Osmoregulation Among Aquatic Vertebrates

Most vertebrates **osmoregulate**—that is, maintain particular ion concentrations in their blood. Osmoregulation is absolutely essential to maintain *homeostasis*, the relative constancy of the internal environment. This is a necessity because ions such as Na⁺, Ca²⁺, K⁺, and PO⁴⁻ greatly affect the workings of the body systems, such as the skeletal, nervous, and muscular systems.

Osmoregulation in general is necessary because few vertebrates have blood that is isotonic to seawater. Not so for the cartilaginous fishes (Fig. 36.3), whose blood is isotonic to seawater, for reasons we will now discuss.

Cartilaginous Fishes

The total concentration of the various ions in the blood of cartilaginous fishes is less than that in seawater. Their blood plasma is nearly isotonic to seawater because they pump it full of urea, and this molecule gives their blood the same tonicity as seawater. Cartilaginous fishes do regulate the concentration of other solutes in their blood and have rectal glands that rid the body of excess salt.

Marine Bony Fishes

A marine environment, which is high in salts, is hypertonic to the blood plasma of bony fishes. Apparently, their common ancestor evolved in fresh water, and only later did some groups invade the sea. Therefore, marine bony fishes must avoid the tendency to become dehydrated (Fig. 36.4a). As the sea washes over their gills, marine bony fishes lose water by osmosis. To counteract this, they drink seawater almost constantly. On the average, marine bony fishes swallow an amount of water equal to 1% of their body weight every hour. This is equivalent to a human drinking about 700 ml of water every hour around the clock. But while they get water by drinking, this habit also causes these fishes to acquire salt. To rid the body of excess salt, they actively transport it into the surrounding seawater at



FIGURE 36.3 Osmoregulation in a shark.

The blood of a shark is isotonic to seawater because the blood contains a high concentration of urea.

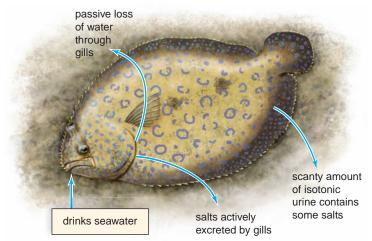
the gills. The kidneys conserve water, and marine bony fishes produce a scant amount of isotonic urine.

Freshwater Bony Fishes

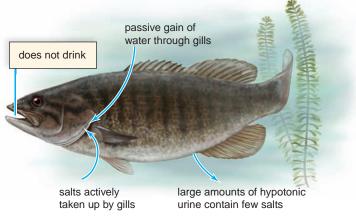
The osmotic problems of freshwater bony fishes and the response to their environment are exactly opposite those of marine bony fishes (Fig. 36.4b). Freshwater fishes tend to gain water by osmosis across the gills and the body surface. As a consequence, these fishes never drink water. They actively transport salts into the blood across the membranes of their gills. They eliminate excess water by producing large quantities of dilute (hypotonic) urine. They discharge a quantity of urine equal to one-third their body weight each day.

Osmoregulation Among Terrestrial Vertebrates

Desert mammals, such as the kangaroo rat, and seabirds, such as a seagull, illustrate different strategies for dealing with extreme terrestrial environments.



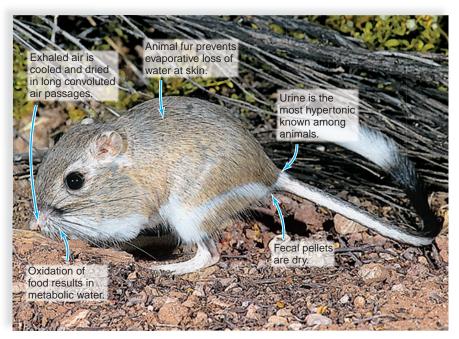
a. Marine bony fish



b. Freshwater bony fish

FIGURE 36.4 Body fluid regulation in bony fishes.

 ${f a.}$ Marine bony fishes employ different mechanisms compared to ${f (b)}$ freshwater fishes in order to osmoregulate their body fluids.



Kangaroo Rat

Dehydration threatens all terrestrial animals, especially those that live in a desert, as does the kangaroo rat. Its fur prevents loss of water to the air, and during the day, it remains in a cool burrow. In addition, the kangaroo rat's nasal passage has a highly convoluted mucous membrane surface that captures condensed water from exhaled air. Exhaled air is usually full of moisture, which is why you can see it on cold winter mornings—the moisture in exhaled air is condensing.

As we shall see, humans mainly conserve water by producing urine that is hypertonic to blood plasma. The kangaroo rat forms a very concentrated urine—20 times more concentrated than its blood plasma. Also, its fecal material is almost completely dry.

Most terrestrial animals need to drink water occasionally to make up for the water lost from the skin and respiratory passages and through urination. However, the kangaroo rat is so adapted to conserving water that it can survive by using metabolic water derived from cellular respiration, and it never drinks water (Fig. 36.5). The adaptations of the kangaroo rat allow it to remain in water-salt balance, even under desert conditions.

Seagulls, Reptiles, and Mammals

Birds, reptiles, and mammals evolved on land, and their kidneys are especially good at conserving water. However, some animals have become secondarily adapted to living near or in the sea. They drink seawater and still manage to survive. If humans drink seawater, we lose more water than we take in just ridding the body of all that salt. Little is known about how whales manage to get rid of extra salt, but we know that their kidneys are enormous. Other animals have been studied, and we have learned that seabirds and reptiles have salt glands that pump out salt (Fig. 36.6). In the two types of animals we

FIGURE 36.5 Adaptations of a kangaroo rat to a dry environment.

A kangaroo rat minimizes water loss in the many ways noted.

will mention, each has commandeered a gland meant for another purpose and used it to pump out the salt from blood plasma and leave behind the water, just as in a desalination plant.

In birds, salt-excreting glands are located near the eyes. The glands produce a salty solution that is excreted through the nostrils and moves down grooves on their beaks until it drips off. In marine turtles, the salt gland is a modified tear (lacrimal) gland, and in sea snakes, a salivary sublingual gland beneath the tongue gets rid of excess salt. The work of the gland is regulated by the nervous system. Osmoreceptors, perhaps located near the heart, are thought to stimulate

the brain, which then orders the gland to excrete salt until the salt concentration in the blood decreases to a tolerable level.

Check Your Progress

36.1

- I. What is the advantage of excreting urea instead of ammonia or uric acid?
- 2. Earthworms have a thin skin for respiration. If they had thicker skin, would it affect the function of the nephridia?
- 3. What evidence do we have that excess salt does not enter the body of a shark?
- 4. Would the tonicity of the urine produced by a seagull be greater than that produced by a human? Explain.

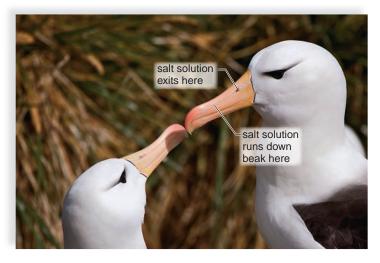


FIGURE 36.6 Adaptations of marine birds to a high salt environment.

Many marine birds and reptiles have glands that pump salt out of the body.

36.2 Urinary System in Humans

The urinary system of humans contains excretory organs called the kidneys (Fig. 36.7). The kidneys are the chief organs of homeostasis in the human body because they are the ultimate regulators of blood composition, as we shall see.

The human **kidneys** are bean-shaped, reddish-brown organs, each about the size of a fist. They are located on either side of the vertebral column just below the diaphragm, in the lower back, where they are partially protected by the lower rib cage. The right kidney is slightly lower than the left kidney. **Urine** [Gk. *urina*, urine] made by the kidneys is conducted from the body by the other organs in the urinary system. Each kidney is connected to a **ureter**, a duct that takes urine from the kidney to the **urinary bladder**, where it is stored until it is voided from the body through the single **urethra**. In males, the urethra passes through the penis, and in females, the opening of the urethra is ventral to that of the vagina. There is no connection between the genital (reproductive) and urinary systems in females, but there is a connection in males. In males, the urethra also carries sperm during ejaculation.

