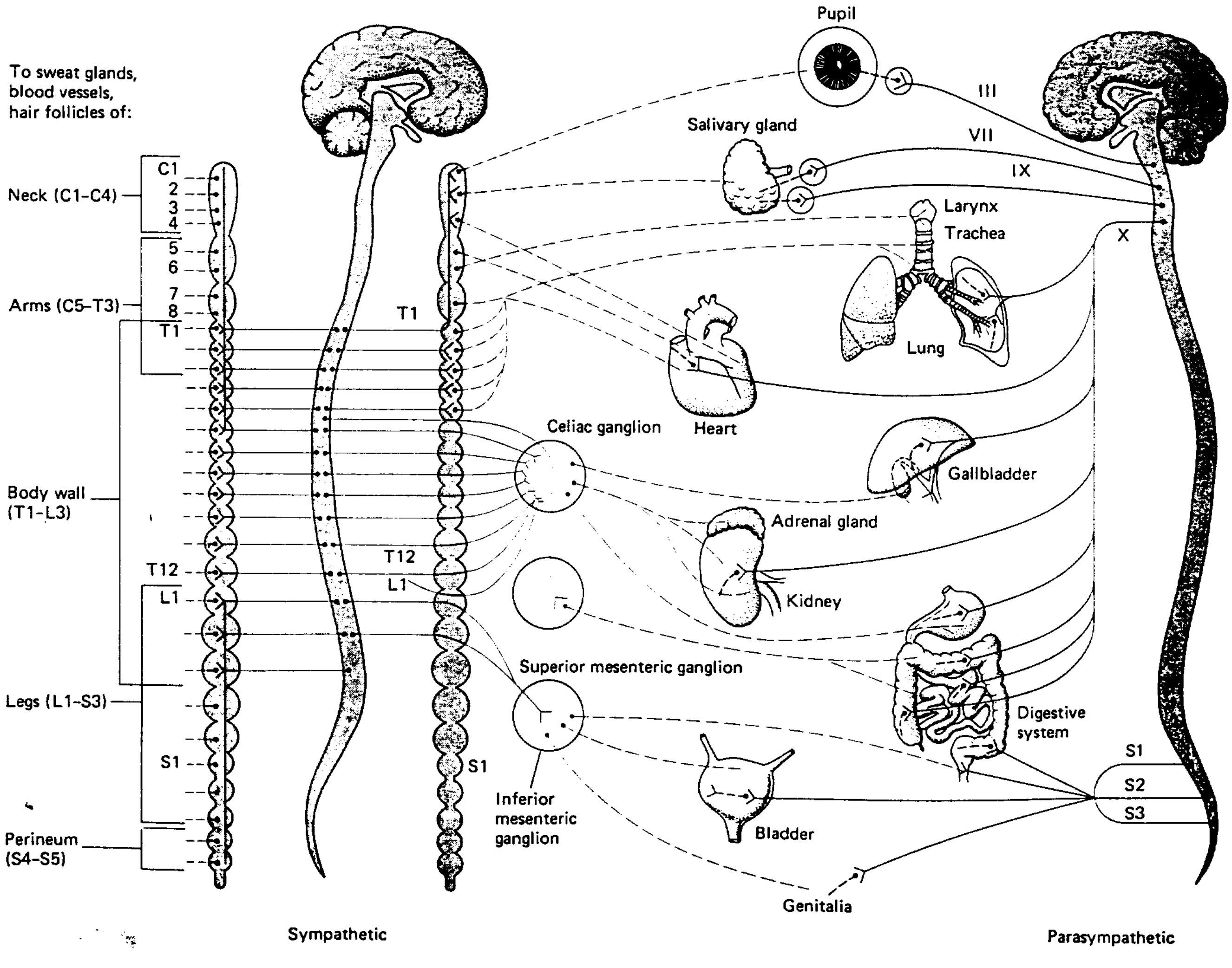


TABLE 40–4
Comparison of Sympathetic with Parasympathetic System

Characteristic	*Sympathetic System*	*Parasympathetic System*
General effect	Prepares body to cope with stressful situations	Restores body to resting state after stressful situation; actively maintains normal configuration of body functions.
Extent of effect	Widespread throughout body	Localized
Transmitter substance released at synapse with effector	Norepinephrine (usually)	Acetylcholine
Duration of effect	Lasting	Brief
Outflow from CNS	Thoracolumbar levels of spinal cord	Craniosacral levels (from brain and spinal cord)
Location of ganglia	Chain and collateral ganglia	Terminal ganglia
Number of postganglionic fibers with which each preganglionic fiber synapses	Many	Few

contraction, increase blood pressure, increase blood sugar concentration, and reroute blood circulation when required so that skeletal and cardiac muscles receive the added amounts of blood needed to support their maximum effort.

The **parasympathetic system** is most active in ordinary, restful situations. After a stressful episode, it decreases the heart rate, decreases blood pressure, and stimulates the digestive system to process food. The parasympathetic system is dominant during relaxation or calm, quiet activities. The sympathetic and parasympathetic systems work together to orchestrate the numerous complex activities continuously taking place within the body (Table 40–5).

Instead of utilizing a single efferent neuron, as in the somatic system, the autonomic system uses a relay of two neurons between the CNS and the effector. The first neuron, called the **preganglionic neuron,** has a cell body and dendrites within the CNS. Its axon, part of a peripheral nerve, ends by synapsing with a **postganglionic neuron.** The dendrites and cell body of the postganglionic neuron are located within a ganglion outside the CNS. Its axon terminates near or on the effector. The sympathetic ganglia are paired, and there is a chain of them on each side of the spinal cord from the neck to the abdomen, the **paravertebral sympathetic ganglion chain.** Some sympathetic preganglionic neurons do not end in these ganglia, but instead pass on to ganglia located in the abdomen close to the aorta and its major branches. These ganglia are known as **collateral ganglia.** Parasympathetic preganglionic neurons synapse with postganglionic neurons in **terminal ganglia** located near or within the walls of the organs they innervate.

The sympathetic and parasympathetic systems also differ in the neurotransmitters they release at the synapse with the effector. Sympathetic postganglionic neurons release norepinephrine (although preganglionic neurons secrete acetylcholine). Both preganglionic and postganglionic parasympathetic neurons secrete acetylcholine. Table 40–4 compares the sympathetic and parasympathetic systems.

The autonomic system got its name from the original belief that it was independent of the CNS, that is, autonomous. Physiologists have shown that this is not so, and that the hypothalamus and many other parts of the CNS help to regulate the autonomic system. Although the autonomic system usually functions automatically, its activities can be consciously influenced. **Biofeedback** provides visual or auditory evidence to a person concerning the status of an autonomic body function; for example, a tone may be sounded when blood pressure reaches a desirable level. Using such techniques, subjects have learned to control certain autonomic activities

TABLE 40–5
Comparison of Sympathetic and Parasympathetic Actions on Selected Effectors*

Effector	*Sympathetic Action*	*Parasympathetic Action*
Heart	Increases rate and strength of contraction	Decreases rate; no direct effect on strength of contraction
Bronchial tubes	Dilates	Constricts
Iris of eye	Dilates pupil	Constricts pupil
Sex organs	Constricts blood vessels; ejaculation	Dilates blood vessels; erection
Blood vessels	Generally constricts	No innervation for many
Sweat glands	Stimulates	No innervation
Intestine	Inhibits motility	Stimulates motility and secretion
Liver	Stimulates glycogenolysis (conversion of glycogen to glucose)	No effect
Adipose tissue	Stimulates free fatty acid release from fat cells	No effect
Adrenal medulla	Stimulates secretion of epinephrine and norepinephrine	No effect
Salivary glands	Stimulates thick, viscous secretion	Stimulates profuse, watery secretion

*Refer to Figure 40–21 as you study this table. Note that many other examples could be added to this list.

such as brain wave pattern, heart rate, blood pressure, and blood sugar level. Even certain abnormal heart rhythms can be consciously modified.

Effects of Drugs on the Nervous System

Among the most widely used drugs in the United States today are tranquilizers, sedatives, alcohol, stimulants, and antidepressants—all drugs that affect mood. Many of these drugs act by altering the levels of neurotransmitters within the brain. For example, amphetamines increase the amount of norepinephrine within the RAS, thus stimulating the CNS. Table 40–6 describes the effects of several types of commonly used and abused drugs.

Many mood drugs, including alcohol, are taken in order to induce a feeling of **euphoria,** or well-being. Habitual or prolonged use of almost any mood drug may result in **psychological dependence,** in which the user becomes emotionally dependent upon the drug. When deprived of it, the user may become irritable and feel unable to carry out normal activities.

Some drugs induce **tolerance** when they are taken continuously for several weeks. This means that increasingly large amounts are required in order to obtain the desired effect. Tolerance is thought to occur when the liver cells are stimulated to produce larger quantities of the enzymes that metabolize and inactivate the drug. Use of some drugs, such as heroin, alcohol, or barbiturates, may also result in **physical addiction,** in which physiological changes take place in body cells, making the user dependent upon the drug. When the drug is withheld, the addict suffers physical illness and characteristic **withdrawal symptoms.**

Physical addiction can also occur because certain drugs, such as morphine, have components similar to substances that body cells normally manufacture on their own. The continued use of such a drug, followed by sudden withdrawal, causes potentially dangerous physiological effects because the body's natural production of these substances has been depressed. It may be some time before homeostasis is reestablished.

TABLE 40–6
Effects of Some Commonly Used Drugs

Name of Drug	*Effect on Mood*	*Actions on Body*	*Dangers Associated with Abuse*
Barbiturates, e.g., Nembutal, Seconal	Sedative-hypnotic;[*] "downers"	Inhibit impulse conduction in RAS: depress CNS, skeletal muscle, and heart; depress respiration; lower blood pressure; cause decrease in REM sleep	Tolerance, physical dependence, death from overdose, especially in combination with alcohol
Methaqualone, e.g., Quāālude, Sopor	Hypnotic	Depresses CNS; depresses certain polysynaptic spinal reflexes	Tolerance, physical dependence, convulsions, death
Meprobamate, e.g., Equanil, Miltown (minor tranquilizers)	Antianxiety drug;[†] induces calmness	Causes decrease in REM sleep; relaxes skeletal muscle; depresses CNS	Tolerance, physical dependence; coma and death from overdose
Diazepam, e.g., Valium; chlordiazepoxide, e.g., Librium (mild tranquilizers)	Reduce anxiety	May reduce rate of impulse firing in limbic system; relax skeletal muscle	Minor EEG abnormalities with chronic use; physical dependence with very large doses
Phenothiazines, e.g., chlorpromazine (major tranquilizers)	Antipsychotic; highly effective in controlling symptoms of psychotic patients	Affect levels of catecholamines in brain (block dopamine receptors, inhibit uptake of NE,[**] dopamine, and serotonin); depress neurons in RAS and basal ganglia	Prolonged intake may result in parkinsonian symptoms
Antidepressants, e.g., Elavil	Elevate mood; relieve depression	Block uptake of NE so that more is available to stimulate nervous system	Central and peripheral neurological disturbances; uncoordination; interference with normal cardiovascular function
Alcohol	Euphoria; relaxation; release of inhibitions	Depresses CNS; impairs vision, coordination, judgment; lengthens reaction time	Physical dependence; damage to pancreas; liver cirrhosis; possible brain damage
Narcotic analgesics, e.g., morphine, heroin	Euphoria; reduction of pain	Depress CNS; depress reflexes; constrict pupils; impair coordination; block action of pain-transmitting neurons	Tolerance; physical dependence; convulsions; death from overdose

[*] Sedatives reduce anxiety; hypnotics induce sleep.
[†] Antianxiety drugs reduce anxiety but are less likely to cause drowsiness than the more potent sedative-hypnotics.
[**] NE = norepinephrine; MAO = monoamine oxidase.

SUMMARY

I. Among invertebrates, nerve nets and radial nervous systems are typical of radially symmetric animals, and bilateral nervous systems are characteristic of bilaterally symmetric animals.
  A. A nerve net consists of nerve cells scattered throughout the body; no CNS is present. Response of these animals to stimuli is generally slow and imprecise.
  B. Echinoderms typically have a nerve ring and nerves that extend into various parts of the body.
  C. In a bilateral nervous system there is a concentration of nerve cells to form nerves, nerve cords, ganglia, and (in complex forms) a brain. There is also an increase in numbers of neurons, especially of the association neurons. This permits greater precision and a wider range of responses.

II. In the vertebrate embryo the brain and spinal cord arise from the neural tube. The anterior end of the tube differentiates into forebrain, midbrain, and hindbrain.
  A. The hindbrain subdivides into the metencephalon and myelencephalon.
    1. The myelencephalon develops into the medulla, which contains the vital centers and other reflex centers.
    2. The metencephalon gives rise to the cerebellum and pons.
      a. The cerebellum is responsible for muscle tone, posture, and equilibrium.
      b. The pons connects various parts of the brain.
  B. The midbrain is the largest part of the brain in fish and amphibians. It is their main association area, linking sensory input and motor output. In reptiles, birds, and mammals the midbrain has a lesser function and is used as a center for certain visual and auditory reflexes. It also contains the red nucleus that integrates information about muscle tone and posture.
  C. The forebrain differentiates to form the diencephalon and telencephalon.

Name of Drug	*Effect on Mood*	*Actions on Body*	*Dangers Associated with Abuse*
Cocaine	Euphoria; excitation followed by depression	CNS stimulation followed by depression; autonomic stimulation; dilates pupils; local anesthesia	Mental impairment; convulsions; hallucinations; unconsciousness; death from overdose
Amphetamines, e.g., Dexedrine	Euphoria; stimulant; hyperactivity; "uppers," "pep pills"	Since chemical structure is almost identical with that of NE, compete with NE for receptor sites; block reuptake of NE into neurons; inhibit MAO;** enhance flow of impulses in RAS; increase heart rate; raise blood pressure; dilate pupils	Tolerance; possible physical dependence; hallucinations; death from overdose
Caffeine	Increases mental alertness; decreases fatigue and drowsiness	Acts upon cerebral cortex; relaxes smooth muscle; stimulates cardiac and skeletal muscle; increases urine volume (diuretic effect)	Very large doses stimulate centers in the medulla (may slow the heart); toxic doses may cause convulsions.
Nicotine	Psychological effect of lessening tension	Stimulates sympathetic nervous system; combines with receptors in the postsynaptic neurons of autonomic system; effect similar to that of acetylcholine, but large amounts result in blocking transmission; stimulates synthesis of lipid in arterial wall	Tolerance; physical dependence; stimulates development of atherosclerosis
LSD (lysergic acid diethylamide)	Overexcitation; sensory distortions; hallucinations	Alters levels of transmitters in brain (may inhibit serotonin and increase NE); potent CNS stimulator; dilates pupils (may appear unequal in size); increases heart rate; raises blood pressure	Irrational behavior
Marijuana	Euphoria	Impairs coordination; impairs depth perception and alters sense of timing; inflames eyes, peripheral vasodilation; exact mode of action unknown	In large doses, sensory distortions, hallucinations; evidence of lowered sperm counts and testosterone (male hormone) levels

1. The diencephalon develops into thalamus and hypothalamus.
    a. The thalamus is a relay center for motor and sensory information.
    b. The hypothalamus controls autonomic functions, links nervous and endocrine systems, controls temperature, appetite, and fluid balance, and is involved in some emotional and sexual responses.
2. The telencephalon develops into the cerebrum and olfactory bulbs.
    a. In fish and amphibians the cerebrum functions mainly to integrate incoming sensory information.
    b. In birds the corpus striatum controls stereotyped but complex behavior patterns. Another part of the cerebrum is thought to govern learning.
    c. The simplest animals possessing a neopallium are certain reptiles. The neopallium is present in birds and mammals, and accounts for about 90% of the cerebral cortex in the human brain. In mammals the cerebrum has complex association functions.

III. The human brain and spinal cord are protected by bone and by three meninges, and are cushioned by cerebrospinal fluid.
   A. The spinal cord consists of ascending tracts, which transmit information to the brain, and descending tracts, which transmit information from the brain. Its gray matter consists of many nuclei that serve as reflex centers.
   B. The human cerebral cortex consists of motor areas, which control voluntary movement; sensory areas, which receive incoming sensory information; and association areas, which link sensory and motor areas and also are responsible for learning, language, thought, and judgment.
      1. The reticular activating system is responsible for maintaining consciousness.
      2. The limbic system affects the emotional aspects of behavior, motivation, sexual behavior, autonomic responses, and biological rhythms.
      3. Alpha wave patterns are characteristic of relaxed

states, beta wave patterns of heightened mental activity, and delta waves of non-REM sleep.
4. Metabolic rate slows during non-REM sleep. REM sleep is characterized by dreaming.
5. Short-term memory may depend upon reverberating circuits in the brain. Mechanisms of long-term memory are not understood.
6. Environmental experience can cause physical and chemical changes in the brain.

IV. The peripheral nervous system consists of sensory receptors and nerves, including the cranial and spinal nerves and their branches.

V. The autonomic system regulates the internal activities of the body.
- *A.* The sympathetic system enables the body to respond to stressful situations.
- *B.* The parasympathetic system influences organs to conserve and restore energy.

VI. Many drugs alter mood by increasing or decreasing the concentrations of specific neurotransmitters within the brain.

POST-TEST

1. The simplest organized nervous system is the ________ ________ found in *Hydra* and other cnidarians.
2. ________ nerves transmit impulses toward a central nervous system whereas ________ nerves transmit impulses away from the CNS.
3. The cerebral ganglia in a flatworm serve as a simple ________.
4. In addition to cerebral ganglia, mollusks typically have ________ ganglia located among the organs and ________ ganglia located in the foot.
5. In vertebrates the embryonic neural tube expands anteriorly to form the ________ and develops posteriorly into the ________ ________.
6. The medulla, pons, and midbrain make up the ________ ________.
7. The fourth ventricle, located within the ________, communicates with the ________ ________ of the spinal cord.

For each group, select the most appropriate answer from Column B for the description given in Column A.

Column A

8. Most prominent part of amphibian brain
9. Links nervous and endocrine systems
10. Most prominent part of mammalian brain
11. Coordinates muscle activity
12. Contains vital centers

Column B

a. Cerebellum
b. Cerebrum
c. Midbrain
d. Medulla
e. Hypothalamus

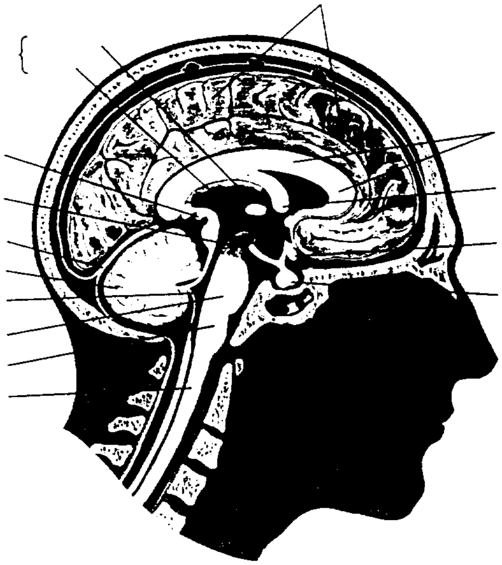
13. Controls innate, complex action patterns in birds
14. Convey voluntary motor impulses from cerebrum down spinal cord
15. Shallow furrows between gyri
16. Makes up most of human cerebral cortex
17. Layers of connective tissue that protect CNS

a. Neopallium
b. Corpus striatum
c. Meninges
d. Pyramidal tracts
e. Sulci

18. Contains primary motor areas
19. Action system concerned with emotional behavior and with reward and punishment
20. Contains the visual centers
21. Maintains wakefulness

a. Limbic system
b. RAS
c. Frontal lobe
d. Temporal lobe
e. None of the above

22. As you answer these questions your brain should be emitting ________ waves.
23. Dreaming takes place during ________ sleep.
24. Cranial nerve X, the ________ nerve, innervates the ________.
25. The sympathetic nervous system mobilizes ________ and helps the body respond to ________.
26. Sensory nerves enter the spinal cord through the ________ root.
27. Some drugs induce tolerance, which means that ________.
28. Label the following diagram. (Refer to Fig. 40–12 as necessary.)