Kidneys

If a kidney is sectioned longitudinally, three major parts can be distinguished (Fig. 36.8). The **renal cortex**, which is the outer region of a kidney, has a somewhat granular appearance. The **renal medulla** consists of six to ten cone-shaped renal pyramids that lie on the inner side of the renal cortex. The innermost part of the kidney is a hollow chamber called the **renal pelvis**. Urine collects in the renal pelvis and then is carried to the bladder by a ureter.

A kidney stone or renal calculus is a hard granule of phosphate, calcium, protein, or uric acid that forms in the renal pelvis. Many are passed unnoticed. However, larger and jagged stones can block the renal pelvis or ureter causing intense pain and damage.

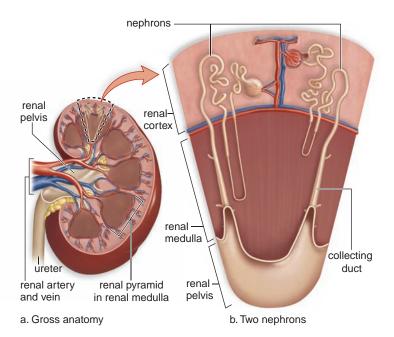
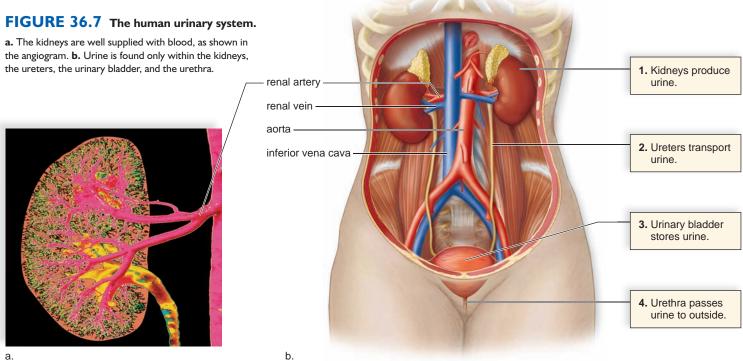


FIGURE 36.8 Macroscopic and microscopic anatomy of the kidney.

a. Longitudinal section of a kidney, showing the location of the renal cortex, the renal medulla, and the renal pelvis. **b.** An enlargement of one renal lobe, showing the placement of nephrons.

Nephrons

Microscopically, each kidney is composed of over 1 million tiny tubules called **nephrons** [Gk. *nephros*, kidney]. The nephrons of a kidney produce urine. Some nephrons are located primarily in the renal cortex, but others dip down into the renal medulla, as shown in Figure 36.8b. Each nephron is made of several parts (Fig. 36.9). The blind end of a nephron is



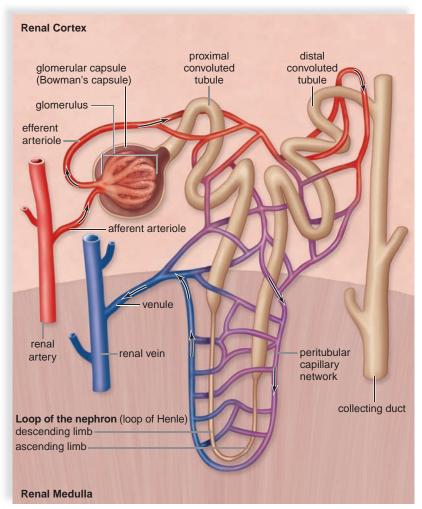
pushed in on itself to form a cuplike structure called the glomerular capsule [L. glomeris, ball] (Bowman's capsule). The outer layer of the glomerular capsule is composed of squamous epithelial cells; the inner layer is composed of specialized cells that allow easy passage of molecules. Leading from the glomerular capsule is a portion of the nephron known as the **proximal convoluted tubule** [L. *proximus*, nearest], which is lined by cells with many mitochondria and tightly packed microvilli. Then, simple squamous epithelium appears in the loop of the nephron (loop of Henle), which has a descending limb and an ascending limb. This is followed by the distal convoluted tubule [L. distantia, far]. Several distal convoluted tubules enter one collecting duct. The collecting duct transports urine down through the renal medulla and delivers it to the renal pelvis. The loop of the nephron and the collecting duct give the pyramids of the renal medulla their striped appearance (see Fig. 36.8).

Each nephron has its own blood supply (Fig. 36.9). The renal artery branches into numerous small arteries, which branch into arterioles, one for each nephron. Each arteriole, called an afferent arteriole, divides to form a capillary bed, the **glomerulus** [L. *glomeris*, ball], which is surrounded by the glomerular capsule. The glomerulus drains into an efferent arteriole, which subsequently branches into a second capillary bed around the tubular parts of the nephron. These capillaries, called peritubular capillaries, lead to venules that join to form veins leading to the renal vein, a vessel that enters the inferior vena cava.

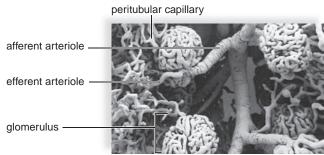
Urine Formation

An average human produces between 1 and 2 liters of urine daily. Urine production requires three distinct processes (see Fig. 36.11), and, as you can see, the entire tubule portion of a nephron participates in the last two steps in urine formation:

- glomerular filtration at the glomerular capsule;
- tubular reabsorption at the convoluted tubules; and
- tubular secretion at the convoluted tubules.



a. A nephron and its blood supply



b. Surface view of glomerulus and its blood supply

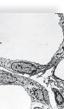


c. Cross sections of proximal and distal convoluted tubules

ascending limb descending limb

capillaries

collecting duct



 $10 \, \mu m$

20 μm

d. Cross sections of a loop of nephron limbs and collecting duct. (The other cross sections are

those of capillaries.)

FIGURE 36.9 Nephron anatomy.

a. You can trace the path of blood about a nephron by following the arrows. A nephron is made up of a glomerular capsule, the proximal convoluted tubule, the loop of the nephron, the distal convoluted tubule, and the collecting duct. The micrographs in (b), (c), and (d) show these structures.

Glomerular Filtration

Glomerular filtration (see Fig. 36.11) is the movement of small molecules across the glomerular wall into the glomerular capsule as a result of blood pressure. When blood enters the glomerulus, blood pressure is sufficient to cause small molecules, such as water, nutrients, salts, and wastes, to move from the glomerulus to the inside of the glomerular capsule, especially since the glomerular walls are 100 times more permeable than the walls of most capillaries elsewhere in the body. The molecules that leave the blood and enter the glomerular capsule are called the glomerular filtrate. Plasma proteins and blood cells are too large to be part of this filtrate, so they remain in the blood as it flows into the efferent arteriole.

Glomerular filtrate is essentially protein free, but otherwise it has the same composition as blood plasma. If this composition were not altered in other parts of the nephron, death from loss of nutrients (starvation) and loss of water (dehydration) would quickly follow. The total blood volume averages about 5 liters, and this amount of fluid is filtered every 40 minutes. Thus 180 liters of filtrate is produced daily, some 60 times the amount of blood plasma in the body. Most of the filtered water is obviously quickly returned to the blood, or a person would actually die from urination. Tubular reabsorption prevents this from happening.

Tubular Reabsorption

Tubular reabsorption (see Fig. 36.11) takes place when substances move across the walls of the tubules into the

associated peritubular capillary network (Fig. 36.10). The osmolarity of the blood is essentially the same as that of the filtrate within the glomerular capsule, and therefore osmosis of water from the filtrate into the blood cannot yet occur. However, sodium ions (Na $^+$) are actively pumped into the peritubular capillary, and then chloride ions (Cl $^-$) follow passively. Now the osmolarity of the blood is such that water moves passively from the tubule into the blood. About 60–70% of salt and water are reabsorbed at the proximal convoluted tubule.