REVIEW QUESTIONS

1. Compare the nervous system of a hydra with that of a planarian flatworm.
2. Compare the flatworm nervous system with that of a vertebrate.
3. Describe characteristics of the bilateral nervous system, and compare it with the radial system.
4. The forebrain, midbrain, and hindbrain give rise to which parts of the brain?
5. What are the functions of each of the following structures in the human brain: medulla, midbrain, cerebellum, thalamus, hypothalamus, and cerebrum.
6. Compare the fish midbrain and cerebrum with that of the mammal.
7. Describe the protective coverings of the human CNS, and give the function of the cerebrospinal fluid.
8. Cite experimental evidence supporting the view that environmental experience can alter the brain.
9. Contrast the structure and function of the sympathetic system with that of the parasympathetic system.
10. Describe how each of the following drugs affects the CNS:
    - *a.* alcohol
    - *b.* phenothiazines
    - *c.* barbiturates
    - *d.* amphetamines

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Sense Organs

OUTLINE

- *I.* What is a sense organ?
- *II.* How sense organs are classified
- *III.* How sense organs work
- *IV.* Sensory coding and sensation
- *V.* Mechanoreceptors
  - *A.* Tactile receptors
  - *B.* Gravity receptors: statocysts
  - *C.* Lateral line organs
  - *D.* Proprioceptors
  - *E.* Equilibrium
    - *1.* Halteres in flies
    - *2.* The labyrinth of the vertebrate ear
  - *F.* Auditory receptors
- *VI.* Chemoreceptors: taste and smell
  - *A.* The sense of taste in insects
  - *B.* The human sense of taste
  - *C.* The sense of smell
- *VII.* Thermoreceptors
- *VIII.* Photoreceptors
  - *A.* The human eye
    - *1.* The chemistry of vision
    - *2.* Color vision
    - *3.* Binocular vision and depth perception
    - *4.* Defects in vision
  - *B.* The compound eye

LEARNING OBJECTIVES

After you have read this chapter you should be able to:

1. Distinguish among exteroceptors, proprioceptors, and interoceptors, and explain the importance of each group.
2. Name the five types of receptors that are classified according to the types of energy to which they respond. Give examples of specific sense organs of each type.
3. Describe how a sense organ functions, including definitions of energy transduction, receptor potential, and adaptation in your answer.
4. Describe how the following mechanoreceptors work: tactile receptors, statocysts, lateral line organs, and proprioceptors.
5. Compare the function of the saccule and utricle with that of the semicircular canals in maintaining equilibrium.
6. Trace the path taken by sound waves through the structures of the ear, and explain how the organ of Corti is able to function as an auditory receptor.
7. Describe the receptors of taste and smell.
8. Describe the ways thermoreceptors are advantageous in various types of animals.
9. Label the structures of the human eye on a diagram, and give the functions of each of the accessory structures.
10. Name the two types of photoreceptors in the human retina, and compare their functions, taking into account the role of rhodopsin.
11. Compare the vertebrate eye with the compound eye of an insect.

Sense organs link organisms with the outside world and enable them to receive information about their environment. The kinds of sense organs an animal has determine just how it perceives the world. We humans live in a world of rich colors, multishapes, and varied sounds. But we cannot hear the high-pitched whistles audible to dogs and cats, or the ultrasonic echoes by which bats navigate (Fig. 41-1). Nor do we ordinarily recognize our friends by their distinctive odors. And although vision is our dominant and most refined sense, we are blind to the ultraviolet hues that light up the world for insects.

What Is a Sense Organ?

A **sense organ** is a specialized structure consisting of one or more **receptor cells** and, sometimes, **accessory cells.** For example, the receptor cells of the human eye are the rod and cone cells located in the retina. The accessory structures include the cornea, lens, iris, and ciliary muscles. Accessory structures enhance the versatility of the sense organ, but in some instances may limit its performance. The lens, for example, enhances the ability of the eye to see by adjusting the focus of the light rays. On the other hand, the lens filters out ultraviolet light before it reaches the retina, so we cannot see it. The cells in the retina can respond to light of this wavelength, however.

Receptor cells may be either neuron endings or specialized cells that are in close contact with neurons. Human taste buds are modified epithelial cells connected to one or more neurons.

How Sense Organs Are Classified

Sense organs can be classified in more than one way. One type of classification focuses on the location of the stimuli affecting the sense organ—the exteroceptors, proprioceptors, and interoceptors. Sense organs that reveal the outside world to

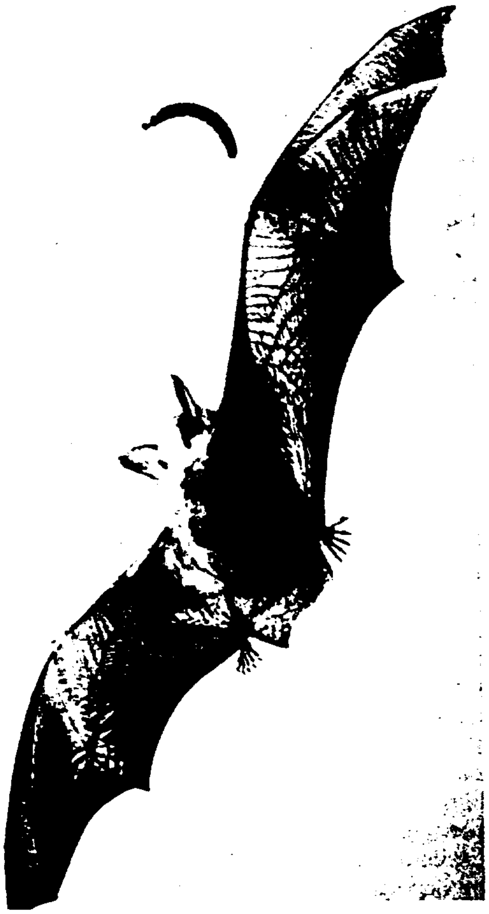


Figure 41–1 Bats navigate by ultrasonic echoes inaudible to the human ear. (Courtesy of Frederic Webster.)

the organism are known as **exteroceptors.** They enable an animal to search for food, find and attract a mate, find shelter, detect enemies, recognize friends, explore the world, and even learn. Exteroceptors are obviously of great importance to the survival of the individual and of the species. **Proprioceptors** are sense organs within muscles, tendons, and joints that enable the animal to perceive the position of the arms, legs, head, and other body parts, along with the orientation of the body as a whole. With the help of our proprioceptors we humans can get dressed or eat in the dark.

Interoceptors are sense organs *within* body organs that detect changes in pH, osmotic pressure, body temperature, and the chemical composition of the blood. We are usually not conscious of messages sent to the CNS by these receptors as they play a continuous role in maintaining homeostasis. We do become aware of their activity when they enable us to perceive such diverse internal conditions as thirst, hunger, nausea, pain, and orgasm. Interoceptors are described not in this chapter but in conjunction with discussions of blood pressure, temperature regulation, respiration, and other specific body functions.

Another way that sense organs can be classified is according to the type of energy to which they respond. **Mechanoreceptors** respond to mechanical energy—touch, pressure, gravity, stretching, or movement. **Chemoreceptors** respond to certain chemical stimuli, while **photoreceptors** detect light energy. **Thermoreceptors** respond to heat or cold. Some fish have well-developed **electroreceptors,** which detect electrical energy.

Traditionally, humans are said to have five senses: touch, smell, taste, sight, and hearing. These are all made possible by sense organs that are classified as exteroceptors. Today, balance is also recognized as a sense, and touch is viewed as a compound sense that involves detection of pressure, pain, and temperature. In this chapter we will also consider some proprioceptors that enable us to sense muscle tension and joint position.

How Sense Organs Work

All receptor cells absorb energy, **transduce** (convert) that energy into electrical energy, and produce a receptor potential (Fig. 41–2). In its capacity as a detector or sensor, a receptor receives a small amount of energy from the environment. Each kind of receptor is especially sensitive to one particular form of energy. Rods and cones in the retina absorb the energy of photons. Temperature receptors respond to radiant energy transferred by radiation, conduction, or convection. Electricity is detected by the energy of electrons. Taste buds and olfactory cells detect the change in energy accompanying the binding of specific molecules to their chemical receptors.

Receptor cells are remarkably sensitive to appropriate stimuli. The rods and cones of the eye, for example, are stimulated by an extremely faint beam of light, whereas only a very strong light can stimulate the optic nerve directly. The negligible amount of vinegar that can be tasted, or the amount of vanilla that can be smelled, would have no effect if applied directly to a nerve fiber.

The various kinds of environmental energy act as triggers, causing the receptor cells to perform biological work. These relationships are best exemplified by a very simple sense organ, the tactile hair of an insect. This hair plus its associated cells constitutes a complete sense organ. But only the bipolar neuron at the base of the hair is a receptor cell. The dendrite of the neuron is attached to the base of the hair near the socket, and the neuron's axon passes directly to the CNS without synapsing.

In its unstimulated state, the neuron maintains a steady resting potential; that is, there is a potential difference between the inside and outside of the neuron. This potential difference exists because the ionic compositions of the fluids on each side of the selectively permeable cell membrane are different. The difference is maintained by sodium-potassium pumps and by metabolic work performed by the cell. When the hair is touched (a mechanical stimulus), its shaft moves in the socket and mechanically deforms the dendrite. This mechanical energy increases the permeability of the neuron membrane to ions, with the result that the potential difference between the two sides of the membrane decreases, disappears, or increases. If it increases, the cell is hyperpolarized. If it decreases or disappears, the cell is said to be **depolarized.**

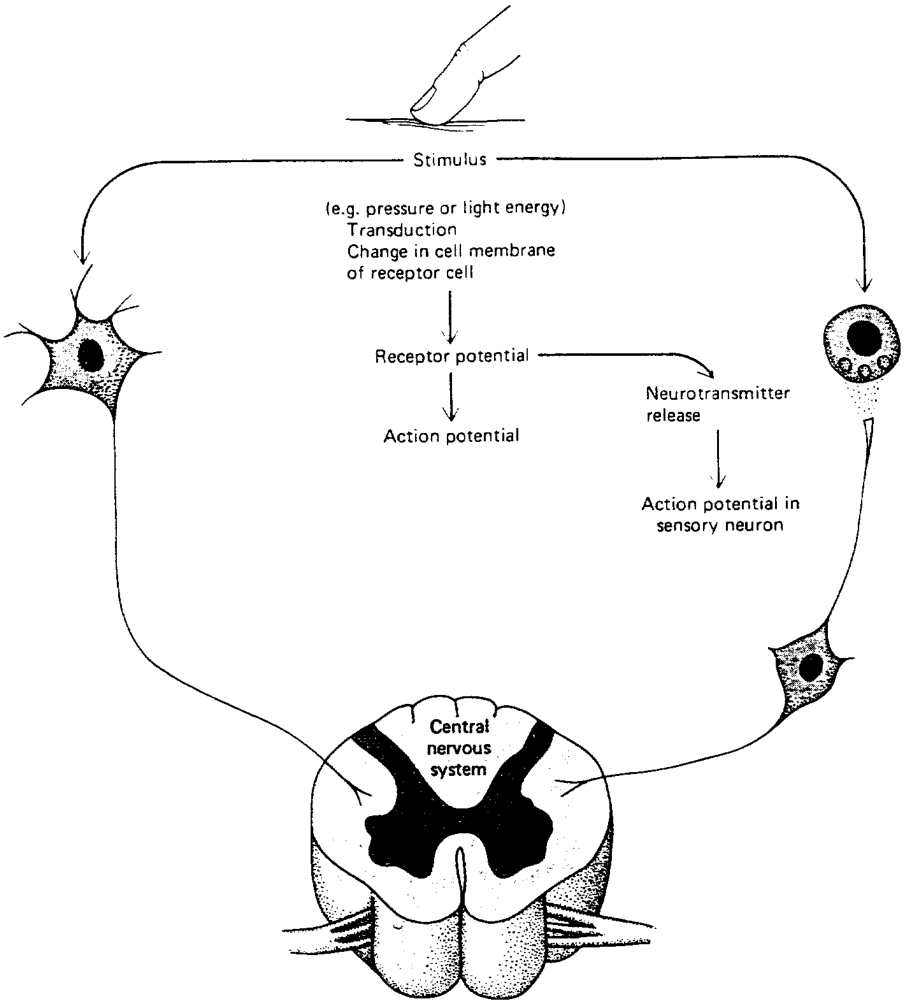


Figure 41–2 How a sense organ works. All receptor cells absorb energy, transduce that energy into electrical energy, and produce a receptor potential. Receptor cells may be either neuron endings themselves or specialized cells in close contact with neuron endings. Both types are shown in the diagram.

The state of depolarization caused by a stimulus is called the **receptor potential**. It spreads relatively slowly down the dendrite, decaying exponentially as it goes. When a special area of the cell near the axon—the axon hillock—becomes depolarized, the threshold level may be reached and an **action potential** is generated. The action potential then travels along the axon to the central nervous system. The receptor thus performs all the essential functions of a sense organ: It detects an event in the environment (a force acting on the hair) by absorbing energy; it converts the energy of the stimulus into electrical energy; and it produces a receptor potential, which may result in an action potential that transmits the information to the CNS. With minor variations, this is how all receptors operate.

The amplitude and duration of the receptor potential are related to the strength and duration of the stimulus. A strong stimulus causes a greater depolarization of the receptor membrane than does a weak one. The action potentials are repetitive, and the frequency at which they are generated is related to the magnitude of the receptor potential. The strength of a stimulus is reflected in the frequency of the action potentials. According to the all-or-none law, the amplitude of each action potential bears no relation to the stimulus; it is characteristic of the particular neuron under the usual recording conditions. In contrast, the receptor potential is a graded response.

Once a stimulus has triggered a receptor to generate action potentials, the stimulus has no further control over them. The situation is analagous to lighting a fuse. The heat of the match is the stimulus. When the end of the fuse reaches the combustion point, the fuse begins to burn, and utilizing its own energy, it ignites adjacent parts of itself. In this way the "message" travels the length of the fuse independently of the temperature of the match flame.

Many receptors do not continue to respond at their initial rate, even if the stimulus remains unabated in intensity. With time, the frequency of action potentials in the sensory neuron decreases. This may occur because the sensory neuron

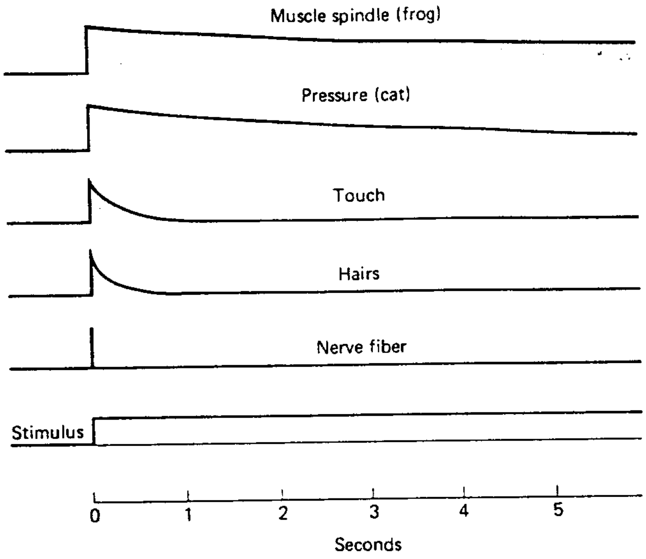


Figure 41–3 The relationship between the stimulus and the different rates of adaptation for different receptors and a nerve fiber. The heights of the curves indicate the rates of discharge of action potentials. (From Adrian, E. D.: *The Basis of Sensation*. London, Chatto and Windus Ltd., 1949.)

becomes less responsive to stimulation, or because the receptor produces a smaller receptor potential, or for both reasons. This diminishing response to a continued, constant stimulus is called **adaptation.**

Some receptors, such as those for pain or cold, adapt so slowly that they continue to trigger action potentials as long as the stimulus persists. Other receptors adapt rapidly, permitting an animal to ignore persistent unpleasant or unimportant stimuli (Fig. 41–3). For example, when you first pull on a pair of tight jeans your pressure receptors let you know that you are being squished and you may feel uncomfortable. Soon, though, these receptors adapt, and you hardly notice the sensation of the tight fit. In the same way we quickly adapt to odors that at first smell seem to assault our senses.

Sensory Coding and Sensation

The stimulation of any sense organ initiates what might be considered a coded message, composed of action potentials transmitted by the nerve fibers and decoded in the brain. Impulses from the sense organ may differ in any of several ways: (1) the total number of fibers transmitting, (2) the specific fibers carrying action potentials, (3) the total number of action potentials passing over a given fiber, (4) the frequency of the action potentials passing over a given fiber, or (5) the time relations between action potentials in specific fibers. These are the possibilities in the "code" sent along the nerve fiber; how the sense organ initiates different codes and how the brain analyzes and interprets them to produce various sensations are not yet understood.

All action potentials are qualitatively the same. Light of the wavelength 400 nanometers (blue), sugar molecules (sweet), and sound waves of 440 hertz (A above middle C) all cause action potentials to be sent to the brain via the appropriate nerves; these action potentials are identical. How can the organism assess its environment accurately? The qualitative differentiation of stimuli must depend either upon the sense organ itself, upon the brain, or upon both. In fact, it depends upon both. Primarily, our ability to discriminate red from green, hot from cold, or red from cold is due to the fact that particular sense organs and their individual sensitive cells are connected to specific cells in particular parts of the brain.

The frequency of the repetitive action potential codes the intensity of the stimulus. Since each receptor normally responds to only one category of stimuli (i.e., light, sound, taste, and so forth), a message arriving in the central nervous system along this nerve is interpreted as meaning that a particular stimulus occurred. Interpretation of the message and, in the case of humans, of the quality of sensation depends upon which central association neurons receive the message. Sensation, when it occurs, occurs in the brain. Rods and cones do not see; only the combination of rods, cones, and centers in the brain see. Furthermore, many sensory messages never give rise to sensations. For example, chemoreceptors in the carotid sinus and the hypothalamus sense internal changes in the body but never stir our consciousness.

Since only those nerve impulses that reach the brain can result in sensations, any blocking of the impulse along the nerve fibers by an anesthetic has the same effect as removing the original stimulus entirely. The sense organs, of course, will continue to initiate impulses that can be detected by the proper electrical apparatus, but the anesthetic prevents them from reaching their destination.

Spatial localization of stimuli impinging on the body, especially mechanical and pain stimuli, also depends upon the destination of specific nerves in the brain. The importance of the brain in localization and in making sensations possible is emphasized by the phenomenon of referred pain. A well-known example of referred pain is that often experienced by persons suffering from heart pains; such persons may complain of pain in the shoulder, upper chest, or left arm. Actually, the stimuli originate in the heart, but the nerve impulses terminate in the same part of the brain as do impulses genuinely originating in the shoulder, chest, or arm.