Nutrients, such as glucose and amino acids, also return to the blood at the proximal convoluted tubule. This is a selective process, because only molecules recognized by carrier proteins in plasma membranes are actively reabsorbed. The cells of the proximal convoluted tubule have numerous microvilli, which increase the surface area, and numerous mitochondria, which supply the energy needed for active transport (Fig. 36.10). Glucose is an example of a molecule that ordinarily is reabsorbed completely because there is a plentiful supply of carrier molecules for it. However, if there is more glucose in the filtrate than there are carriers to handle it, glucose will exceed its renal threshold, or transport maximum. When this happens, the excess glucose in the filtrate will appear in the urine. In diabetes mellitus, there is an abnormally large amount of glucose in the filtrate because the liver fails to store glucose as glycogen. The presence of glucose in the filtrate results in less water being absorbed; the increased thirst and frequent urination in un-

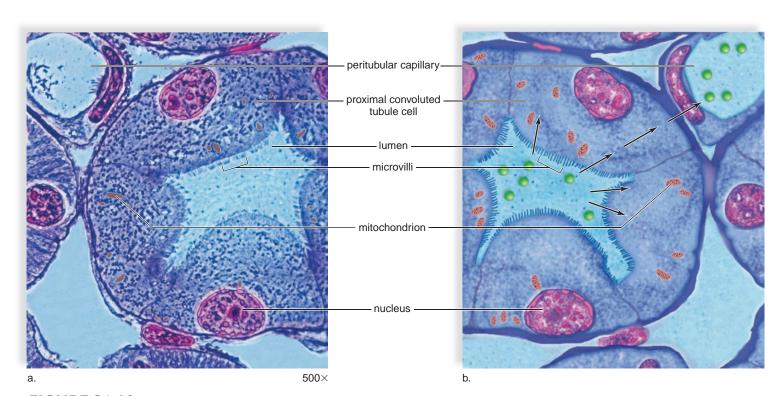


FIGURE 36.10 Proximal convoluted tubule.

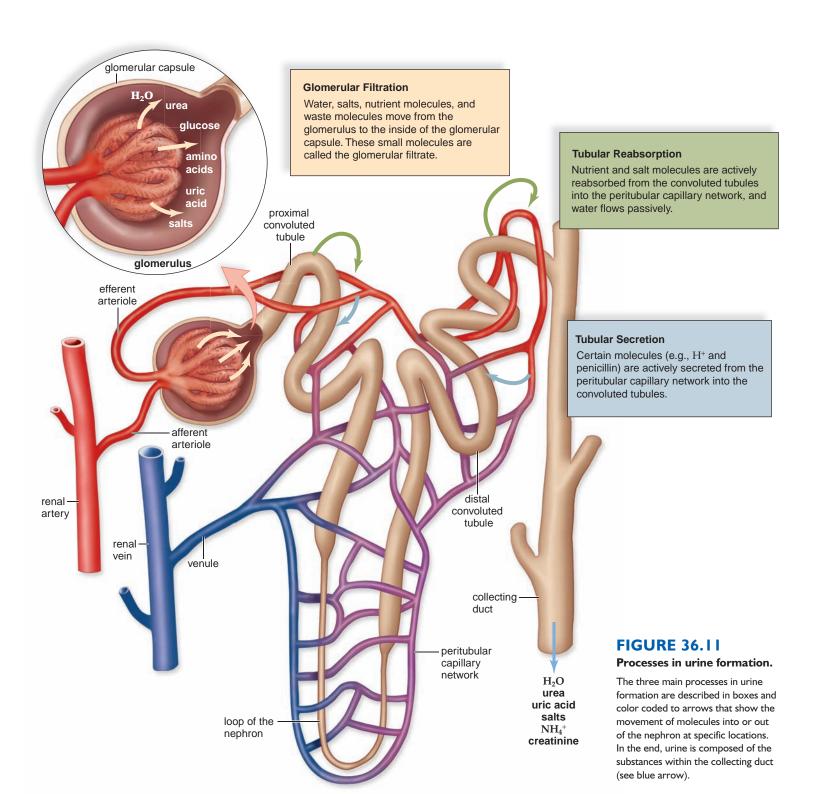
a. This photomicrograph shows that the cells lining the proximal convoluted tubule have a brush border composed of microvilli, which greatly increases the surface area exposed to the lumen. The peritubular capillary adjoins the cells. b. Diagrammatic representation of (a) shows that each cell has many mitochondria, which supply the energy needed for active transport, the process that moves molecules (green) from the lumen of the tubule to the capillary, as indicated by the arrows.

treated diabetics are due to less water being reabsorbed into the peritubular capillary network.

Urea is an example of a substance that is passively reabsorbed from the filtrate. At first, the concentration of urea within the filtrate is the same as that in blood plasma. But after water is reabsorbed, the urea concentration is greater than that of peritubular plasma. In the end, about 50% of the filtered urea is reabsorbed.

Tubular Secretion

Tubular secretion is the second way substances are removed from blood and added to tubular fluid (Fig. 36.11). Substances such as uric acid, hydrogen ions, ammonia, creatinine, histamine, and penicillin are eliminated by tubular secretion. The process of tubular secretion may be viewed as helping to rid the body of potentially harmful compounds that were not filtered into the glomerulus.



The Kidneys and Homeostasis

The kidneys are organs of homeostasis for four main reasons: The kidneys (1) excrete metabolic wastes such as urea, which is the primary nitrogenous waste of humans; (2) maintain the water-salt balance in a way to be described; (3) maintain the acid-base balance and, therefore, the pH balance; and (4) secrete hormones. One of the hormones secreted by the kidneys boosts the number of red blood cells when insufficient oxygen is being delivered to its cells. This hormone, called **erythropoietin**, stimulates the stem cells in the bone marrow to produce more red blood cells. Another hormone produced by the kidneys, called renin, will be discussed in this part of the chapter.

Maintaining the Salt-Water Balance

Most of the water and salt (NaCl) present in the filtrate is reabsorbed across the wall of the proximal convoluted tubule. The excretion of a hypertonic urine (one that is more concentrated than blood) is dependent on the reabsorption of water from the loop of the nephron and the collecting duct. During the process of reabsorption, water passes through recently discovered water channels called **aquaporins**.

Loop of the Nephron. A long loop of the nephron, which typically penetrates deep into the renal medulla, is made up of a descending (going down) limb and an ascending (going up) limb. Salt (NaCl) passively diffuses out of the lower portion of the ascending limb, but the upper, thick portion of the limb actively extrudes salt out into the tissue of the outer renal medulla (Fig. 36.12). Less and less salt is available for transport as fluid moves up the thick portion of the ascending limb. Because of these circumstances, there is an osmotic gradient within the tissues of the renal medulla: The concentration of salt is greater in the direction of the inner medulla. (Note that water cannot leave the ascending limb because the limb is impermeable to water.)

The innermost portion of the inner medulla has the highest concentration of solutes. This cannot be due to salt because active transport of salt does not start until fluid reaches the thick portion of the ascending limb. Urea is believed to leak from the lower portion of the collecting duct, and it is this molecule that contributes to the high solute concentration of the inner medulla.

Because of the osmotic gradient within the renal medulla, water leaves the descending limb along its entire length. This is a countercurrent mechanism: As water diffuses out of the descending limb, the remaining fluid within the limb encounters an even greater osmotic concentration of solute; therefore, water will continue to leave the descending limb from the top to the bottom. Filtrate within the collecting duct also encounters the same osmotic gradient mentioned earlier (Fig. 36.12). Therefore, water diffuses out of the collecting duct into the renal medulla, and the urine within the collecting duct becomes hypertonic to blood plasma.

Antidiuretic hormone (ADH) [Gk. anti, against; L. ouresis, urination] released by the posterior lobe of the pituitary plays a role in water reabsorption at the collecting duct. To understand the action of this hormone, consider its name. Diuresis

means increased amount of urine, and *antidiuresis* means decreased amount of urine. When ADH is present, more water is reabsorbed (blood volume and pressure rise), and a decreased amount of urine results. In practical terms, if an individual does not drink much water on a certain day, the posterior lobe of the pituitary releases ADH, causing more water to be reabsorbed and less urine to form. On the other hand, if an individual drinks a large amount of water and does not perspire much, ADH is not released. Now more water is excreted, and more urine forms. Diuretics, such as caffeine and alcohol, increase the flow of urine by interfering with the action of ADH.

Hormones Control the Reabsorption of Salt. Usually, more than 99% of sodium (Na⁺) filtered at the glomerulus is returned to the blood. Most sodium (67%) is reabsorbed at the proximal convoluted tubule, and a sizable amount (25%) is extruded by the ascending limb of the loop of the nephron. The rest is reabsorbed from the distal convoluted tubule and collecting duct.