Cross-fiber patterning, another method of coding information, is probably the one used in olfactory organs. An olfactory organ does not contain a specific receptor for each of the thousands of individual odors that can be recognized. Instead, there is evidence that a limited number of categories of receptors exists. Several receptors are thought to react to each odor. The brain probably makes a statistical analysis of the pattern of responding receptors and from this pattern infers the odor.

The **temporal pattern** of action potentials generated in a single neuron may serve as a code for different stimuli. The single taste receptors of flies, for example, generate action potentials at an even, regular frequency when the stimulus is salt, but generate irregular frequencies when the stimulus is acid.

In invertebrates it is usual for the axon of a sensory neuron to extend all the way to the CNS without synapsing. In these circumstances the message generated at the periphery arrives unaltered. However, in the compound eye of the arthropod, as in many vertebrate sense organs, many interneurons are interposed between the receptor and the CNS. The vertebrate retina or olfactory bulb has an exceptionally complicated neural circuitry. As a consequence of all these synaptic connections, the original message is altered and may lose or gain some of its information.

Mechanoreceptors

Mechanoreceptors respond to touch, pressure, gravity, stretch, or movement. Some of these sense organs are concerned with enabling an organism to maintain its primary body attitude with respect to gravity (for us, head up and feet down; for a dog, dorsal side up and ventral side down; for a tree sloth, ventral side up and dorsal side down).

Mechanoreceptors are also concerned with maintaining postural relations (i.e., the position of one part of the body with respect to another). This information is essential for all forms of locomotion and for all coordinated and skilled movements, from spinning a cocoon to completing a reverse one-and-a-half dive with twist. In addition, mechanoreceptors provide information about the shape, texture, weight, and topographical relations of objects in the external environment. Finally, mechanoreceptors affect the operation of some internal organs. They supply, for example, information about the presence of food in the stomach, feces in the rectum, urine in the bladder, or a fetus in the uterus.

TACTILE RECEPTORS

The simplest mechanoreceptors are free nerve endings in the skin that are directly stimulated by contact with any object on the body surface. Somewhat more complex are the tactile receptors that lie at the base of a hair or bristle (Fig. 41–4). They are stimulated indirectly when the hair is bent or displaced. A receptor potential then develops, and a few action potentials may be generated. Because this type of receptor responds only when the hair is moving, it is known as a **phasic** receptor. Even though the hair may be maintained in a displaced position, the receptor is not stimulated unless there is motion. Such tactile hairs are found in many inverte-

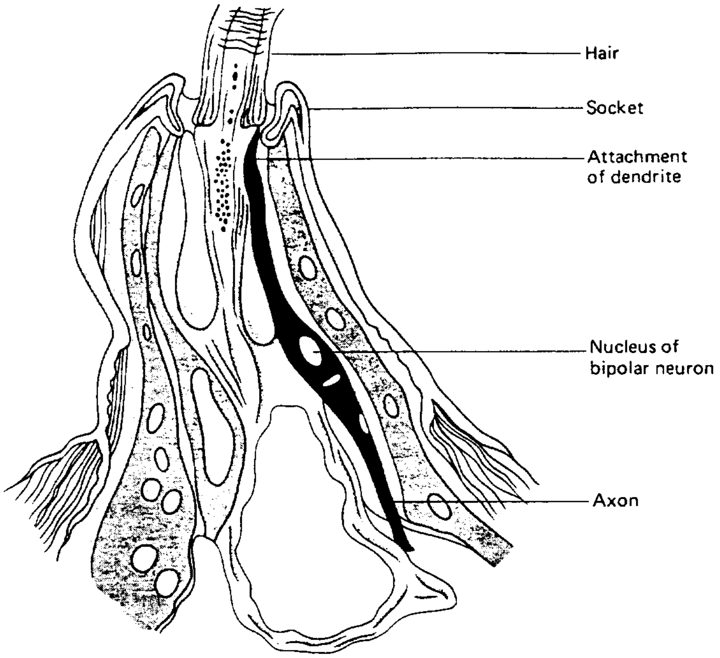


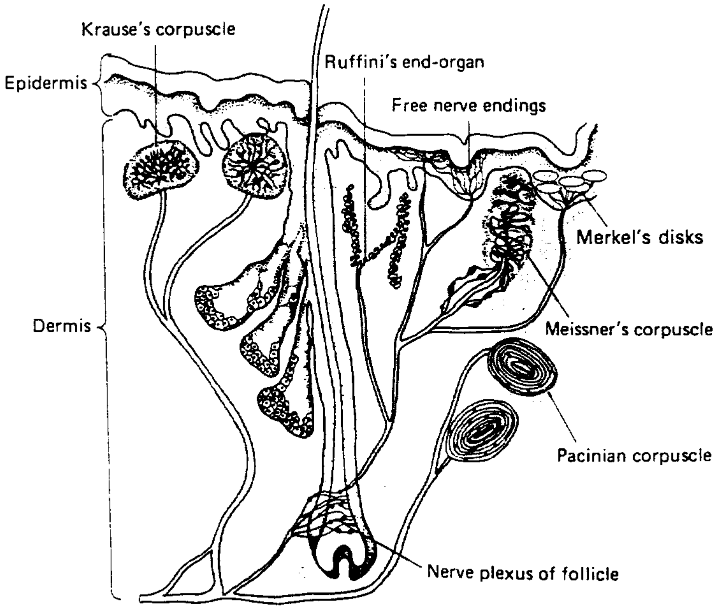
Figure 41–4 A tactile hair from a caterpillar, showing the attachment of the dendrite of the bipolar neuron (the mechanoreceptor) at the point where the shaft of the hair enters the socket.

brates as well as vertebrates and are involved in orientation to gravity, in postural orientation, and in the reception of vibrations in air and water, as well as in contacts with other objects.

The remarkable tactile sensitivity of human skin, especially on the fingertips and lips, is due to a large and diverse number of sense organs (Fig. 41–5). By making a careful point-by-point survey of a small area of skin, using a stiff bristle to test for touch, a hot or cold metal stylus to test for temperature, and a needle to test for pain, it has been found that receptors for each of these sensations are located at different spots. By comparing the distribution of the different types of sense organs and the types of sensations produced, it has been found that the free nerve endings are responsible for pain perception, that a variety of tiny sense organs (e.g., Meissner's corpuscles, Ruffini's end organs, and Merkel's disks) are responsible for touch, that Krause's corpuscles may be responsible for sensations of cold and warmth, and that pacinian corpuscles mediate the sensation of deep pressure.

The pacinian corpuscle has been particularly well studied. The bare nerve ending is surrounded by connective tissue layers (lamellae) interspersed with fluid. Compression causes displacement of the lamellae, which provides the deformation

Figure 41–5 Diagrammatic section through the human skin showing the types of sense organs present. The free nerve endings respond to pain; Krause's corpuscles are thought to respond to hot and cold stimuli; tactile hairs, Merkel's disks, Ruffini's end organs, and Meissner's corpuscles respond to touch; pacinian corpuscles respond to deep pressure.



stimulating the axon. Even though the displacement is maintained under steady compression, the receptor potential rapidly falls to zero and action potentials cease—an excellent example of adaptation. The pacinian corpuscle is a phasic receptor responding to velocity (rapid movement of the tissue).

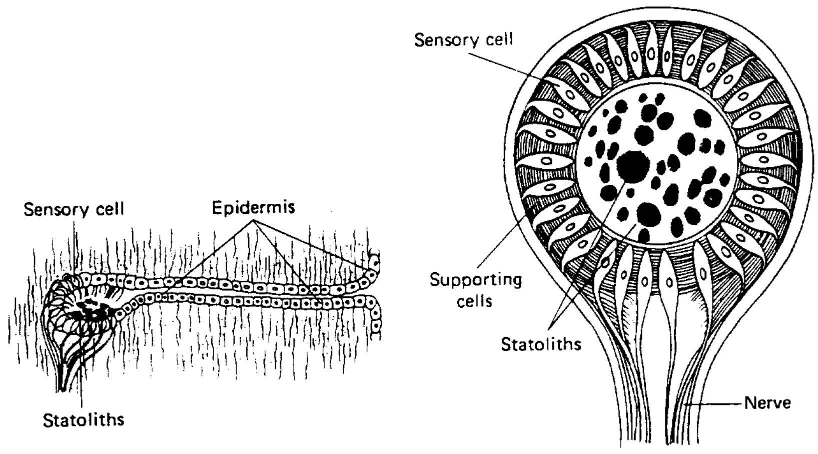
GRAVITY RECEPTORS: STATOCYSTS

All organisms are oriented in a characteristic way with respect to gravity. When displaced from this normal position, they quickly adjust the body to reassume it. To accomplish this, receptors must continually send information regarding the position and movements of the body to the CNS.

Many invertebrates have specialized sense organs called **statocysts** that serve as gravity receptors. A statocyst is basically an infolding of the epidermis lined with receptor cells that have hairs (Fig. 41–6). The cavity contains a **statolith** (sometimes more than one), which is a tiny granule of loose sand grains or calcium carbonate. The particles are held together by an adhesive material secreted by cells of the statocyst. Normally the particles are pulled downward by gravity and stimulate the hair cells. When the position of the statolith changes, the hairs of the receptor cells are bent. This mechanical displacement results in receptor potentials and action potentials that inform the CNS of the change in position. By "knowing" which hair cells are firing, the animal knows where down is, and so can correct any abnormal orientation.

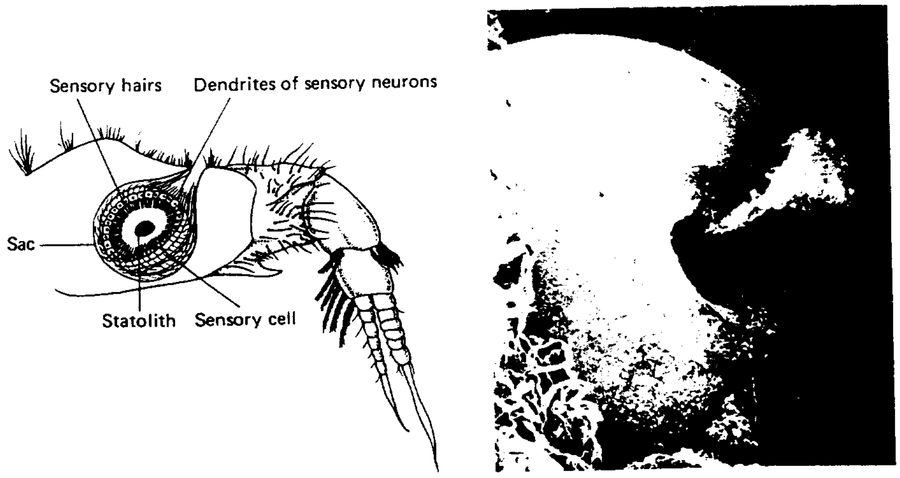
In a classic experiment on crayfish, the function of the statocyst was demonstrated by substituting iron filings for sand grains in the statocyst. The force of gravity was overcome by holding magnets above the animals. The iron filings were

Figure 41–6 Many invertebrates have statocysts, which serve as sensors of gravitational force. ((*d*), Courtesy of J. Derrenbacher.)



(*a*) A type of statocyst found in mollusks

(*b*) A statocyst from an annelid polychaete



(*c*) Statocyst in the antennule of a decapod crustacean

(*d*) Sea urchin statocyst

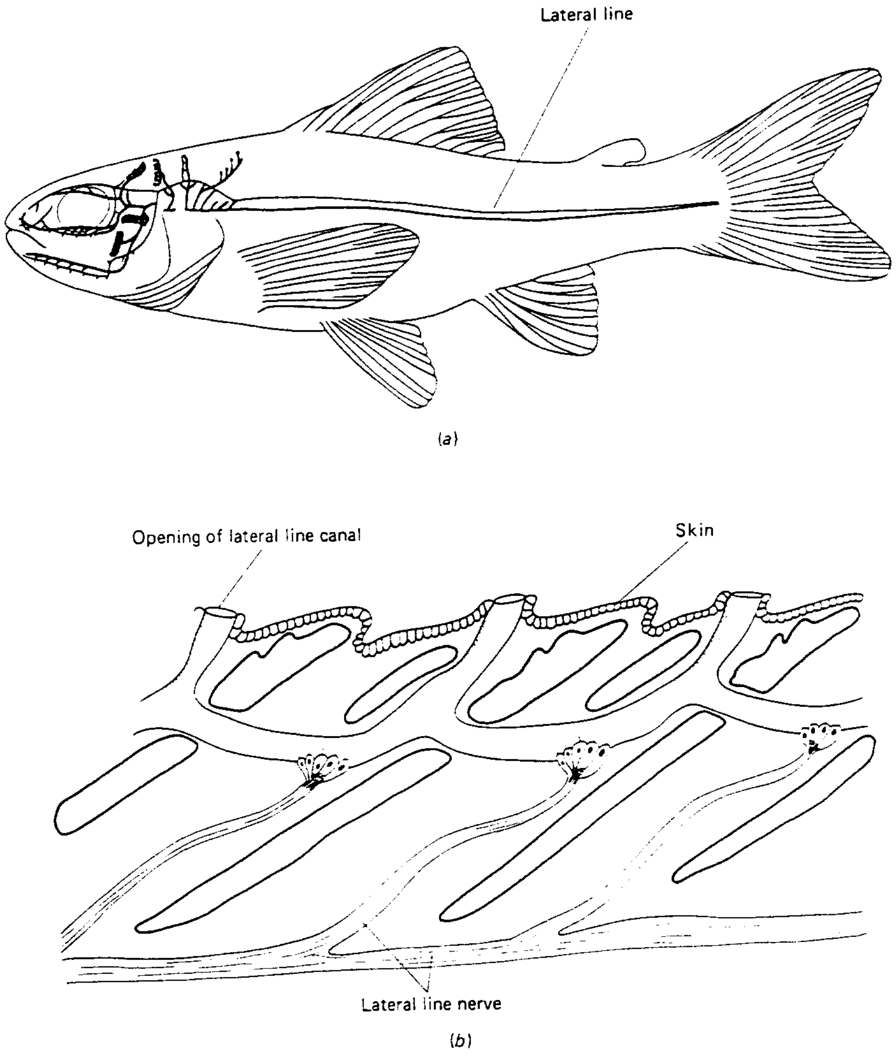


Figure 41–7 The receptor cells of the lateral line organ respond to waves, currents, or disturbances in the water, informing the fish of obstacles or moving objects.

attracted upward toward the magnets, and the crayfish began to swim upside down in response to the new information provided by their gravity receptors.

LATERAL LINE ORGANS

Lateral line organs are found in fishes, and in aquatic and larval amphibians. Typically this sense organ consists of a long canal running the length of the body and continuing into the head on both sides of the animal (Fig. 41–7). The canals are lined with receptor cells that have hairs. Above the hairs and enclosing their tips is a mass of gelatinous material, called a **cupula,** secreted by the receptor cells.

The receptor cells are thought to respond to waves, currents, or disturbances in the water. The water moves the cupula and causes the hairs to bend. This results in messages being dispatched to the CNS. The lateral line organ is thought to supplement vision by informing the fish of obstacles in its way or of moving objects such as prey or enemies.

PROPRIOCEPTORS

Proprioceptors are sense organs that respond continuously to tension and movement in muscles and joints. Vertebrates have three main types: **muscle spindles,** which detect muscle movement (Fig. 41–8); **Golgi tendon organs,** which determine stretch in the tendons that attach muscle to bone; and **joint receptors,** which detect movement in ligaments. These are **tonic** (static) sense organs. In contrast to that in phasic receptors, the receptor potential is maintained (though not at constant magnitude) as long as the stimulus is present and action potentials continue to be generated. Thus, information about the position of the organ concerned is continuously supplied.

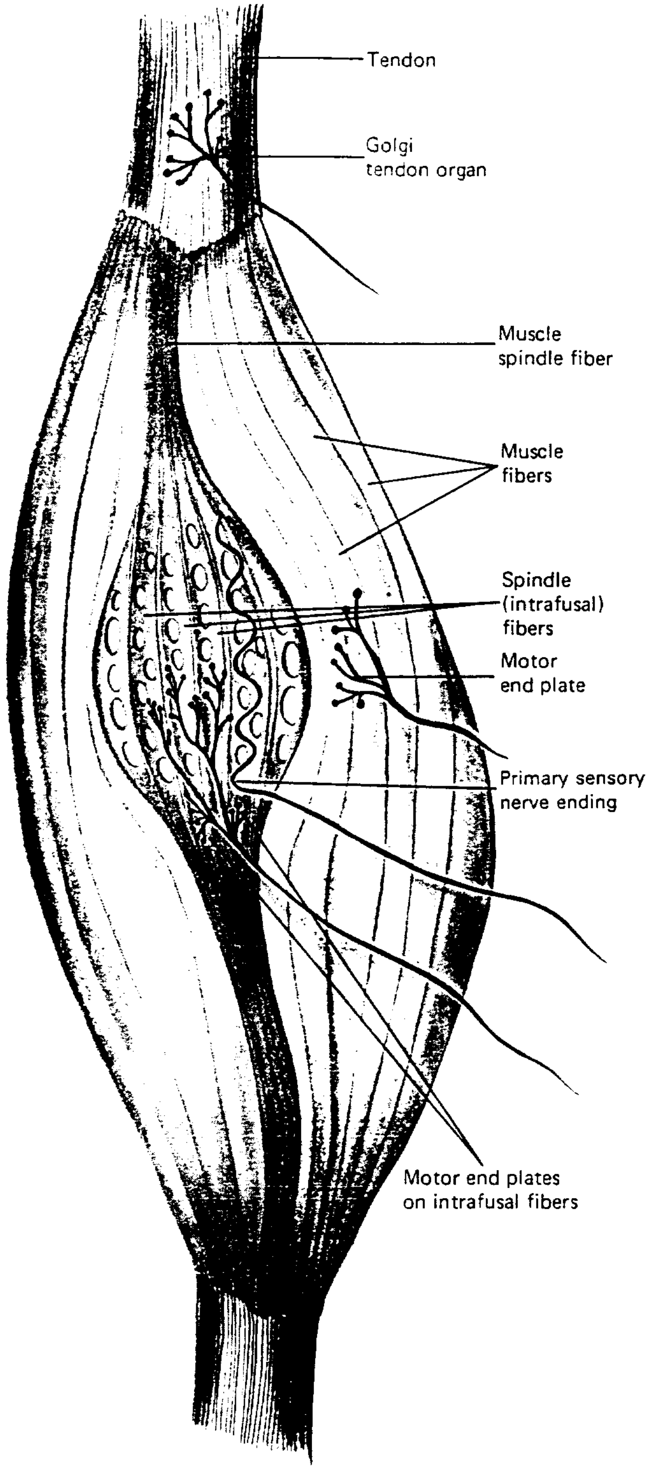


Figure 41–8 A muscle spindle and Golgi tendon organ. Muscle spindles detect muscle movement; Golgi tendon organs determine stretch in tendons.

By means of these sense organs we can, even with our eyes closed, perform manual acts such as dressing or tying knots. Impulses from the proprioceptors are also extremely important in ensuring the harmonious contraction of different muscles involved in a single movement; without such receptors, complicated skillful acts would be impossible. Impulses from these organs are also important in maintaining balance. Proprioceptors, which were discovered only a little more than 100 years ago, are probably more numerous and more continuously active than any of the other sense organs, although we are less aware of them than most of the others. We obtain some idea of what life without proprioceptors would be like when a leg or arm "goes to sleep"—a feeling of numbness, which results in part from the lack of proprioception.