Blood volume and pressure is, in part, regulated by salt reabsorption. When blood volume, and therefore blood pressure, is not sufficient to promote glomerular filtration, the kidneys secrete renin. **Renin** is an enzyme that changes angiotensinogen (a large plasma protein produced by the liver) into

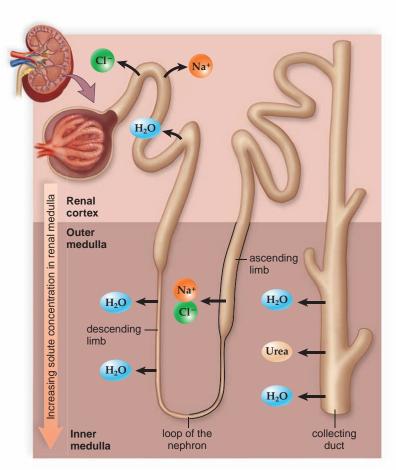


FIGURE 36.12 Reabsorption of salt and water.

Salt (NaCl) diffuses and is actively transported out of the ascending limb of the loop of the nephron into the renal medulla; also, urea leaks from the collecting duct and enters the tissues of the renal medulla. This creates a hypertonic environment, which draws water out of the descending limb and the collecting duct. This water is returned to the cardiovascular system.

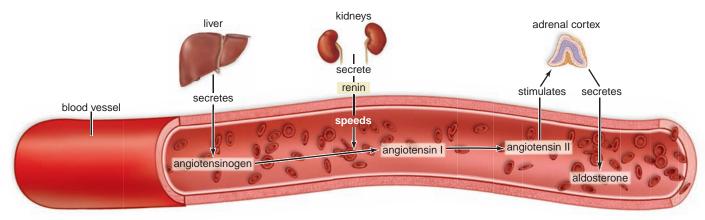


FIGURE 36.13 The renin-angiotensin-aldosterone system.

The liver secretes angiotensinogen into the bloodstream. Renin from the kidneys initiates the chain of events that results in angiotensin II. Angiotensin II acts on the adrenal cortex to secrete aldosterone, which causes reabsorption of sodium ions by the kidneys and a subsequent rise in blood pressure.

angiotensin I. Later, angiotensin I is converted to **angiotensin** II, a powerful vasoconstrictor that also stimulates the adrenal glands, which lie on top of the kidneys, to release aldosterone (Fig. 36.13). **Aldosterone** is a hormone that promotes the excretion of potassium ions (K^+) and the reabsorption of sodium ions (Na^+) at the distal convoluted tubule. The reabsorption of sodium ions is followed by the reabsorption of water. Therefore, blood volume and blood pressure increase.

Atrial natriuretic hormone (ANH) is a hormone secreted by the atria of the heart when cardiac cells are stretched due to increased blood volume. ANH inhibits the secretion of renin by the juxtaglomerular apparatus and the secretion of aldosterone by the adrenal cortex. Its effect, therefore, is to promote the excretion of Na⁺—that is, natriuresis. When Na⁺ is excreted, so is water, and therefore blood volume and blood pressure decrease.

These examples show that the kidneys regulate the water balance in blood by controlling the excretion and the reabsorption of ions. Sodium (Na $^+$) is an important ion in plasma that must be regulated, but the kidneys also excrete or reabsorb other ions, such as potassium ions (K $^+$), bicarbonate ions (HCO $_3^-$), and magnesium ions (Mg $^{2+}$), as needed.

Maintaining the Acid-Base Balance

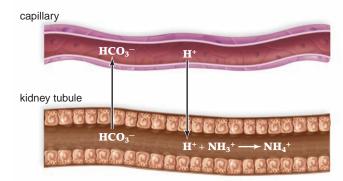
The functions of cells are influenced by pH. Therefore regulation of pH is extremely important to good health. The *bicarbonate* (HCO_3^-) *buffer system* and breathing work together to help maintain the pH of the blood. Central to the mechanism is this reaction, which you have seen before:

$$H^+ + HCO_3^- \Longrightarrow H_2CO_3 \Longrightarrow H_2O + CO_2$$

The excretion of carbon dioxide (CO₂) by the lungs helps keep the pH within normal limits, because when carbon dioxide is exhaled, this reaction is pushed to the right, and hydrogen ions are tied up in water. Indeed, when blood pH decreases, chemoreceptors in the carotid bodies (located in the carotid arteries) and in aortic bodies (located in the aorta) stimulate the respiratory control center, and the rate and depth of breathing increase. On the other hand, when blood pH begins to rise, the respiratory control center is

depressed, and the amount of bicarbonate ion increases in the blood.

As powerful as this system is, only the kidneys can rid the body of a wide range of acidic and basic substances. The kidneys are slower acting than the buffer/breathing mechanism, but they have a more powerful effect on pH. For the sake of simplicity, we can think of the kidneys as reabsorbing bicarbonate ions and excreting hydrogen ions as needed to maintain the normal pH of the blood:



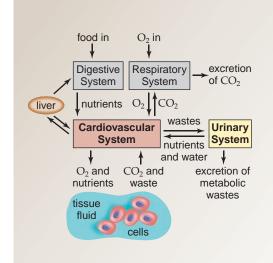
If the blood is acidic, hydrogen ions are excreted and bicarbonate ions are reabsorbed. If the blood is basic, hydrogen ions are not excreted and bicarbonate ions are not reabsorbed. The fact that urine is usually acidic (pH about 6) shows that usually an excess of hydrogen ions are excreted. Ammonia (NH₃) provides a means for buffering these hydrogen ions in urine: (NH₃ + H⁺ \longrightarrow NH₄⁺). Ammonia (whose presence is quite obvious in the diaper pail or kitty litter box) is produced in tubule cells by the deamination of amino acids. Phosphate provides another means of buffering hydrogen ions in urine.

Check Your Progress

36.2

- 1. Which of the organs shown in Figure 36.7 are organs of homeostasis involved in osmoregulation and excretion?
- 2. The kidneys function on a take-back system. Explain.
- 3. What does the renin-angiotensin-aldosterone system accomplish?

Connecting the Concepts



We have seen that the cardiovascular system works with the digestive and respiratory systems to maintain homeostasis, and now we wish to consider the contribution of the urinary system. The kidneys are the chief regulators of the internal environment because they have ultimate control over what is removed and what is retained in blood. They remove nitrogenous wastes such as urea (produced by the liver) and also uric acid. Even more important, the kidneys maintain the watersalt balance and the pH balance of blood. Hormones affect the workings of the kidneys. Too low a concentration of Na+ in the blood causes blood pressure to lower and activates the renin-aldosterone sequence, and then

the kidneys increase $\mathrm{Na^+}$ reabsorption. Take in too much salt and ADH from the pituitary gland causes the kidneys to reabsorb more water. The kidneys work with the respiratory system to maintain pH. The respiratory system excretes $\mathrm{CO_2}$ and this helps lower pH, but the kidneys can retain $\mathrm{HCO_3}^-$, which helps raise pH. The kidneys can also retain or excrete H+ ions. Ion composition of the blood affects osmolarity and the workings of other body systems.

The kidneys affect homeostasis another way. They produce erythropoietin, a hormone that stimulates red blood cell formation, and in this way, they help the cardiovascular and respiratory systems.

summary

36.1 Excretion and the Environment

Animals excrete nitrogenous wastes. The amount of water and energy required to excrete nitrogenous wastes differs. Aquatic animals usually excrete ammonia (needs much water to excrete), and land animals excrete either urea or uric acid (needs much energy to produce).

Animals often have an excretory organ. The flame cells of planarians rid the body of excess water. Earthworm nephridia exchange molecules with the blood in a manner similar to that of vertebrate kidneys. Malpighian tubules in insects take up metabolic wastes and water from the hemolymph. Later, the water is absorbed by the gut.

Osmotic regulation is important to animals. Most have to balance their water and salt intake and excretion to maintain normal solute and water concentration in body fluids. Marine fishes constantly drink water, excrete salts at the gills, and pass an isotonic urine. Freshwater fishes never drink water; they take in salts at the gills and excrete a hypotonic urine. Terrestrial animals that live in extreme environments also have adaptations. For example, the kangaroo rat can survive on metabolic water because of its many ways of conserving water; marine birds and reptiles have glands that extrude salt.

36.2 Urinary System in Humans

The kidneys, excretory organs, are part of the human urinary system. Microscopically, each kidney is made up of nephrons, each of which has several parts and its own blood supply.