The mammalian muscle spindle is one of the more versatile stretch receptors. It consists of a bundle of specialized muscle fibers, the intrafusal fibers. In the center of the muscle spindle is a region in which filaments are absent. This region is encircled by two types of sensory nerve endings: primary endings and secondary endings. Both types respond statically; they continue to transmit signals for a prolonged period of time, and they do so in proportion to the degree of stretch. The primary endings also exhibit a strong dynamic response. They respond very actively to a rapid rate of change in length, but only while the length is actually increasing.

EQUILIBRIUM

In addition to monitoring events within its body and outside, an organism must have a way of sensing its own orientation. The state of balance or adjustment between opposing forces that enables an organism to maintain this orientation is known as **equilibrium.** Most creatures employ the force of gravity to provide this information, but other cues, such as the direction of the prevailing light, may also be used. Two examples of orientational sensing are the more typical human mechanism, which is based largely on the force of gravity, and a more unusual method employed by flies.

Halteres in Flies

Long before humans invented the gyroscope, flies evolved a balancing organ to stabilize flight. Any flying machine must maintain stability if it is to be controllable in the air. Flies must be able to control lift and stabilize in all three planes of rotation; that is, they must correct for pitch, roll, and yaw. They accomplish this with information derived from the **halteres,** a pair of marvelously modified hind wings. Each is a heavy mass of tissue on a thin stalk (Fig. 41–9) and resembles an Indian club. The base is folded and articulated in a complicated fashion and is equipped with about 418 mechanoreceptors. These respond to strains produced in the cuticle by gyroscopic torque produced by the beating of the halteres. These oscillating masses generate forces at the base of the stalk as the whole fly rotates. They probably do not act as stabilizing gyroscopes of the sort placed in ships to offset their

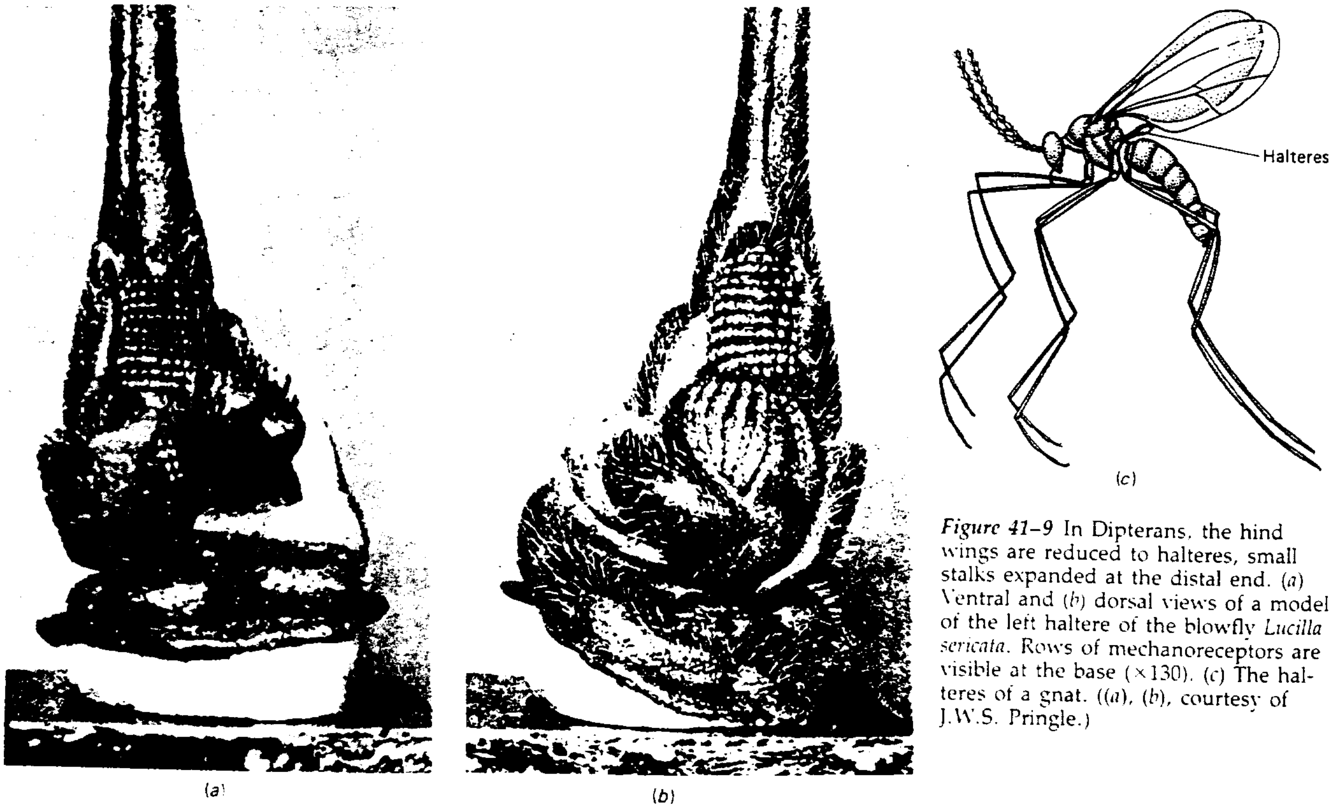


Figure 41–9 In Dipterans, the hind wings are reduced to halteres, small stalks expanded at the distal end. (*a*) Ventral and (*b*) dorsal views of a model of the left haltere of the blowfly *Lucilla sericata*. Rows of mechanoreceptors are visible at the base (×130). (*c*) The halteres of a gnat. ((*a*), (*b*), courtesy of J.W.S. Pringle.)

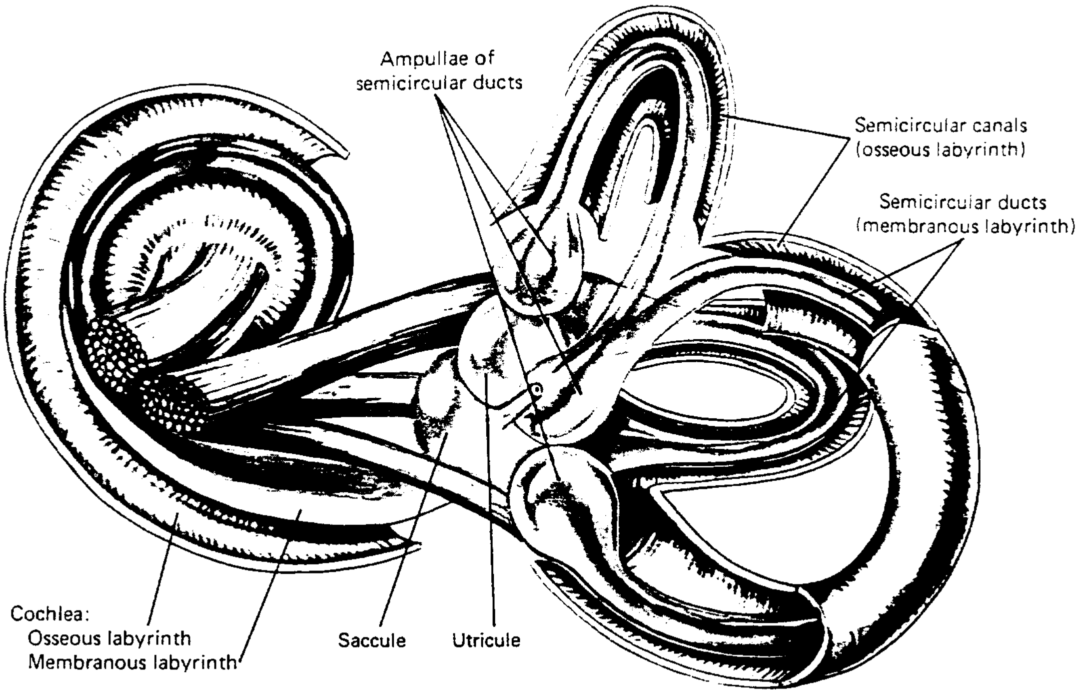


Figure 41–10 The human inner ear with the membranous labyrinth exposed. Because this is a posterior view the utricle and saccule can be seen. Note that the membranous labyrinth is shown in color only within the semicircular canals and is not colored in the cochlea.

movement. Their action is indirect in that their mechanoreceptors signal the CNS to make the necessary corrections in flight.

The Labyrinth of the Vertebrate Ear

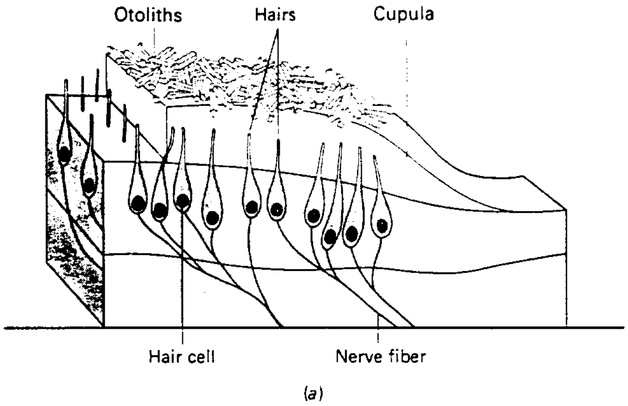
When we think of the ear, we think of hearing. However, fishes do not use their ears for hearing. In fact, in all vertebrates the basic function of the ear is to help maintain equilibrium. Typically the ear also contains gravity receptors. Although many vertebrates do not have outer or middle ears, all of them have inner ears.

The inner ear consists of a complicated group of interconnected canals and sacs, often referred to as the **labyrinth.** In jawed vertebrates the labyrinth consists of two saclike chambers, the **saccule** and **utricle,** and three **semicircular canals,** as well as the **cochlea.**

Collectively, the saccule, utricle, and semicircular canals are referred to as the **vestibular apparatus** (Fig. 41–10). Destruction of the vestibular apparatus leads to a considerable loss of the sense of equilibrium. A pigeon in which these organs have been destroyed is unable to fly, but in time can relearn how to maintain equilibrium using visual stimuli. Equilibrium in the human depends not only upon stimuli from the organs in the inner ear but also upon the sense of vision, stimuli from the proprioceptors, and stimuli from cells sensitive to pressure in the soles of the feet.

The saccule and utricle house gravity detectors in the form of small calcium carbonate ear stones called **otoliths** (Fig. 41–11). The sensory cells of these structures are similar to those of the lateral line organ. They consist of groups of hair cells surrounded at their tips by a gelatinous cupula. The receptor cells in the saccule and utricle lie in different planes. Normally, the pull of gravity causes the otoliths to press against particular hair cells, stimulating them to initiate impulses sent to the brain by way of sensory nerve fibers at their bases. When the head is tilted, or in linear acceleration (change in speed when the body is moving in a straight line), the otoliths press upon the hairs of other cells and stimulate them. This enables the animal to perceive the direction of gravity and of linear acceleration or deceleration when the head is in any position.

Information about turning movements is furnished by the three semicircular canals. Each of these is connected with the utricle, and lies in a plane at right angles to the other two. Each canal is a hollow ring filled with fluid called **endolymph.** At one of the openings of each canal into the utricle is a small, bulblike enlargement, the **ampulla.** Within each ampulla is a clump of hair cells called a **crista,** similar to those in the utricle and saccule, but lacking otoliths. These receptor cells are stimulated by movements of the endolymph in the canals (Fig. 41–12).



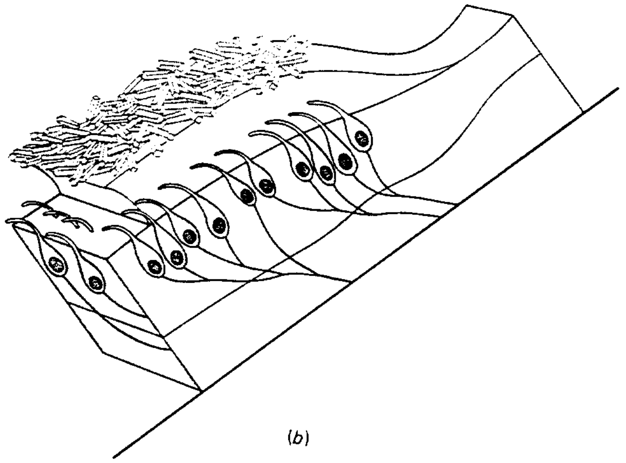
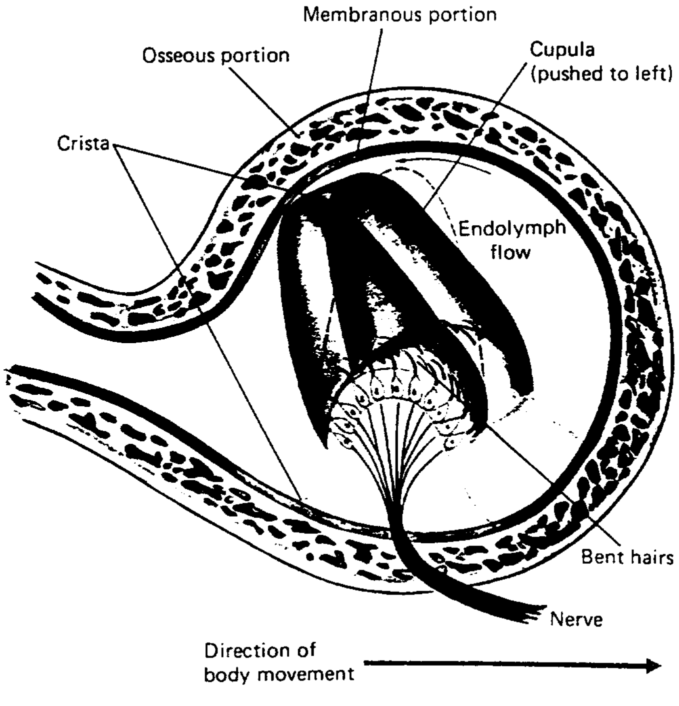


Figure 41–11 The saccule and utricle. Compare the positions of the otoliths and hairs in (*a*) with those in (*b*). Changes in head position cause the force of gravity to distort the cupula, which in turn distorts the hairs of the hair cells; the hair cells respond by sending impulses down the vestibular nerve (part of the auditory nerve) to the brain.

When the head is turned, there is a lag in the movement of the fluid within the canals, so that the hair cells move in relation to the fluid and are stimulated by its flow. This stimulation produces not only the consciousness of rotation but also certain reflex movements in response to it—movements of the eyes and head in a direction opposite to the original rotation. Since the three canals are located in three

Figure 41–12 How movement of the endolymph within the semicircular ducts of the ampulla distorts the cupula. The hair cells of the cupula then are bent, reporting any change to the brain via the vestibular nerve.



different planes, a movement of the head in any direction will stimulate the movement of the fluid in at least one of the canals.

We humans are used to movements in the horizontal plane, which stimulate certain semicircular canals, but we are unused to vertical movements parallel to the long axis of the body. Movements such as the motion of an elevator, or of a ship pitching in a rough sea, stimulate the semicircular canals in an unusual way, and may cause sea sickness or motion sickness, with their resulting nausea or vomiting. When a person so affected lies down, the movement stimulates the semicircular canals in a different way, and nausea is less likely to occur.

AUDITORY RECEPTORS

Some fish hear by means of receptors in the utricle, but hearing does not seem to be important to them. Hearing is an important sense in tetrapods, however. Both birds and mammals have a highly developed sense of hearing based in the cochlea, a structure in the inner ear that contains mechanoreceptor hair cells that detect pressure waves.

Part of the labyrinth of the inner ear, the cochlea is a spiral tube coiled two-and-a-half turns and resembling a snail's shell (Fig. 41-13). If the cochlea were uncoiled, as in Figure 41-14, it would be seen to consist of three canals separated from each other by thin membranes and coming almost to a point at the apex. Two of these canals, or ducts, the **vestibular duct** and the **tympanic duct**, are connected with one another at the apex of the cochlea and are filled with a fluid known as **perilymph**. The middle canal, the **cochlear duct**, is filled with endolymph and contains the actual auditory receptor, the **organ of Corti**. Each organ of Corti contains about 24,000 hair cells arranged in five rows extending the entire length of the coiled cochlea. Each cell is equipped with hairlike projections extending into the cochlear duct. These cells rest upon the **basilar membrane**, which separates the cochlea from the tympanic duct. Overhanging the hair cells is another membrane, the **tectorial membrane**, attached along one edge to the membrane on which the hair cells rest, with its other edge free. The hair cells initiate impulses in the fibers of the cochlear (auditory) nerve.

In terrestrial vertebrates, accessory structures in the outer and middle ear change sound waves in air to pressure waves in the cochlear fluid. In the human

Figure 41-13 The anatomy of the human ear.