Urine formation by a nephron requires three steps: glomerular filtration, when nutrients, water, and wastes enter the nephron's glomerular capsule; tubular reabsorption, when nutrients and most water are reabsorbed into the peritubular capillary network; and tubular secretion, when additional wastes are added to the convoluted tubules.

Humans excrete a hypertonic urine. The ascending limb of the loop of the nephron actively extrudes salt so that the renal medulla is increasingly hypertonic relative to the contents of the descending limb and the collecting duct. Since urea leaks from the lower end of the collecting duct, the inner renal medulla has the highest concentration of solute. Therefore, a countercurrent mechanism ensures that water will diffuse out of the descending limb and the collecting duct.

Three hormones are involved in maintaining the water content of the blood. The hormone ADH (antidiuretic hormone), which makes the collecting duct more permeable, is secreted by the posterior pituitary in response to an increase in the osmotic pressure of the blood. The hormone aldosterone is secreted by the adrenal cortex after low blood pressure has caused the kidneys to release renin. The presence of renin leads to the formation of angiotensin II, which causes the adrenal cortex to release aldosterone. Aldosterone acts on the kidneys to retain Na⁺; therefore, water is reabsorbed and blood pressure rises. The atrial natriuretic hormone prevents the secretion of renin and aldosterone.

The kidneys keep blood pH within normal limits. They reabsorb HCO_3^- and excrete H^+ as needed to maintain the pH at about 7.4.

understanding the terms

aldosterone 675 ammonia 666 angiotensin II 675 antidiuretic hormone (ADH) 674 aquaporin 674 atrial natriuretic hormone (ANH) 675 collecting duct 671 distal convoluted tubule 671 erythropoietin 674 excretion 666 flame cell 667 glomerular capsule 671 glomerular filtration 672 glomerulus 671 kidneys 670 loop of the nephron 671

Malpighian tubule nephridium 667 nephron 670 osmoregulate 668 proximal convoluted tubule 671 renal cortex 670 renal medulla 670 renal pelvis 670 renin 674 tubular reabsorption 672 tubular secretion 673 urea 666 ureter 670 urethra 670 uric acid 666 urinary bladder urine 670

Match the terms to these definitions:

- Blind, threadlike excretory tubule near the anterior end of an insect hindgut.
- b. _____ Cuplike structure that is the initial portion of a nephron; where glomerular filtration occurs.

c.	Main nitrogenous waste of terrestrial
	amphibians and most mammals.
d.	Hormone secreted by the adrenal cortex that
	regulates the sodium and potassium ion balance of the blood.
e.	Main nitrogenous waste of insects, reptiles, and
	birds

reviewing this chapter

- 1. Relate the three primary nitrogenous wastes to the habitat of animals 666
- 2. Describe how the excretory organs of the earthworm and the insect function. 667
- 3. Contrast the osmotic regulation of a marine bony fish with that of a freshwater bony fish. 668
- 4. Give examples of how other types of animals regulate their water and salt balance. 668-69
- 5. Describe the path of urine in humans, and give a function for each structure mentioned. 670
- 6. Describe the macroscopic anatomy of a human kidney, and relate it to the placement of nephrons. 670–71
- 7. List the parts of a nephron, and give a function for each structure mentioned. 670-71
- 8. Describe how urine is made by outlining what happens at each part of the nephron. 671-73
- 9. Describe the reabsorption of water and salt along the length of the nephron. Include the contribution of the loop of the nephron. 674-75
- 10. Name and describe the action of antidiuretic hormone (ADH), the renin-aldosterone connection, and the atrial natriuretic hormone (ANH). 674-75
- 11. How does the nephron regulate the pH of the blood? 675

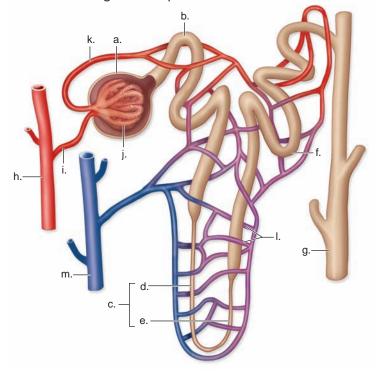
testing yourself

Choose the best answer for each question.

- 1. Which of these pairs is mismatched?
 - a. insects-excrete uric acid
 - b. humans—excrete urea
 - c. fishes-excrete ammonia
 - d. birds-excrete ammonia
 - e. All of these are correct.
- 2. One advantage of urea excretion over uric acid excretion is that
 - a. requires less energy than uric acid to form.
 - b. can be concentrated to a greater extent.
 - c. is not a toxic substance.
 - d. requires no water to excrete.
 - e. is a larger molecule.
- 3. Freshwater bony fishes maintain water balance by
 - a. excreting salt across their gills.
 - b. periodically drinking small amounts of water.
 - c. excreting a hypotonic urine.
 - d. excreting wastes in the form of uric acid.
 - e. Both a and c are correct.
- 4. Animals with which of these are most likely to excrete a semisolid nitrogenous waste?
 - a. nephridia
- d. flame cells
- b. Malpighian tubules c. human kidneys
- e. All of these are correct.

- 5. In which of these human structures are you least apt to find
 - a. large intestine
 - b. urethra
 - c. collecting duct
 - d. bladder
 - e. Both a and c are correct.
- 6. Excretion of a hypertonic urine in humans is associated best with
 - a. the glomerular capsule.
 - b. the proximal convoluted tubule.
 - c. the loop of the nephron.
 - d. the collecting duct.
 - e. Both c and d are correct.
- 7. The presence of ADH (antidiuretic hormone) causes an individual to excrete
 - a. less salt.
 - h less water
 - c. more water.
 - d. more salt.
 - e. Both a and c are correct.
- 8. In humans, water is
 - a. found in the glomerular filtrate.
 - b. reabsorbed from the nephron.
 - c. in the urine.
 - d. reabsorbed from the collecting duct.
 - e. All of these are correct.
- 9. Which of these is out of order first?
 - a. glomerular capsule
 - b. proximal convoluted tubule
 - c. distal convoluted tubule
 - d. loop of the nephron
 - e. collecting duct
- 10. Normally in humans, glucose
 - a. is always in the filtrate and urine.
 - b. is always in the filtrate with little or none in urine.
 - c. undergoes tubular secretion and is in urine.
 - d. undergoes tubular secretion and is not in urine.
 - e. is not in the filtrate and is not in the urine.
- 11. Which of these causes blood pressure to decrease?
 - a. aldosterone
 - b. antidiuretic hormone (ADH)
 - c. renin
 - d. atrial natriuretic hormone (ANH)
- 12. If a drug inhibits the kidneys' ability to reabsorb bicarbonate so that bicarbonate is excreted in the urine, the blood will become
 - a. acidic.
 - b. alkaline.
 - c. first acidic and then alkaline.
 - d. first alkaline and then acidic.
- 13. Which of these materials is not filtered from the blood at the glomerulus? a. water d. glucose
 - b. urea
 - e. sodium ions c. protei
- 14. The renal medulla has a striped appearance due to the presence of which structures?
 - a. loop of the nephron
 - b. collecting ducts
 - c. peritubular capillaries
 - d. Both a and b are correct.