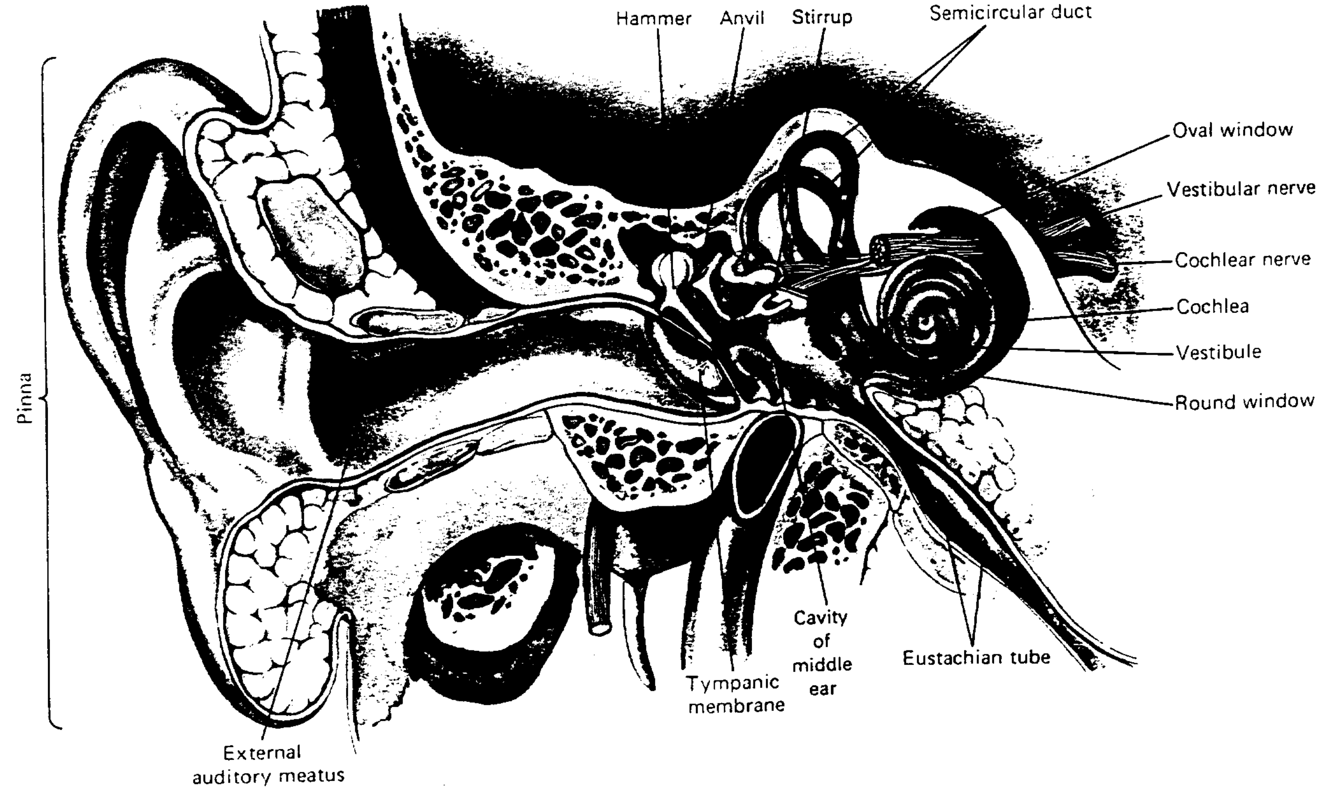
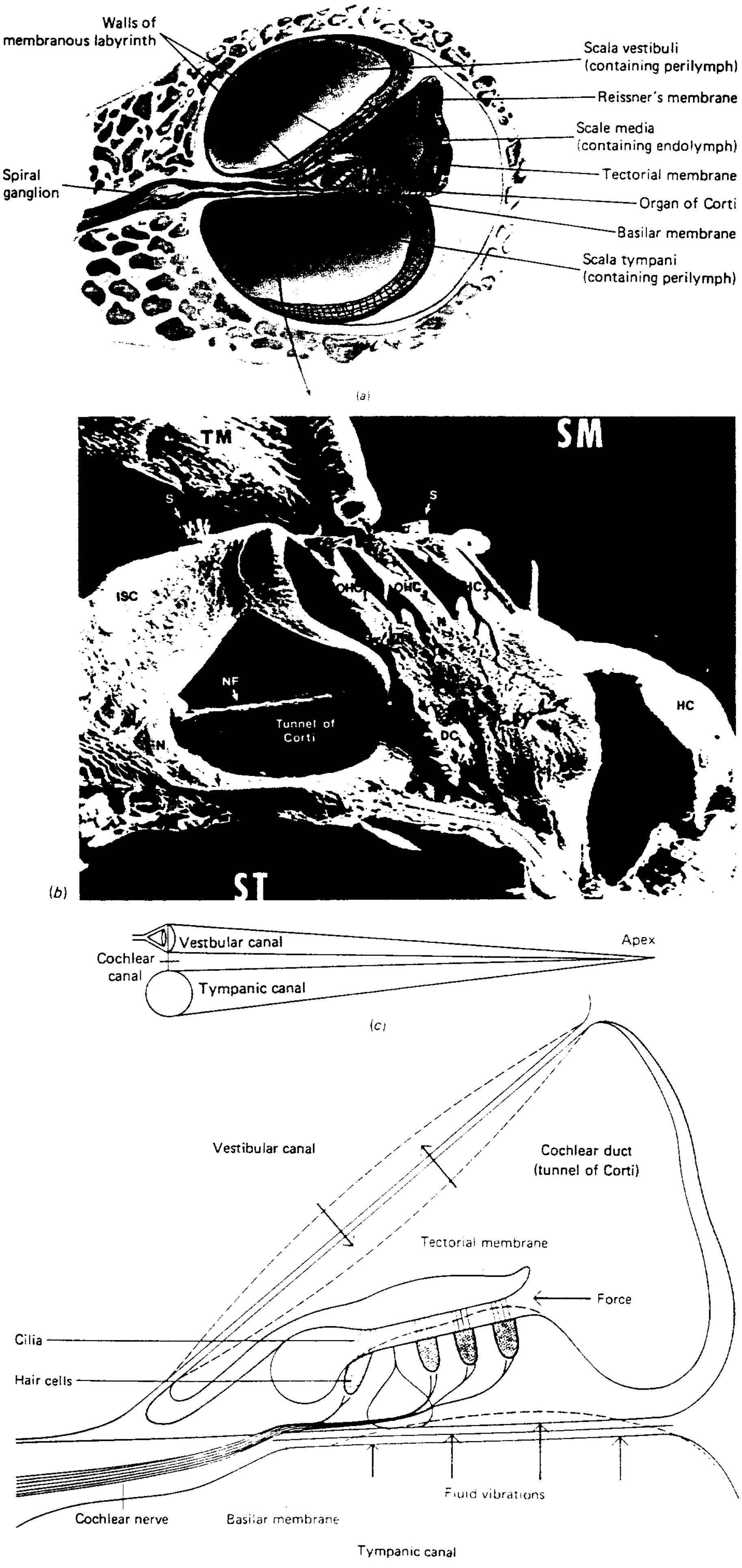


Figure 41–14 The cochlea is the part of the inner ear concerned with hearing. (*a*) Cross section through the cochlea to show the organ of Corti resting on the basilar membrane and covered by the tectorial membrane. (*b*) Scanning electron micrograph of guinea pig organ of Corti showing inner hair cells, *IHC*, and three rows of outer hair cells, *OHC 1–3* (magnification ×1,790). *N*, nucleus; *S*, stereocilia; *TM*, tectorial membrane; *SM*, scala media (cochlear duct); *ST*, scala tympani (tympanic duct); *black arrows*, basilar membrane; *HC, DC, PC*, various supporting cells. (Courtesy of Dr. L. G. Duckert, University of Washington.) (*c*) Diagram of the cochlea uncoiled and drawn out in a straight line. (*d*) The organ of Corti. Vibrations transmitted by the hammer, anvil, and stirrup set the fluid in the vestibular canal in motion; these vibrations are transmitted to the basilar membrane and the organ of Corti. The hair cells of the organ of Corti are the receptor cells for hearing and are innervated by the cochlear nerve, a branch of the auditory nerve.



ear, for example, sound waves pass through the **external auditory meatus** (the canal of the outer ear) and set the **eardrum** (the membrane separating outer ear and middle ear) vibrating. These vibrations are transmitted across the middle ear by three tiny bones, the **hammer, anvil,** and **stirrup** (so called because of their shapes). The hammer is in contact with the eardrum, and the stirrup is in contact with the membrane at the opening of the inner ear called the **oval window**. The vibrations pass through the oval window to the fluid in the vestibular canal.

Since liquids cannot be compressed, the oval window could not cause movement of the fluid in the vestibular duct unless there were an escape valve for the pressure. This is provided by the **round window** at the end of the tympanic duct. The pressure wave presses upon the membranes separating the three ducts, is transmitted to the tympanic canal, and causes a bulging of the round window. The movements of the basilar membrane produced by these pulsations are believed to rub the hair cells of the organs of Corti against the overlying tectorial membrane, thus stimulating them and initiating nerve impulses in the dendrites of the cochlear nerve lying at the base of each hair cell.

Since sounds differ in pitch, intensity, and quality, any theory of hearing must account for the ability to differentiate between these characteristics of sound. Microscopic examination of the organ of Corti reveals that the fibers of the basilar membrane along the coiled cochlea are of different lengths, being longer at the apex and shorter at the base of the coil, thus resembling the strings of a harp or piano. Sounds of a given frequency (and pitch) set up resonance waves in the fluid in the cochlea that cause a particular section of the basilar membrane to vibrate. The vibration stimulates the particular group of hair cells in that section. In this way the brain infers the pitch of a sound by taking note of the particular hair cells that are stimulated. Loud sounds cause resonance waves of greater amplitude and lead to a more intense stimulation of the hair cells and to the initiation of a greater number of impulses per second passing over the auditory nerve to the brain. The nerve impulses produced by particular sounds have the same frequency as those sounds; thus the brain may recognize particular pitches by the frequency of the nerve impulses reaching it, as well as by the identity of the nerve fibers conducting the impulses.

Variations in the quality of sound, such as are evident when an oboe, a cornet, and a violin play the same note, depend upon the number and kinds of **overtones,** or **harmonics,** present. These stimulate different hair cells in addition to the main stimulation common to all three. Thus, differences in quality are recognized by the *pattern* of the hair cells stimulated. Careful histological work has shown that the nerve fibers from each particular part of the cochlea are connected to particular parts of the auditory area of the brain, so that certain brain cells are responsible for the perception of sensations of high tones, others for low tones.

The human ear is equipped to register sound frequencies between about 20 and 20,000 cycles per second, although there are great individual differences. Some animals—dogs, for example—can hear sounds of much higher frequencies. The human ear is more sensitive to sounds between 1000 and 2000 cycles per second than to higher or lower ones. Within this range, the ear is extremely sensitive. In fact, when the energy of audible sound waves is compared with the energy of visible light waves, the ear is 10 times more sensitive than the eye.

The normal human ear is extremely efficient. Any further increase in sensitivity would probably be useless, since it would pick up the random movement of air molecules, which would result in a constant hiss or buzzing. Similarly, if the eye were more sensitive, a steady light would appear to flicker because the eye would be sensitive to the individual photons (light particles) impinging upon it.

There is little fatigue connected with hearing. Even though the ear is constantly assailed by noises, it retains its acuity and fatigue disappears after a few minutes. When one ear is stimulated for some time by a loud noise, the other ear also shows fatigue (i.e., loses acuity), indicating, not unexpectedly, that some of the fatigue is in the brain rather than in the ear itself.

Deafness may be caused by injuries or malformations of either the sound-transmitting mechanisms of the outer, middle, or inner ears, or of the sound-perceiving mechanism of the latter. The external ear may become obstructed by wax secreted by the glands in its wall; the middle-ear bones may become fused after an infection; or, more rarely, the inner ear or auditory nerve may be injured by a local inflammation or by the fever accompanying some disease.

When the ear is subjected to intense sound, the organ of Corti is injured. This was demonstrated by an experiment in which guinea pigs were exposed to continuous pure tones for a period of several weeks. When their cochleas were examined microscopically after death, it was found that the guinea pigs subjected to high-pitched tones suffered injury only in the lower part of the cochlea, while those subjected to low-pitched tones suffered injury only in the upper part of the cochlea. Members of rock bands, boilermakers, and other workers subjected to loud, high-pitched noises over a period of years frequently become deaf to high tones because the cells near the base of the organ of Corti become injured.

Chemoreceptors: Taste and Smell

Throughout the animal kingdom many feeding, social, sexual, and reproductive activities are initiated, regulated, or influenced in some way by specific chemical cues in the environment. Insects, for example, use many chemicals in communication, in defense from predators, and in recognizing specific foods. Many vertebrates employ chemical secretions to mark territory, to attract their sexual partners, and to defend themselves. Chemoreception is also used to help carnivores track prey and to help the intended prey elude the carnivores.

The sensitivity of chemoreceptors varies greatly. Some, such as those in the skin of a frog, may be gross and nonspecific. A frog is thus unable to differentiate between certain stimuli and will scratch its back when dilute acid or concentrated solutions of inorganic salts are applied to the skin. Free nerve endings are the chemoreceptors involved. This common chemical sense is widely distributed among aquatic animals. Among mammals it is restricted to moist areas of the body. Recall how your eye smarts and waters in the presence of ammonia fumes or a peeled onion, and how a broken blister stings if touched by a nonphysiological solution.

Two highly sensitive chemoreceptive systems are the senses of **taste** and **smell** (olfaction). These are easily distinguishable in humans and other terrestrial organisms. However, in aquatic organisms, especially members of lower phyla, it becomes increasingly difficult to decide what is taste and what is olfaction.

THE SENSE OF TASTE IN INSECTS

One of the most thoroughly studied organs of taste is the taste hair of the fly (Fig. 41–15). The terminal segments of the legs and the mouthparts of flies, moths, butterflies, and a number of other insects are equipped with very sensitive hairs. In the fly, each one of these contains four taste receptors and a tactile receptor. All are primary neurons. One taste receptor is more-or-less specific to sugars, one to water, and two to salts. If water is placed on one hair of a thirsty fly, action potentials generated by the water cell pass directly to the CNS and cause the fly to respond by extending its retractable proboscis and drinking. Similarly, sugar on a particular hair stimulates the sugar receptor and causes feeding. Salt causes the fly to reject the solution.

THE HUMAN SENSE OF TASTE

The organs of taste in humans are budlike structures known as **taste buds,** which are located predominantly on the tongue and soft palate. They are found mainly in tiny elevations, or papillae, on the surface of the tongue. There is a rapid turnover of taste bud cells; every 10 to 30 hours the cells are completely replaced.

A taste bud is an oval body that consists of an epithelial capsule containing several taste receptors. Each taste receptor is an epithelial cell with a border of microvilli at its free surface (Figs. 41–16 and 41–17). A hairlike projection extends to the external surface of the taste bud through an opening called the taste pore. The connections between the taste receptors and the nerve cells that innervate them are complicated, with each taste receptor being innervated by more than one neuron. Furthermore, some neurons are connected with one taste cell, while others are connected with many. This complexity of connections renders interpretation of taste-sensory physiology difficult.

Traditionally there are four basic tastes: sweet, sour, salty, and bitter. Although it is true that the greatest sensitivity to each of these tastes is restricted to a

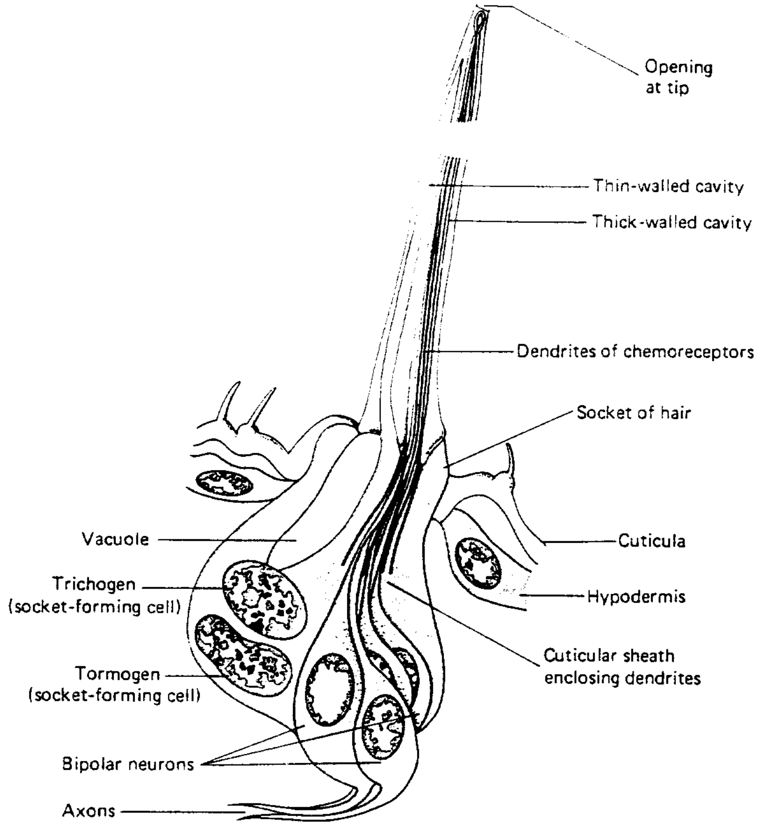


Figure 41–15 A chemoreceptive hair of the blowfly. Four of the five neurons are shown.

given area of the human tongue (Fig. 41–16), not all papillae are restricted in their sensitivity to a single category of taste. Some indeed are responsive specifically to salty, bitter, or sweet taste, but the majority respond to two or more categories of taste. Nor is a single taste bud restricted in its sensitivity to a single type of chemi-

Figure 41–16 The distribution on the surface of the tongue of taste buds sensitive to sweet, bitter, sour, and salt.

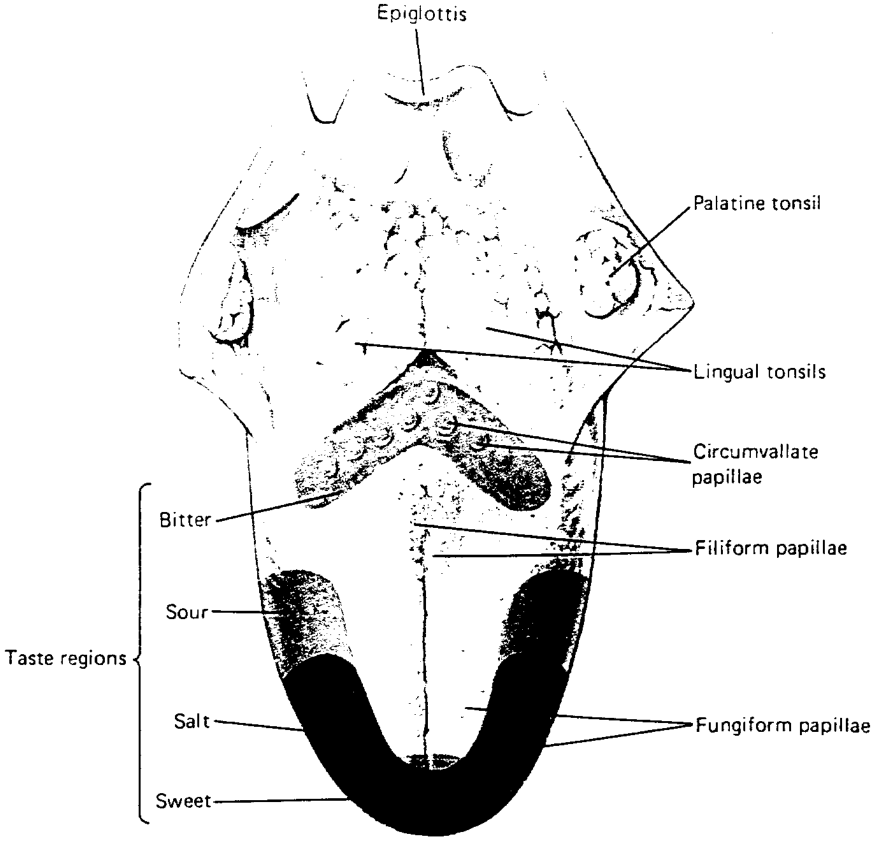


Figure 41–17 Electron micrograph of papillae of the tongue containing taste buds. The taste buds are the oval bodies (approximately ×400). (Biophoto Associates, Photo Researchers, Inc.)

cal. A single taste receptor may respond to more than one category of taste. Thus the detection and processing of information in the taste organs of the tongue are very complex. Taste discrimination probably depends on a code that consists of cross-fiber patterning; that is, each receptor responds to more than one kind of chemical, but no two respond exactly alike, so that the total pattern of messages going to the brain is different for different solutions.

Flavor does not depend on the perception of taste alone. It is actually compounded of taste, smell, texture, and temperature. Smell affects flavor because odors pass from the mouth to the nasal chamber via the internal nares. No doubt you have observed that when you have a cold, food seems to have little "taste." Actually, the taste buds are not affected, but the blockage of nasal passages severely reduces the participation of olfactory reception in the composite sensation of flavor.

THE SENSE OF SMELL

In terrestrial vertebrates, olfaction occurs in the nasal epithelium. In humans the **olfactory epithelium** is located in the roof of the nasal cavity (Fig. 41–18). This epithelium contains specialized olfactory cells with axons that extend upward as the fibers of the olfactory nerves. These fibers penetrate the exceedingly thin cribriform plate of the ethmoid bone on the cranial floor through many sievelike pores. The end of each olfactory cell on the epithelial surface bears several olfactory hairs that are believed to react to odors (chemicals) in the air.

Unlike the taste buds, which are sensitive to only a few chemical sensations, the olfactory epithelium is thought to react to as many as 50. Mixtures of these primary smell sensations produce the broad spectrum of odors that we are capable of perceiving. The olfactory organs respond to remarkably small amounts of a substance. For example, ionone, the synthetic substitute for the odor of violets, can be detected by most people when it is present in a concentration of only one part in more than 30 billion parts of air.

Despite its sensitivity smell is perhaps the sense that adapts most quickly. The olfactory receptors adapt about 50% in the first second or so after stimulation, so that even offensively odorous air may seem odorless after only a few minutes. Part of this adaptation is thought to take place in the CNS.

Thermoreceptors

Heat is another form of radiant energy to which all living things respond. Although not much is known about specific thermoreceptors in invertebrates, many invertebrates are sensitive to gradations in temperature. In very small animals, the CNS itself may respond to temperature change. In others, free nerve endings in the integument may be responsible for detection of heat. Mosquitoes and other blood-sucking insects and ticks must use thermoreception in their search for a warm-blooded host. Some have temperature receptors on their antennae sensitive to changes of less than 0.5°C.

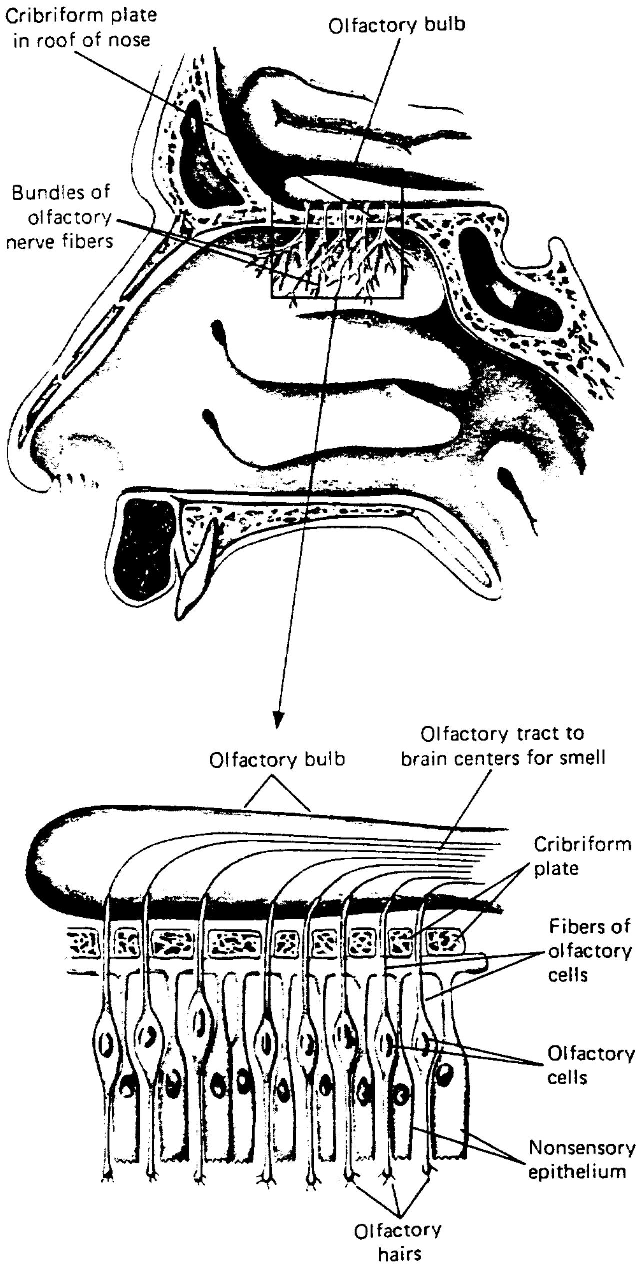


Figure 41–18 Location and structure of the olfactory epithelium. Note that the receptor cells are located in the epithelium itself.

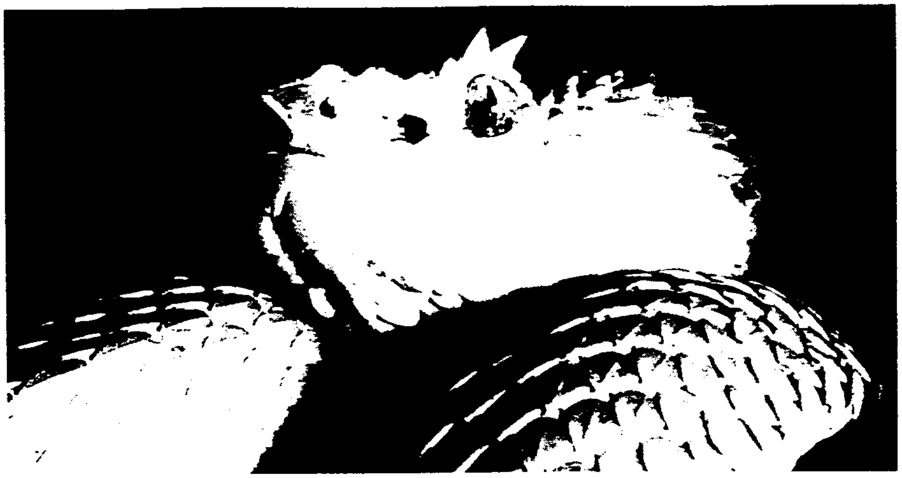
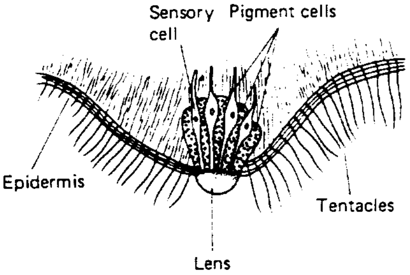


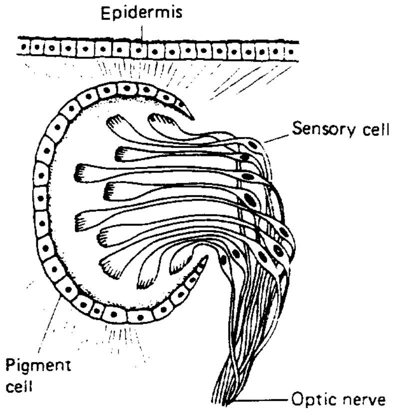
Figure 41–19 A golden eye-lash viper showing a pit organ, a sensory structure located between each eye and nostril. The pit organ can detect the heat from a warmblooded animal up to a distance of one to two meters. (Tom McHugh, Steinhart Aquarium, Photo Researchers, Inc.)

Certain snakes (pit vipers and boas) use thermoreceptors to locate warm-blooded prey. Pits in the heads of these snakes are thermoreceptors that can detect heat generated by a small animal as far as a half meter away (Fig. 41–19). The snake orients its head so that the pits on both sides of its head detect the same amount of heat. This position indicates that the snake is facing its prey directly, and presumably improves the snake's "aim" when striking. Each pit organ consists of a cavity 1 to 5 mm in diameter in the head of the snake. In rattlesnakes, a very thin membrane is suspended across the cavity. About 7000 heat sensitive axons (of the trigeminal nerve) are located along the membrane surface. When warmed, each of these axons can send action potentials to the snake's brain.

In mammals, free nerve endings and specialized receptors in the skin and tongue detect temperature changes. Thermoreceptors in the hypothalamus of the brain detect internal changes in temperature and receive and integrate information from thermoreceptors on the body surface. The hypothalamus then initiates homeostatic mechanisms that ensure a constant body temperature.



(*a*) Simple invertebrate eye (Ocellus from cell of jellyfish)



(*b*) Ocellus of planarian worm

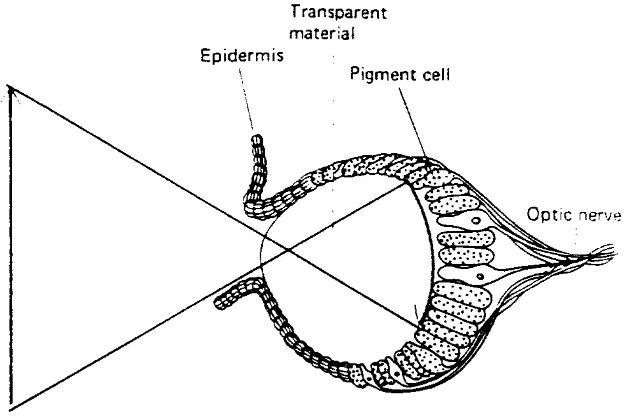
Figure 41–20 Simple invertebrate eyes. (*a*) Ocellus from bell of jellyfish. (*b*) Ocellus of planarian worm.

Photoreceptors

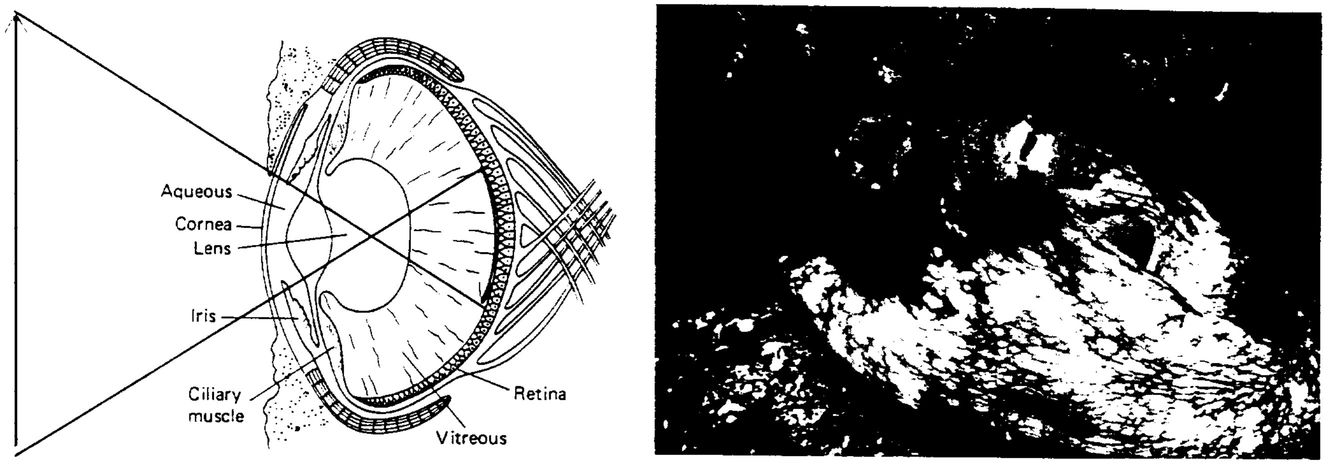
Just as matter consists of atoms, light consists of units called **photons.** The energy content of one photon is defined as one **quantum.** In photoreception, quanta of light energy striking the light-sensitive cells trigger the receptor cell to transmit a nerve impulse. Light energy is absorbed by certain pigments. **Rhodopsins** are the photosensitive pigments found in the eyes of cephalopod mollusks, arthropods, and vertebrates.

Cells are sensitive to radiant energy, including light, but this general sensitivity (found even among protozoa) is not considered photoreception. Some protozoa have eyespots, which are more sensitive to light than the rest of the cell surface, but on the evolutionary scale, the first true light-sensitive organs are found in certain cnidarians and in flatworms. Their photoreceptor organs, comparable to simple eyes, are called **ocelli.** In planarian flatworms they are bowl-shaped structures containing black pigment (Fig. 41–20). At the bottom of the pigment are clusters of light-sensitive cells. The pigment shades these light-sensitive cells from all light except that coming from above and slightly to the front. This arrangement enables the planarian to detect the direction of the source of light. These photoreceptors can also distinguish light intensity. Planarians have other light-sensitive cells over the body surface and therefore can continue to react to light even after their ocelli have been destroyed. However, their responses become random and slow.

Animals with eyespots or very simple eyes can detect light, but they cannot see objects. Effective image formation, called **vision,** requires a more complex eye, usually with a lens that can focus an image on the light-sensitive cells. A necessary first step in the evolution from photoreceptor to true eye, therefore, was the development of a lens to concentrate light on a group of photoreceptors. As better lens systems evolved, the photoreceptors were able to form images, and an eye in the strict sense of the word evolved. Two fundamentally different types of complex eyes are the camera eye of some cephalopods (squids and octopuses) and verte-

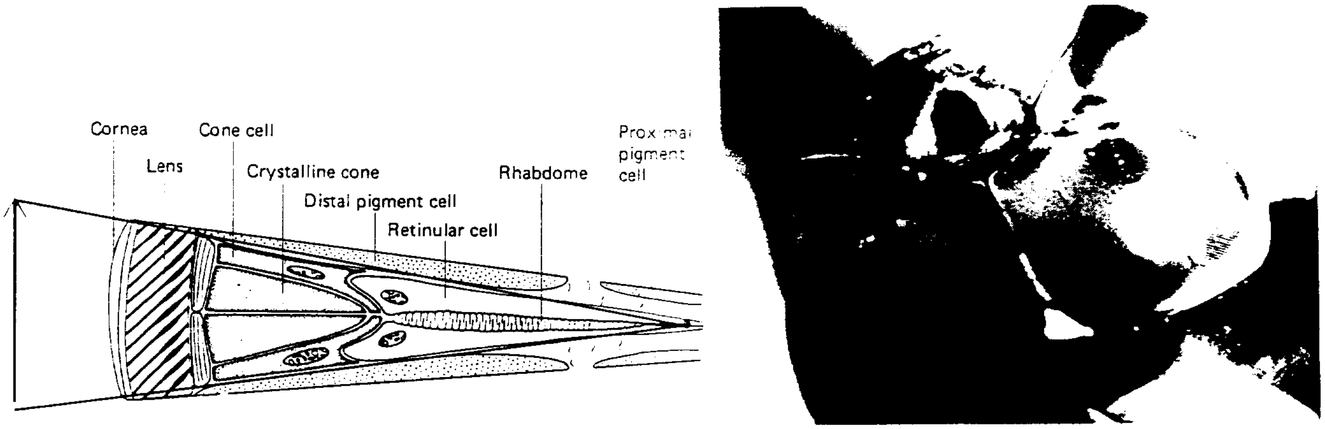


(*a*) Simple mollusk eye (abalone)



(*b*) Octopus eye

(*c*)



(*d*) Arthropod eye (spider)

(*e*)

Figure 41–21 Comparison of different types of eyes. (*a*) Some mollusks have a simple eye that lacks a lens and works like a pinhole camera. (*b*), (*c*) Some cephalopods have eyes that work like vertebrate eyes. An adjustable lens is present. (*d*) A unit from the compound eye of an insect or crustacean. This type of eye registers changes in light and shade so that the insect can detect movement. The compound eyes of most of these organisms do not actually form images. (*e*) The eyes of a darning needle (an insect). ((*c*), Charles Seaborn; (*e*), Luci Giglio.)

brates, and the compound eye of the arthropods (Fig. 41–21). (The vertebrate eye and the cephalopod eyes are analogous structures; that is, they evolved independently of one another and are functionally but not structurally similar.)

THE HUMAN EYE

The eye of a squid or octopus is rather like a simple box camera equipped with "slow" (requiring much light for development) black-and-white film, whereas the human eye is like a 35-millimeter camera loaded with extremely sensitive color film.

The analogy between the human eye and a camera is an especially apt one. The eye (Fig. 41–22) has a **lens** that can be focused for different distances; a diaphragm, the **iris**, which regulates the size of the light opening (the pupil); and a light-sensitive **retina** located at the rear of the eye, corresponding to the film of the

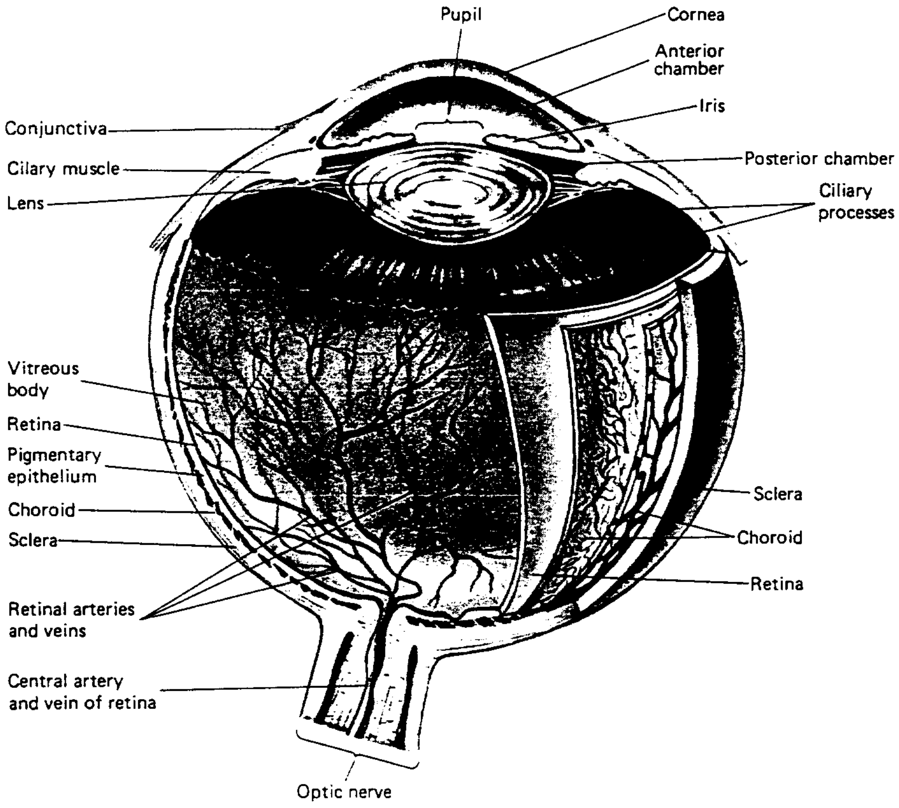


Figure 41–22 Structure of the human eye.

camera. Next to the retina is a sheet of cells filled with black pigment that absorbs extra light and prevents internally reflected light from blurring the image (cameras are also painted black on the inside). This sheet, called the **choroid coat,** also contains the blood vessels that nourish the retina.

The outer coat of the eyeball, called the **sclera,** is a tough, opaque, curved sheet of connective tissue that protects the inner structures and helps to maintain the rigidity of the eyeball. On the front surface of the eye this sheet becomes the thinner, transparent **cornea,** through which light enters.

The lens is a transparent, elastic ball located just behind the iris. It bends the light rays coming in and brings them to a focus on the retina. The lens is aided by the curved surface of the cornea and by the refractive properties of the liquids inside the eyeball. The cavity between the cornea and the lens is filled with a watery substance, the **aqueous fluid.** The larger chamber between the lens and the retina is filled with a more viscous fluid, the **vitreous body.** Both fluids are important in maintaining the shape of the eyeball. The aqueous fluid is secreted by the **ciliary body,** a doughnut-shaped structure that attaches the ligament holding the lens to the eyeball.

The eye has the power of **accommodation,** meaning it can change focus for near or far vision by changing the curvature of the lens. This is made possible by the stretching and relaxing of the lens by the **ciliary muscle,** a part of the ciliary body that is attached to the lens by tiny fibers called zonules. Because of the pressure of the fluids within, the eyeball is under tension transmitted by the ciliary muscle to the lens. Relaxation of the ciliary muscle fibers places tension on the zonules and flattens the lens; this focuses the eye for far vision, the condition of the eye at rest. When contracted, tension on the zonules lessens, the elastic lens assumes a more spherical shape for near vision.

As people grow older, the lens enlarges and becomes less elastic and thereby less able to accommodate for near vision. When this occurs, spectacles with one portion ground for distance vision and one portion ground for near vision (bifocals) may be worn to accomplish what the eye can no longer do.