- 15. By what process are most molecules secreted from the blood into the convoluted tubules?
 - a. osmosis
 - b. diffusion
 - c. active transport
 - d. facilitated diffusion
- 16. Which of these is not correct?
 - a. Uric acid is produced from the breakdown of amino acids.
 - b. Urea is produced from the breakdown of proteins.
 - c. Ammonia results from the deamination of amino acids.
 - d. All of these are correct.
- 17. When tracing the path of blood, the blood vessel that follows the renal artery is the
 - a. peritubular capillary.
 - b. efferent arteriole.
 - c. afferent arteriole.
 - d. renal vein.
 - e. glomerulus.
- 18. Absorption of the glomerular filtrate occurs at
 - a. the convoluted tubules.
 - b. only the distal convoluted tubule.
 - c. the loop of the nephron.
 - d. the collecting duct.
- 19. Label this diagram of a nephron.



thinking scientifically

- High blood pressure often is accompanied by kidney damage. In some people, the kidney damage is subsequent to the high blood pressure, but in others the kidney damage is what caused the high blood pressure. Explain how a low-salt diet would enable you to determine whether the high blood pressure or the kidney damage came first?
- 2. The renin-angiotensin-aldosterone system can be inhibited in order to reduce high blood pressure. Usually, the angiotensin-converting enzyme, which converts angiotensin I to angiotensin II, is inhibited by drug therapy. Why would this enzyme be an effective point to disrupt the system?

bioethical issue

Increasing Life Span

As a society, we are accustomed to thinking that as we grow older, diseases such as urinary disorders will begin to occur. Almost everyone is aware that most males are subject to enlargement of the prostate as they age, and that cancer of the prostate is not uncommon among older men. However, as with many illnesses associated with aging, medical science now knows how to treat or even cure prostate problems. Because of these successes, our life span has lengthened. A child born in the United States in 1900 lived to, say, the age of 47. If that same child were born today, he or she would probably live to at least 76. Even more exciting is the probability that scientists will improve the life span still further. People could live beyond 100 years and have the same vigor and vitality they had when they were young.

Most people are appreciative of living longer, especially if they can expect to be free of the illnesses and inconveniences associated with aging. But have we examined how we feel about longevity as a society? We are accustomed to considering that if the birthrate increases, so does the size of a population. But what about the death rate? If the birthrate stays constant and the death rate decreases, obviously population size also increases. Most experts agree that population growth depletes resources and increases environmental degradation. Having more people in the older population can also put a strain on the economy if they are unable to meet their financial needs, including medical expenses, without government assistance.

What is the ethical solution to this problem? Should we just allow the population to increase as older people live longer? Should we decrease the birthrate? Should we reduce government assistance to older people so they realize that they must be able to take care of themselves? Or should we call a halt to increasing the life span through advancements in medical science?

Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

http://www.mhhe.com/maderbiology I 0



37

Neurons and Nervous Systems

hrough input from sensory receptors, the nervous system receives a continuous barrage of information, which it integrates before it stimulates effectors, such as muscles and glands. An impairment of these operations can have serious consequences for the individual. Spinal cord injuries can result in paralysis when commands from the brain and spinal cord fail to reach the nerves that bring about muscle contraction. Similarly, disease can cause paralysis. Amyotrophic lateral sclerosis (ALS), also known as Lou Gehrig disease (for a famous baseball player with ALS), is a fatal degenerative disease characterized by the death of neurons, which signal muscle contraction. People with ALS gradually lose the ability to move, and eventually cannot even breathe on their own; however, their intellectual ability is not impaired. Professor Stephen Hawking, pictured below, is a renowned physicist and author who is afflicted with ALS.

In this chapter, you will explore the structure, evolution, and function of nervous systems in invertebrate and vertebrate animals.



concepts

37.1 EVOLUTION OF THE NERVOUS SYSTEM

- A survey of invertebrates shows a gradual increase in the complexity of the nervous system. 680
- All vertebrates have a well-developed brain, but the forebrain is largest in mammals, particularly humans. 681–82

37.2 NERVOUS TISSUE

- Nervous tissue is made up of cells called neurons, which are specialized to carry nerve impulses; and neuroglia, which support and protect neurons. 683
- A nerve impulse is a self-propagating electrochemical change that travels along the length of a neuron. Transmission of impulses between neurons is usually accomplished by means of chemicals called neurotransmitters. 684–87

37.3 CENTRAL NERVOUS SYSTEM: BRAIN AND SPINAL CORD

- The spinal cord carries out reflex actions and communicates with the brain. 688
- The cerebrum is the largest part of the brain, and it coordinates the activities of the other parts of the brain, which are concerned with sensory input or motor control and homeostasis. 689–91

37.4 PERIPHERAL NERVOUS SYSTEM

- The peripheral nervous system contains nerves that conduct nerve impulses between the central nervous system and all body parts. 692
- The somatic system controls skeletal muscles; the autonomic system regulates the activity of cardiac and smooth muscles and glands. 693-95

37.1 Evolution of the Nervous System

The nervous system is vitally important in complex animals, enabling them to seek food and avoid danger. It ceaselessly monitors internal and external conditions and makes appropriate changes to maintain homeostasis. A comparative study of animal nervous system organization indicates the evolutionary trends that may have led to the nervous system of vertebrates.

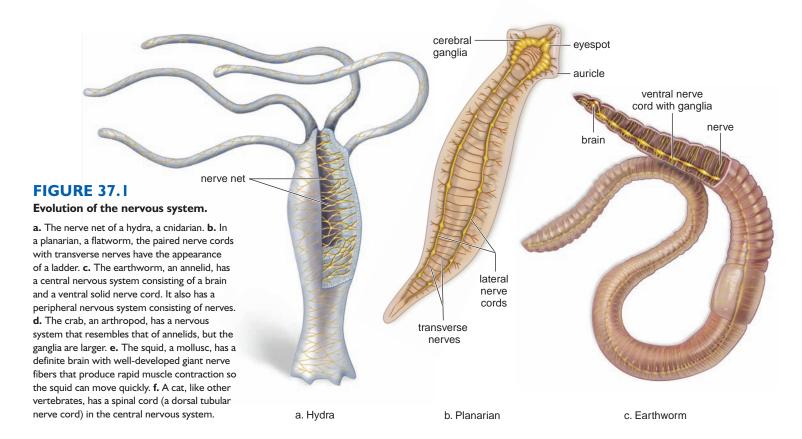
Invertebrate Nervous Organization

Simple animals, such as sponges, which have the cellular level of organization, can respond to stimuli; the most common observable response is closure of the osculum (central opening). Hydras, which are cnidarians with the tissue level of organization, can contract and extend their bodies, move their tentacles to capture prey, and even turn somersaults. They have a **nerve net** that is composed of neurons (nerve cells) in contact with one another and with contractile cells in the body wall (Fig. 37.1a). Sea anemones and jellyfishes, which are also cnidarians, seem to have two nerve nets. A fast-acting one allows major responses, particularly in times of danger, and the other coordinates slower and more delicate movements.

Planarians, which are flatworms, have a nervous organization that reflects their bilateral symmetry. They have a **ladderlike nervous system**, with two ventrally located lateral or longitudinal nerve cords (bundles of nerves) that extend from the cerebral ganglia to the posterior end

of their body. Transverse nerves connect the nerve cords, as well as the cerebral ganglia, to the eyespots. Cephalization has occurred, as evidenced by a concentration of neurons and sensory receptors in a head region. A cluster of neurons is called a ganglion (pl., ganglia), and the anterior cerebral ganglia receive sensory information from photoreceptors in the eyespots and sensory cells in the auricles (Fig. 37.1b). The two lateral nerve cords allow a rapid transfer of information from the cerebral ganglia to the posterior end, and the transverse nerves between the nerve cords keep the movement of the two sides coordinated. Bilateral symmetry plus cephalization are two significant trends in the development of a nervous organization that is adaptive for an active way of life. Also, the nervous organization in planarians is a foreshadowing of the central nervous system and peripheral nervous system seen in vertebrates.

Annelids (e.g., earthworm, Fig. 37.1c), arthropods (e.g., crab, Fig. 37.1d), and molluscs (e.g., squid, Fig. 37.1e) are complex animals with true nervous systems. The annelids and arthropods have the typical invertebrate nervous system. There is a brain and a ventral nerve cord having a ganglion in each segment. The brain, which normally receives sensory information, controls the activity of the ganglia and assorted nerves so that the muscle activity of the entire animal is coordinated. The crab and squid show marked cephalization—the anterior end has a well-defined brain, and there are well-developed sense organs, such as eyes. The presence of a brain and other ganglia in the body of all these animals indicates an increase in the number of neurons among more complex invertebrates.



Vertebrate Nervous Organization

In vertebrates (e.g., cat), cephalization, coupled with bilateral symmetry, results in several types of paired sensory receptors, including the eyes, ears, and olfactory structures that allow the animal to gather information from the environment. Paired cranial and spinal nerves contain numerous nerve fibers. Vertebrates have many more neurons than do invertebrates. For example, an insect's entire nervous system may contain a total of about 1 million neurons, while a vertebrate's nervous system may contain many thousand to many billion times that number. A vertebrate's central nervous system (CNS), consisting of a spinal cord and brain, develops from an embryonic dorsal neural tube. The spinal cord is continuous with the brain because the embryonic neural tube becomes the spinal cord posteriorly, while the vertebrate brain is derived from the enlarged anterior end of the neural tube. Ascending tracts carry sensory information to the brain, and descending tracts carry motor commands to the neurons in the spinal cord that control the muscles.