The amount of light entering the eye is regulated by the **iris,** a ring of smooth muscle that appears as blue, green, or brown, depending on the amount and nature of pigment present. The iris is composed of two mutually antagonistic sets of muscle fibers; one that is arranged circularly and contracts to decrease the size of the pupil, and one that is arranged radially and contracts to increase the size of the pupil. The response of these muscles to changes in light intensity is not instantaneous, but requires from 10 to 30 seconds. Thus when a person steps from a light to a dark area, some time is needed for the eyes to adapt to the dark, and when a person steps from a dark room to a brightly lighted area, the eyes are dazzled until the size of the pupil is decreased. The retina of the eye (soon to be discussed) is also able to adapt to changes in light intensity.

Each eye has six muscles stretching from the surface of the eyeball to various points in the bony socket. These enable the eye as a whole to move and be oriented in a given direction. These muscles are innervated by cranial nerves in such a way that the eyes normally move together and focus on the same area.

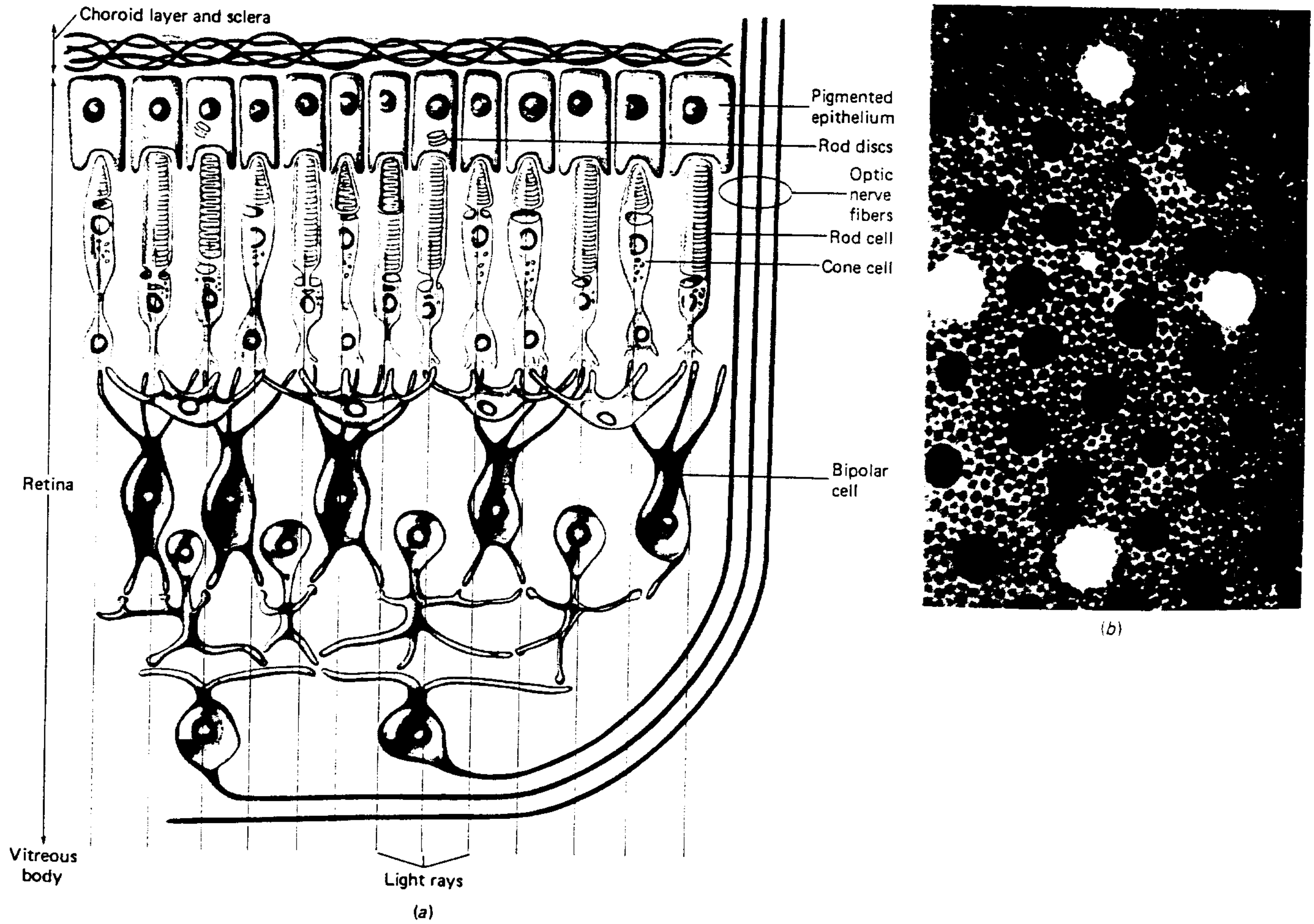
The light-sensitive part of the human eye is the retina, a hemisphere made up of an abundance of receptor cells called, according to their shape, **rods** and **cones.** There are about 125 million rods and 6.5 million cones. In addition, the retina contains many sensory and connector neurons and their axons. Curiously, the sensitive cells are at the *back* of the retina; to reach them, light must pass through several layers of connecting neurons (Fig. 41–23).

At a point in the back of the eye, the individual axons of the sensory neurons unite to form the **optic nerve,** which then passes out of the eyeball. Here there are no rods and cones. This area is called the "blind spot" since images falling on it cannot be perceived. Its existence can be demonstrated by closing the left eye and focusing the right eye on the X in Figure 41–24. Starting with the page about 13 cm from the eye, move it away until the circle disappears. At that position the image of the circle is falling on the blind spot and so is not perceived.

In the center of the retina, directly in line with the center of the cornea and lens, is the region of keenest vision, a small depressed area called the **fovea.** Here are concentrated the light-sensitive cones, responsible for bright-light vision, for the perception of fine detail, and for color vision.

The other light-sensitive cells, the rods, are more numerous in the periphery of the retina, away from the fovea. These function in twilight or dim light and are

Figure 41–23 The retina. (*a*) Neuronal connections in the retina. The elaborate interconnections among the various layers of cells allow them to interact and to influence one another in a number of ways. (*b*) High-power view of the retinal surface, showing the geometric, spatial arrangement of the cone cells. Blue-sensitive cones appear as bright spots in this photomicrograph. Cones sensitive to others colors of light appear as dark, round holes. Rods appear as a dark cobblestone mesh interspersed among the various cones. The brain infers the color of light by observing the pattern of cone response in the part of the retina on which the light is falling. If the bright cones were responding more than the others, the light would appear blue. (Courtesy of Francisco M. de Monasterio, S. J. Schein, and E. P. McCrane.)



(*a*)

(*b*)

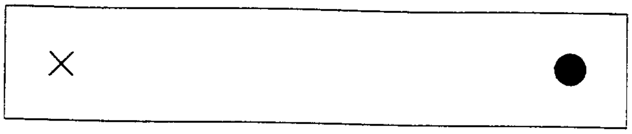


Figure 41–24 Demonstration of the blind spot on the retina. See text for details.

insensitive to colors. We are not ordinarily aware that only those objects more or less directly in front of our eyes can be perceived in color, but this can be demonstrated by a simple experiment. Close one eye and focus the other on some point straight ahead. As a colored object is gradually brought into view from the side, you will be aware of its presence and of its size and shape before you are aware of its color. Only when the object is brought closer to the direct line of vision, so that its image falls on a part of the retina containing cones, can its color be determined. The rods are actually more sensitive in dim light than are the cones. Since the rods are located not in the center but in the periphery of the retina, it is a curious fact that you can see an object better in dim light if you look at it not directly (when its image would fall on the cones in the center of the retina) but slightly to one side of it, so that its image falls on the rods in the periphery of the retina.

The Chemistry of Vision

The substance primarily responsible for the ability to see is **rhodopsin** (also called visual purple), found only in the rod cells, together with a series of very closely related pigments found in the cone cells. Rhodopsin consists of a large protein called opsin, chemically joined with a carotenoid called **retinal,** which is made from vitamin A. Two isomers of retinal exist: the 11-*cis* form and the all-*trans* form.

When light strikes rhodopsin, it transforms **11-*cis* retinal** to **all-*trans*-retinal.** This change in shape causes the breakdown of rhodopsin into its components, opsin and retinal. The breakdown somehow triggers a depolarization of the rod cell that contains the rhodopsin; this in turn produces an impulse that is transmitted to other neurons in the retina, and, if not inhibited, ultimately to the brain. The all-*trans* retinal is converted back to the 11-*cis* form by an enzyme. Then the retinal combines with opsin to produce rhodopsin once again. This sequence of reactions is known as the visual cycle (Fig. 41–25).

It has been shown that a single quantum of light can be absorbed by a single molecule of rhodopsin and lead to the excitation of a single rod. When the eye is exposed to a flash of light lasting only a millionth of a second, it sees an image of light that persists for nearly a tenth of a second. This is the length of time that the retina remains stimulated following a flash. This persistence of images in the retina enables your eye to fuse the successive flickering images on a motion picture or screen, so that what is actually a rapid succession of still pictures is perceived as moving persons and objects.

The ability to see an exceedingly faint light depends on the amount of rhodopsin present in the retinal rods. This in turn depends on the relative rates of synthesis and breakdown of rhodopsin. In bright light, much of the rhodopsin is broken down to free retinal and opsin. The synthesis of rhodopsin is a relatively slow process, and the concentration of rhodopsin in the retina is never very great so long as the eye is exposed to bright light. When the eye is suitably shielded from light, the breakdown of rhodopsin is prevented and its concentration gradually builds up until essentially all of the opsin has been converted to rhodopsin. The sensitivity of the eye to light, a function of the amount of rhodopsin present, can increase 1 million-fold if the eye is dark-adapted for as much as an hour.

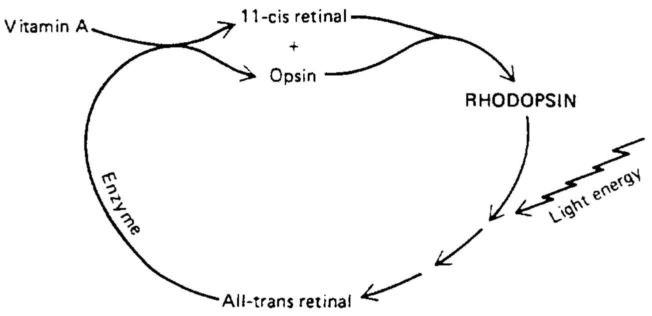


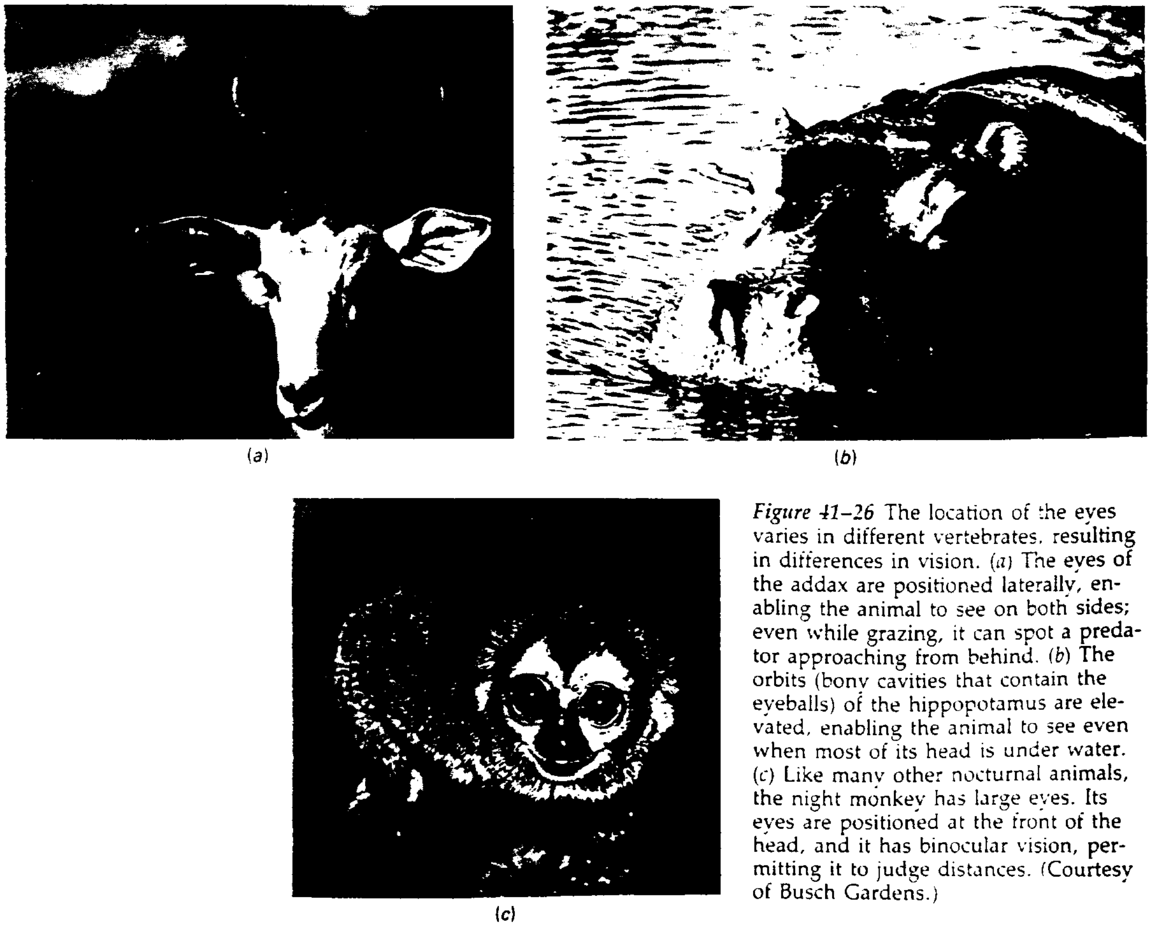
Figure 41–25 The visual cycle. When light strikes rhodopsin, it breaks down depolarizing the rod cell which contains it. This produces an impulse. See text for further explanation.

Color Vision

The chemistry of the cones and of color vision is less well understood. There are three different types of cones and three different cone pigments. One cone pigment, **iodopsin**, is composed of retinal and an opsin different from that found in the rods. The cones are considerably less sensitive to light than the rods and cannot provide vision in dim light. The prime function of the cones is to perceive colors. The evidence from certain psychological tests is consistent with the hypothesis that there are three different types of cones, which respond respectively to blue, green, and red light. This has been substantiated recently by the extraction of three kinds of color receptors—red, green, and blue—from human and other primate retinas. Each type can respond to light with a considerable range of wavelengths. The green cones, for example, can respond to light of any wavelength from 450 to 675 nanometers (i.e., blue, green, yellow, orange, and red light), but they respond to green light more strongly than to any of the others. Intermediate colors other than blue, green, and red are perceived by the simultaneous stimulation of two or more types of cones. The "red" cones are actually more sensitive to yellow light than to red, but they respond to red before any of the others do, and therefore behave as red receptors. By a comparison of the rate at which various receptors respond, the brain is able to detect light colors of intermediate frequency. Color blindness results when one or more of the three types of cones is absent. This is an inherited sex-linked condition (see Chapter 11).

Binocular Vision and Depth Perception

The position of the eyes in the head of humans and certain other higher vertebrates permits both of them to be focused on the same object (Fig. 41-26). This **binocular vision** is an important factor in judging distance and depth. To focus on a near object, the eyes must converge (turn inward so that the animal becomes slightly cross-eyed). The proprioceptors in the eye muscles causing this convergence are


(a)

(b)

(c)

Figure 41-26 The location of the eyes varies in different vertebrates, resulting in differences in vision. (*a*) The eyes of the addax are positioned laterally, enabling the animal to see on both sides; even while grazing, it can spot a predator approaching from behind. (*b*) The orbits (bony cavities that contain the eyeballs) of the hippopotamus are elevated, enabling the animal to see even when most of its head is under water. (*c*) Like many other nocturnal animals, the night monkey has large eyes. Its eyes are positioned at the front of the head, and it has binocular vision, permitting it to judge distances. (Courtesy of Busch Gardens.)

stimulated by this contraction to send impulses to the brain. Thus part of judgment of distance and depth depends upon impulses originating when the sensory fibers in those muscles are stimulated. In addition, the eyes, being some distance apart (a little over 5 cm in humans), see things from slightly different angles and therefore get slightly different views of a close object. The images of a given object that the two eyes perceive differ most for a near object and least for a distant object. By comparing the differences, the brain is able to infer distances. Depth perception is also made possible by the differential size of near and far objects on the retina, by perspective, by overlap and shadow, by distance over the horizon, and by the increasing dimness of distant objects.

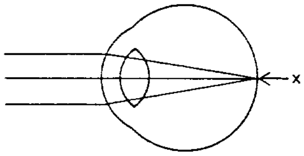
Defects in Vision

The most common defects of the human eye are **nearsightedness** (myopia), **farsightedness** (hypermetropia), and **astigmatism.** In the normal eye, as shown in Figure 41–27(*a*), the shape of the eyeball is such that the retina is the proper distance behind the lens for the light rays to converge in the fovea. In a nearsighted eye, illustrated in Figure 41–27(*b*), the eyeball is too long and the retina is too far from the lens. The light rays converge at a point in front of the retina, and are again diverging when they reach it, resulting in a blurred image. In a farsighted eye, the eyeball is too short and the retina too close to the lens (part (*c*) of the figure). Light rays strike the retina before they have converged, again resulting in a blurred image. Concave lenses correct for the nearsighted condition by bringing the light rays to a focus at a point farther back, and convex lenses correct for the farsighted condition by causing the light rays to converge farther forward.

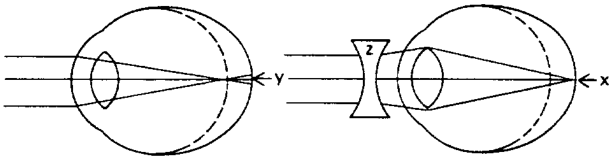
In astigmatism the cornea is curved unequally in different planes, so that the light rays in one plane are focused at a different point from those in another plane, as shown in Figure 41–27(*d*). To correct for astigmatism, lenses must be ground unequally to compensate for the unequal curvature of the cornea.

THE COMPOUND EYE

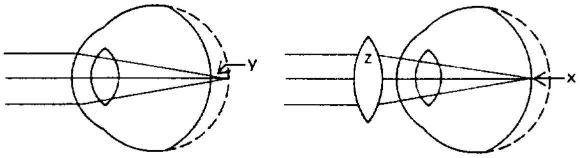
Compound eyes are found in crustaceans and insects. Not only do these eyes look different from vertebrate eyes, but they also see differently (Fig. 41–28). The surface of a compound eye appears faceted. Each **facet** is the convex cornea of one of its



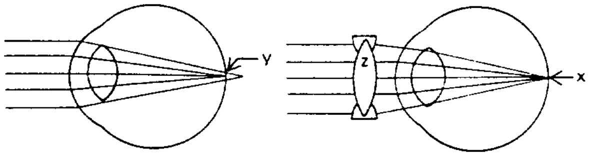
(*a*) Normal eye



(*b*) Nearsighted eye



(*c*) Farsighted eye



(*d*) Astigmatic eye

x, Sharp image y, Blurred image z, Correction

Figure 41–27 Common abnormalities of the eye that result in defects in vision. (*a*) Normal eye, in which parallel rays coming from a point in space are focused as a point on the retina. (*b*) Nearsighted eye, in which the eyeball is elongated so that parallel light rays are brought to a focus in front of the retina (on dotted line, which represents the position of the retina in a normal eye) and so form a blurred image on the retina. This is corrected by placing a concave lens in front of the eye, which diverges the light rays, making it possible for the eye to focus these rays on the retina. (*c*) Farsighted eye, in which the eyeball is shortened and light rays are focused behind the retina. A convex lens converges the light rays so that the eye focuses them onto the retina. (*d*) Astigmatic eye, in which light rays passing through one part of the eye are focused on the retina, while light rays passing through another area of the lens are not focused on the retina. This is a result of the unequal curvature of the lens or cornea. A cylindrical lens corrects this by bending light rays going through only certain parts of the eye.