It is customary to divide the vertebrate brain into the hindbrain, midbrain, and forebrain (Fig. 37.2). The hindbrain is the most ancient part of the brain. Nearly all vertebrates have a well-developed hindbrain that regulates motor activity below the level of consciousness. In humans, for example, the lungs and heart function even when we are sleeping. The medulla oblongata contains control centers for breathing and heart rate. Coordination of motor activity associated with limb movement, posture, and balance eventually became centered in the cerebellum.

The optic lobes are part of the midbrain, which was originally a center for coordinating reflexes involving the

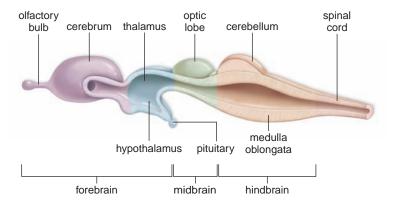
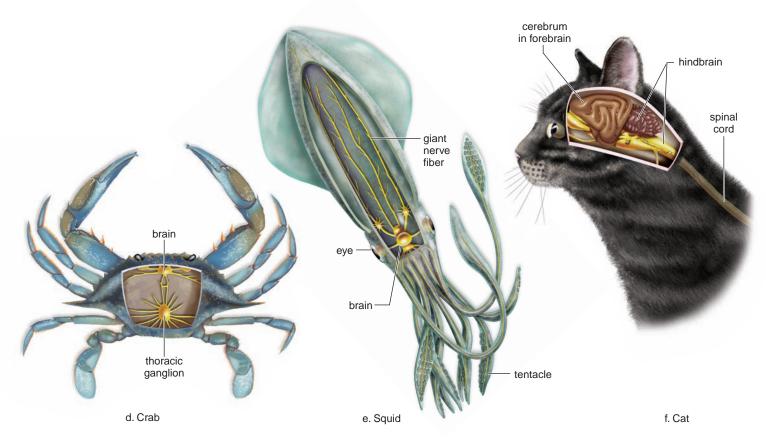


FIGURE 37.2 Organization of the vertebrate brain.

The vertebrate brain is divided into the forebrain, the midbrain, and the hindbrain.

eyes and ears. Starting with the amphibians and continuing in the other vertebrates, the forebrain processes sensory information. Originally, the forebrain was concerned mainly with the sense of smell. Later, the thalamus evolved to receive sensory input from the midbrain and the hindbrain and to pass it on to the cerebrum, the anterior part of the forebrain in vertebrates. In the forebrain, the hypothalamus is particularly concerned with homeostasis, and in this capacity, the hypothalamus communicates with the medulla oblongata and the pituitary gland.

The cerebrum, which is highly developed in mammals, integrates sensory and motor input and is particularly associated with higher mental capabilities. In humans, the outer layer of the cerebrum, called the cerebral cortex, is especially large and complex.



The Human Nervous System

The human nervous system has three specific functions: (1) it receives sensory input-sensory receptors in skin and other organs respond to external and internal stimuli by generating nerve impulses that travel to the central nervous system (CNS); (2) it performs integration—the CNS sums up the input it receives from all over the body; and (3) it generates motor output—nerve impulses from the CNS go to the muscles and glands. Muscle contractions and gland secretions are responses to stimuli received by sensory receptors. As an example, consider the events that occur as a person raises a glass to the lips. Continual sensory input to the CNS from the eyes and hand informs the CNS of the position of the glass, and the CNS continually sums up the incoming data before commanding the hand to proceed. At any time, integration with other sensory data might cause the CNS to command a different motion instead.

In humans, the central nervous system (CNS) consists of the brain and spinal cord (Fig. 37.3). The brain is housed in the skull and the spinal cord is housed in the vertebral

brain cranial nerves cervical nerves thoracic nerves spinal cord lumbar nerves radial nerve median nerve sacral ulnar nerve nerves sciatic nerve tibial nerve common fibular nerve a.

column. The peripheral nervous system (PNS) [Gk. periphereia, circumference] consists of all the nerves and ganglia that lie outside the central nervous system. The paired cranial and spinal nerves are part of the PNS. In the PNS, the somatic nervous system has sensory and motor functions that control the skeletal muscles. The autonomic nervous system controls smooth muscle, cardiac muscle, and the glands. It is further divided into the sympathetic and parasympathetic divisions.

The components and functions of the central and peripheral nervous systems are complex. For an organism to maintain homeostasis, both systems have to work in harmony.

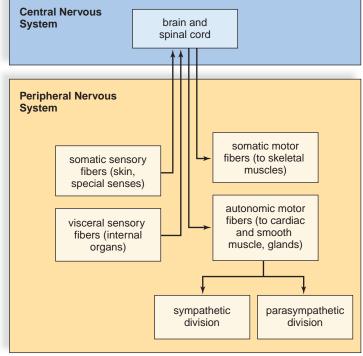
Check Your Progress

37. I

- I. What is a ganglion?
- 2. What is the advantage for an animal having cephalization in addition to bilateral symmetry?
- 3. Distinguish between the CNS and the PNS.

FIGURE 37.3 Organization of the nervous system in humans

a. The central nervous system (CNS) is composed of brain and spinal cord; the peripheral nervous system (PNS) consists of nerves. b. In the somatic system of the PNS, nerves conduct impulses from sensory receptors located in the skin and internal organs to the CNS and motor impulses from the CNS to the skeletal muscles. In the autonomic system, consisting of the sympathetic and parasympathetic divisions, motor impulses travel to smooth muscle, cardiac muscle, and glands.



37.2 Nervous Tissue

Although complex, nervous tissue is composed of two principal types of cells. **Neurons**, also known as nerve cells, are the functional units of the nervous system. They receive sensory information, convey the information to an integration center such as the brain, and conduct signals from the integration center to effector structures such as the glands and muscles. **Neuroglia** serve as supporting cells, providing support and nourishment to the neurons.

Neurons and Neuroglia

Neurons [Gk. *neuron*, nerve] vary in appearance depending on their function and location. They consist of three major parts: a cell body, dendrites, and an axon (Fig. 37.4). The **cell body** contains a nucleus and a variety of organelles. The **dendrites** [Gk. *dendron*, tree] are short, highly branched processes that receive signals from the sensory receptors or other neurons and transmit them to the cell body. The **axon** [Gk. *axon*, axis] is the portion of the neuron that conveys information to another neuron or to other cells. Axons can be bundled together to form nerves. For this reason, axons are often called **nerve fibers**. Many axons are covered by a white insulating layer called the **myelin sheath** [Gk. *myelos*, spinal cord].

Neuroglia, or glial cells, which were discussed on page 583, greatly outnumber neurons in the brain. There are several different types in the CNS, each with specific functions. Some (microglia) help remove bacteria and debris, some (astrocytes) provide metabolic and structural support directly to the neurons. The myelin sheath is formed from the membranes of tightly spiraled neuroglia. In the PNS, Schwann cells perform this function, leaving gaps called nodes of Ranvier. In the CNS, neuroglial cells called oligodendrocytes perform this function.

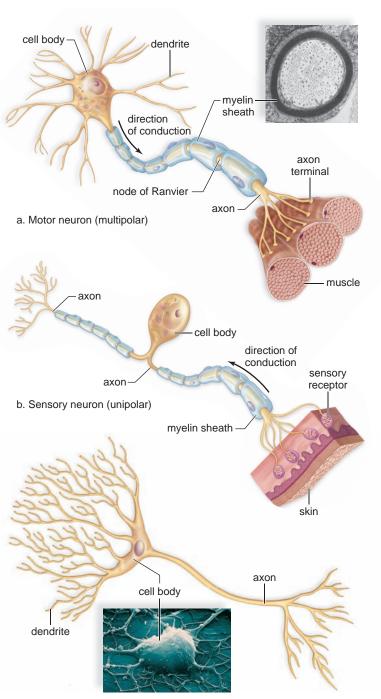
Types of Neurons

Neurons can be described in terms of their function and shape. **Motor (efferent) neurons** take nerve impulses from the CNS to muscles or glands. Motor neurons are said to have a multipolar shape because they have many dendrites and a single axon (Fig. 37.4a). Motor neurons cause muscle fibers to contract or glands to secrete, and therefore they are said to innervate these structures.