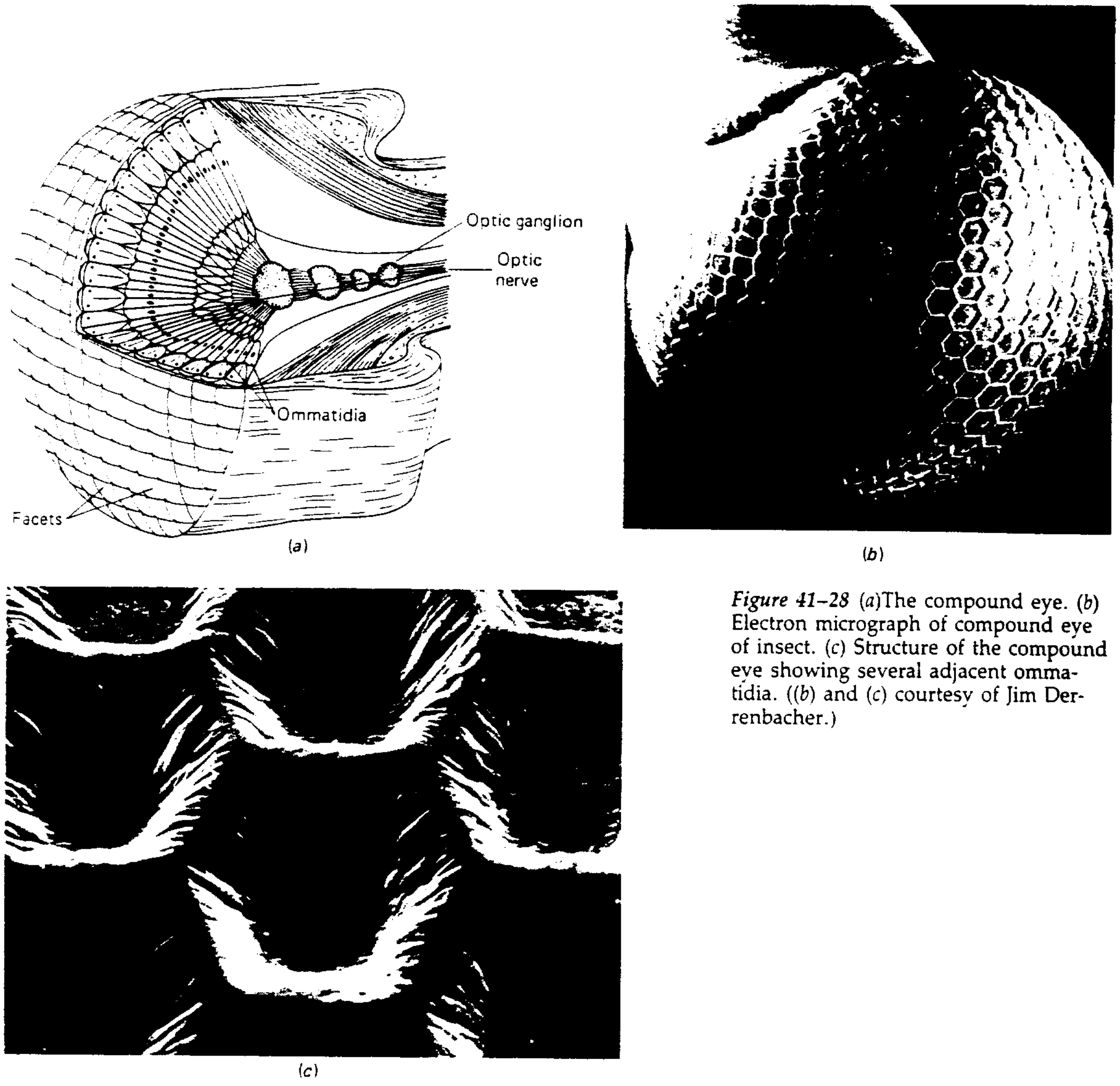


Figure 41–28 (*a*)The compound eye. (*b*) Electron micrograph of compound eye of insect. (*c*) Structure of the compound eye showing several adjacent ommatidia. ((*b*) and (*c*) courtesy of Jim Derrenbacher.)

visual units called an **ommatidium.** The number of ommatidia varies in different species. For example, there may be only 20, as in the eye of certain crustaceans, or as many as 28,000, as in the eye of a dragonfly.

Each ommatidium consists of a cornea, a lens, and a light-sensitive **rhabdome,** the central core of the ommatidium. The rhabdome is surrounded by retinular cells, which transmit the sensory stimulus (Fig. 41–29). A sheath of pigmented cells envelops each ommatidium. Arthropod eyes usually adapt to different intensities of light. In nocturnal and crepuscular (dark- or dusk-loving) insects and many crustaceans, pigment is capable of migrating proximally and distally. When the pigment is in the proximal position, each ommatidium is shielded from its neighbor and only light entering directly along its axis can stimulate the receptors. When the pigment is in the distal position, light striking at an angle may pass through several ommatidia and stimulate many retinal units. As a result, in dim light, sensitivity of the eye is increased, and in bright light, the eye is protected from excessive stimulation. Pigment migration is under neural control in insects and under hormonal control in crustaceans. In some species it follows a daily rhythm.

Compound eyes do not perceive form well. Although the lens system of each ommatidium is adequate to focus a small inverted image on the retinular cells, there is no evidence that such images are actually perceived as images by the organism. However, all the ommatidia together do produce a composite image. Each ommatidium, in gathering a point of light from a narrow sector of the visual field, is in fact

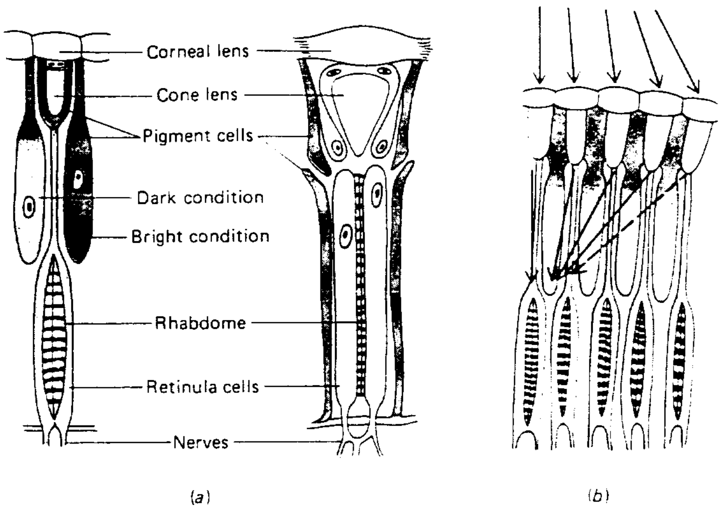


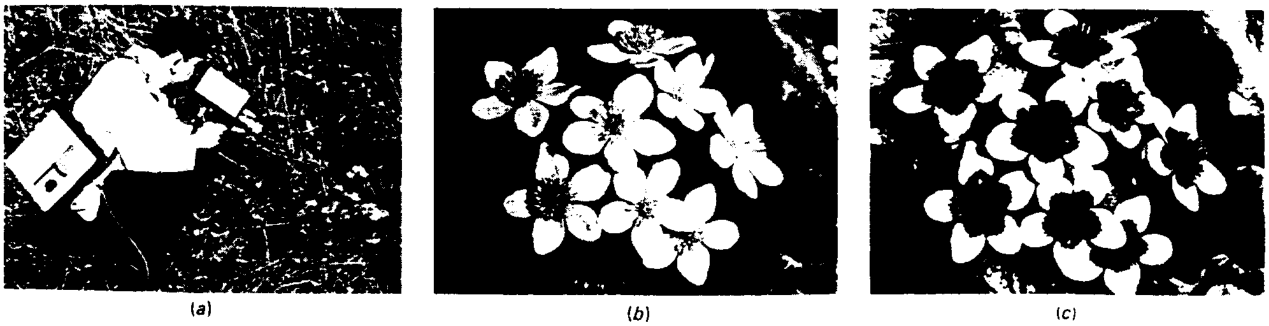
Figure 41–29 (*a*) Insect ommatidia, showing a diurnal type (*left*) and a nocturnal type (*right*). In the diurnal type, the pigment is shown in two positions: adapted for very dark conditions on the left side, and for relatively bright conditions on the right. (*b*) Nocturnal type of eye adapted for dark conditions, showing how light can be concentrated upon one rhabdome from several lenses. If the pigment moved downward, light from peripheral lenses would be screened out.

sampling a mean intensity from that sector. All of these points of light taken together form a **mosaic** picture. To appreciate the nature of this mosaic picture we need only look at a newspaper photograph through a magnifying glass; it is a mosaic of many dots of different intensities. The clearness and definition of the picture will depend upon how many dots there are per unit area—the more dots, the better the picture. So it is with the compound eye. The image as perceived by the animal is probably much better in quality than might be suspected from the structure of the compound eye. The nervous system of an insect is apparently capable of image processing similar to that employed to improve the quality of photographs sent to the earth by robot spacecraft.

Although the compound eye can form only coarse images, it compensates for this by being able to follow **flicker** to higher frequencies. Flies are able to detect flickers up to about 265 per second. In contrast, the human eye can detect flickers of only 45 to 53 per second; because flickering lights fuse above these values, we see motion pictures as smooth movement and the ordinary 60-cycle light in the room as steady. To an insect, both motion pictures and room lighting must flicker horribly. However, because the insect has such a high critical flicker fusion rate, any movement of prey or enemy is immediately detected by one of the eye units. Hence the compound eye is peculiarly well-suited to the arthropod's way of life.

Compound eyes are superior to our eyes in two other respects. They are sensitive to different wavelengths of light ranging from the red into the ultraviolet (UV), and they are able to analyze the **plane of polarization** of light. Accordingly, an insect can see UV light well, and its world of color is much different from ours. Since different flowers deflect UV light to different degrees, two flowers that appear identically colored to us may appear strikingly different to insects. How the world appears to an insect with UV vision can be appreciated by viewing the landscape through a television camera with an UV light-transmitting lens (Fig. 41–30). A sky that appears equally blue to us in all quadrants reveals quite different patterns to an insect, because the plane of polarization of the light is not the same in all parts of the sky, and the insect's eye can detect the difference. Honey bees and some other arthropods employ this ability as a navigational aid.

Figure 41–30 (*a*) UV video-viewing of marsh marigolds, *Caltha palustris*, in the field. (*b*) The marsh marigold appears to be uniformly yellow to the human eye. (*c*) When viewed with UV film the flowers have darker areas that represent light-absorbing centers. (From Eisner, T.: *Science* 28: 1172, 1969.)



(*a*) (*b*) (*c*)

SUMMARY

I. A sense organ consists of one or more receptor cells, and sometimes, accessory cells. Receptor cells may be neuron endings or specialized cells in close contact with neurons.

II. Exteroceptors are sense organs that receive information from the outside world. Proprioceptors are sense organs within muscles, tendons, and joints, which enable the animal to perceive orientation of the body and position of its parts. Interoceptors are sense organs within body organs.

III. Sense organs also may be classified on the basis of the type of energy to which they respond. Thus there are mechanoreceptors, chemoreceptors, photoreceptors, thermoreceptors, and electroreceptors.

IV. Receptor cells absorb energy, transduce that energy into electrical energy, and produce receptor potentials.

V. Adaptation of a receptor to a continuous stimulus results in diminished perception. For this reason, adaptation to an unpleasant odor or noise occurs after a few moments.

VI. Mechanoreceptors respond to touch, pressure, gravity, stretch, or movement.
  - *A.* The tactile receptors in the skin are mechanoreceptors that respond to mechanical displacement of hairs or of the receptor cells themselves.
  - *B.* Statocysts are gravity receptors found in many invertebrates.
    1. When the position of the statolith within the statocyst changes, hairs of receptor cells are bent.
    2. Messages sent to the CNS inform an animal which hairs have been stimulated; from this the animal can determine where "down" is, and can correct for any abnormal orientation.
  - *C.* Lateral line organs supplement vision in fish and some amphibians by informing the animal of moving objects or objects in its path.
  - *D.* Muscle spindles, Golgi tendon organs, and joint receptors are proprioceptors that respond continuously to tension and movement in the muscles and joints.
  - *E.* The saccule and utricle of the vertebrate ear contain otoliths that change position when the head is tilted or when the body is moving forward. The hair cells stimulated by the otoliths send impulses to the brain, enabling the animal to perceive the direction of gravity.
  - *F.* The semicircular canals of the vertebrate ear inform the brain about turning movements. Their cristae are stimulated by movements of the endolymph.
  - *G.* The organ of Corti within the cochlea is the auditory receptor in birds and mammals.
    1. Sound waves pass through the external auditory meatus, cause the eardrum to vibrate, and are transmitted through the middle ear by the hammer, anvil, and stirrup.
    2. Vibrations pass through the oval window to fluid within the vestibular duct. Pressure waves press upon the membranes separating the three ducts of the cochlea.
    3. Movements of the basilar membrane rub the hair cells of the organ of Corti against the overlying tectorial membrane, thus stimulating them.
    4. Nerve impulses are initiated in the dendrites of the auditory neurons lying at the base of each hair cell.

VII. Chemoreceptors include receptors for taste and smell.
  - *A.* Taste receptors are specialized epithelial cells located in taste buds.
  - *B.* The olfactory epithelium contains specialized olfactory cells with axons that extend upward as fibers of the olfactory nerves.

VIII. Thermoreceptors are important in warm-blooded animals in providing cues about body temperature. In some invertebrates they are used to locate a warm-blooded host.

IX. Photoreceptors in very simple eyes detect light, but these eyes do not form images effectively. Effective image formation and interpretation is called vision.
  - *A.* In the human eye, light enters through the cornea, is focused by the lens, and sensed as an image by the retina. The iris regulates the amount of light that can enter.
  - *B.* When light strikes rhodopsin in the rod cells, a chemical change in retinal occurs that breaks down the rhodopsin, triggering depolarization of the rod cell.
  - *C.* The rods form images in black and white, whereas the cones function in color vision.
  - *D.* The compound eye found in insects and crustaceans consists of ommatidia, which collectively form a mosaic image.

POST-TEST

1. A sense organ consists of one or more ______________ cells and, sometimes, ______________ cells.

2. Exteroceptors are sense organs that ______________; proprioceptors enable an animal to perceive ______________, along with the ______________ of the body as a whole.

3. ______________ detect light energy; ______________ respond to touch, gravity, or movement.

4. Receptor cells absorb ______________, transduce this energy into ______________ energy, and produce a ______________ ______________.

5. The diminishing response of a receptor to a continued, constant stimulus is called ______________.

6. Statocysts serve as ______________ receptors; their action depends upon mechanical displacement of receptor cell hairs by change in position of a ______________.

7. The lateral line organ of fishes is thought to supplement ______________; its canals are lined with recep-

tor cells that have ____________; the receptor cells secrete a mass of gelatinous material called a ____________.

8. Three main types of vertebrate proprioceptors are ____________ ____________, which detect muscle movement; ____________ ____________ organs, which determine stretch in tendons; and ____________ receptors, which detect movement in ligaments.

9. Phasic receptors respond only to ____________; tonic sense organs respond as long as the ____________ is present.

10. ____________ are balancing organs that stabilize flight in flies.

11. The basic function of the vertebrate ear is to help maintain ____________.

12. The inner ear consists of interconnected canals and sacs called the ____________; in jawed vertebrates this structure consists of two saclike chambers, the ____________ and ____________, and three ____________ canals, as well as the cochlea.

13. The rocks in your head (within the saccule and utricle) called ____________ are actually ____________ detectors.

14. Each semicircular canal is filled with fluid called ____________; at one of the openings of each canal into the utricle is a small enlargement, the ____________.

15. The cochlea, located in the ____________ ear, contains mechanoreceptor hair cells that detect ____________ waves.

16. The actual auditory receptor is the organ of ____________; it is located within the ____________ canal.

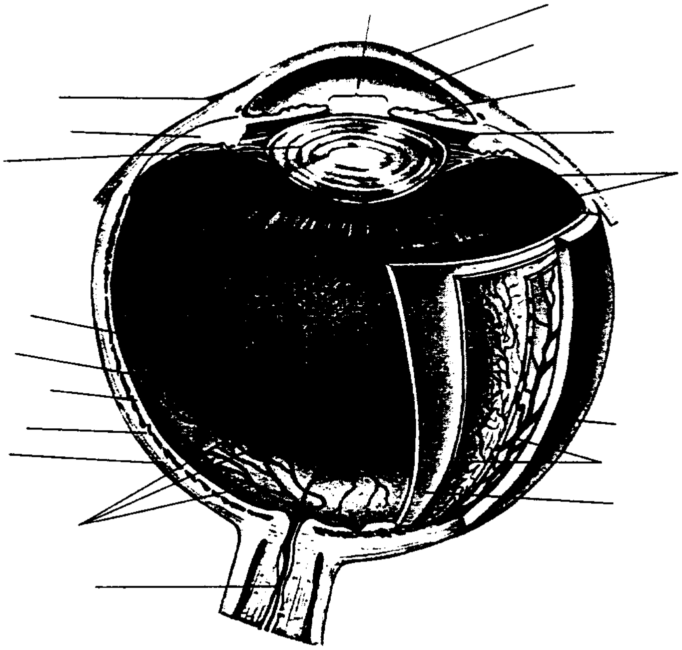
17. The senses of taste and smell depend upon ____________.

18. The photosensitive pigments in the eyes of vertebrates and arthropods are ____________.

Select the most appropriate answer in Column B for each description in Column A.

Column A	*Column B*
19. Light-sensitive part of human eye	a. Ommatidium
20. Regulates size of pupil	b. Cones
21. Perceive color	c. Retina
22. Region of keenest vision	d. Iris
23. Visual unit in compound eye	e. Fovea

24. Label the diagram below. (Refer to Fig. 41–22 as necessary.)



REVIEW QUESTIONS

1. What are mechanoreceptors? Give three examples.
2. What is a proprioceptor? What is its function in the mammalian body?
3. How do anesthetics reduce or eliminate the sensation of pain?
4. Draw a diagram of the human eye, labeling all parts. How are rods and cones distributed in the retina?
5. Discuss the mechanism by which photoreceptors are stimulated by light. What is the function of rhodopsin? How is it regenerated?
6. Describe the anatomical abnormality that produces each of the following visual defects:
    - *a.* myopia
    - *b.* hypermetropia
    - *c.* astigmatism
7. How does the human eye adjust to near and far vision and to bright and dim lights?
8. Draw a diagram of the human ear, labeling all parts.
9. Discuss the mechanism by which the sensory cells of the ear are stimulated by sound waves.
10. What are otoliths and what is their role in maintaining equilibrium?
11. Contrast the function of the insect's compound eye with that of the vertebrate eye.