Sensory (afferent) neurons take nerve impulses from sensory receptors to the CNS. The sensory receptor, which is the distal end of the long axon of a sensory neuron, may be as simple as a naked nerve ending (a pain receptor), or may be built into a highly complex organ, such as the eye or ear. Almost all sensory neurons have a structure that is termed unipolar (Fig. 37.4b). In unipolar neurons, the process that extends from the cell body divides into a branch that extends to the periphery and another that extends to the CNS. Since both of these extensions are long and myelinated and transmit nerve impulses, it is now generally accepted to refer to them as an axon.

Interneurons [L. *inter*, between; Gk. *neuron*, nerve] occur entirely within the CNS. Interneurons, which are typi-

cally multipolar in shape (Fig. 37.4c), convey nerve impulses between various parts of the CNS. Some lie between sensory neurons and motor neurons; some take messages from one side of the spinal cord to the other or from the brain to the cord, and vice versa. They also form complex pathways in the brain where processes accounting for thinking, memory, and language occur.



c. Interneuron (multipolar)

FIGURE 37.4 Neuron anatomy.

a. Motor neuron. Note the branched dendrites and the single, long axon, which branches only near its tip. b. Sensory neuron with dendritelike structures projecting from the peripheral end of the axon. c. Interneuron (from the cortex of the cerebellum) with very highly branched dendrites.

Transmission of the Nerve Impulses

In the early 1900s, Julius Bernstein at the University of Halle, Germany, suggested that the nerve impulse is an electrochemical phenomenon involving the movement of unequally distributed ions on either side of an axonal membrane, the plasma membrane of an axon. It was not until later, however, that investigators developed a technique that enabled them to support this hypothesis. A. L. Hodgkin and A. F. Huxley, English neurophysiologists, received the Nobel Prize in 1963 for their work in this field. They and a group of researchers, headed by K. S. Cole and J. J. Curtis at Woods Hole, Massachusetts, managed to insert a tiny electrode into the giant axon of the squid Loligo. This internal electrode was then connected to a voltmeter, an instrument with a screen that shows voltage differences over time (Fig. 37.5). Voltage is a measure of the electrical potential difference between two points, which in this case is the difference between two electrodes—one placed inside and another placed outside the axon. (An electrical potential difference across a membrane is called the membrane potential.) When a membrane potential exists, we can say that a plus pole and a minus pole exist; therefore, the voltmeter indicates the existence of polarity and records polarity changes.

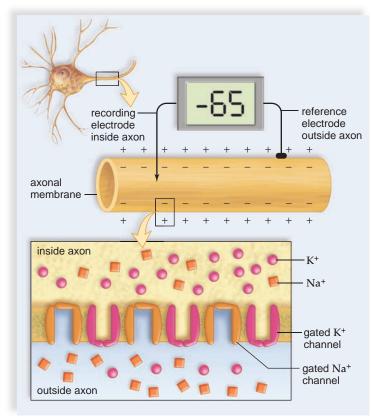
Resting Potential

When the axon is not conducting an impulse, the voltmeter records a membrane potential equal to about -65 mV (millivolts), indicating that the inside of the neuron is more negative than the outside (Fig. 37.5a). This is called the **resting potential** because the axon is not conducting an impulse.

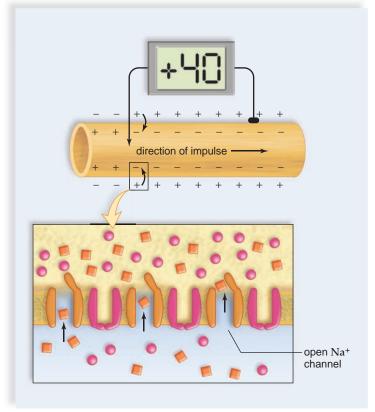
The existence of this polarity can be correlated with a difference in ion distribution on either side of the axonal membrane. As Figure 37.5a shows, there is a higher concentration of sodium ions (Na+) outside the axon and a higher concentration of potassium ions (K⁺) inside the axon. The unequal distribution of these ions is in part due to the activity of the sodium-potassium pump (see page 94). This pump is an active transport system in the plasma membrane that pumps three sodium ions out of and two potassium ions into the axon. The pump is always working because the membrane is somewhat permeable to these ions and they tend to diffuse toward their lesser concentration. Since the membrane is more permeable to potassium ions than to sodium ions, there are always more positive ions outside the membrane than inside; this accounts for some of the polarity recorded by the voltmeter. There are also large, negatively charged proteins in the cytoplasm of the axon; altogether, then, the

FIGURE 37.5 Resting and action potential of the axonal membrane.

a. Resting potential. A voltmeter that records voltage changes indicates the axonal membrane has a resting potential of -65 mV. There is a preponderance of Na⁺ outside the axon and a preponderance of K⁺ inside the axon. The permeability of the membrane to K⁺ compared to Na⁺, and the presence of large, negatively charged proteins (not shown) within the axon, causes the inside to be negative compared to the outside. **b.** Action potential. Depolarization occurs when Na⁺ gates open and Na⁺ moves inside the axon, and (c) repolarization occurs when K⁺ gates open and K⁺ moves outside the axon. **d.** Graph of the action potential.



a. Resting potential: more Na^+ outside the axon and more K^+ inside the axon causes polarization.



 Action potential begins: depolarization occurs when Na⁺ gates open and Na⁺ moves to inside the axon.

voltmeter records that the inside is -65 mV compared to the outside. This is the resting potential.

Action Potential

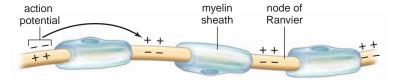
An **action potential** is a rapid change in polarity across a portion of an axonal membrane as the nerve impulse occurs. An action potential uses two types of gated ion channels in the axonal membrane. In the axonal membrane, a gated ion channel allows sodium (Na^+) to pass through the membrane, and another allows potassium (K^+) to pass through the membrane. In contrast to ungated ion channels, which constantly allow ions across the membrane, gated ion channels open and close in response to a stimulus such as a signal from another neuron.

Threshold is the minimum change in polarity across the axonal membrane that is required to generate an action potential. Therefore, the action potential is an all-or-none event. During depolarization, the inside of a neuron becomes positive because of the sudden entrance of sodium ions. If threshold is reached, many more sodium channels open, and the action potential begins. As sodium ions rapidly move across the membrane to the inside of the axon, the action potential swings up from -65 mV to +40 mV (Fig. 37.5b). This reversal in polarity causes the sodium channels to close and the potassium channels to open. As potassium ions leave the axon, the action potential swings down from +40 mV to -65 mV. In other words, a repolarization occurs (Fig. 37.5c). An action potential only takes 2 milliseconds. In order to visualize such rapid fluctuations in voltage across the axonal membrane, researchers generally find it useful to plot the voltage changes over time (Fig. 37.5*d*).

 c. Action potential ends: repolarization occurs when K⁺ gates open and K⁺ moves to outside the axon.

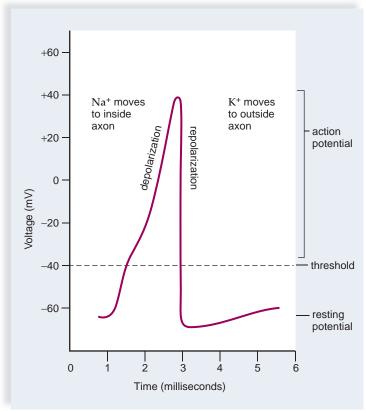
Propagation of Action Potentials

In nonmyelinated axons, the action potential travels down an axon one small section at a time, at a speed of about 1 m/second. In myelinated axons, the gated ion channels that produce an action potential are concentrated at the nodes of Ranvier. Just as taking giant steps during a game of "Simon Says" is more efficient, so ion exchange only at the nodes makes the action potential travel faster. *Saltar* in Spanish means "to jump," and so this mode of conduction, called **saltatory conduction**, means that the action potential "jumps" from node to node:



Speeds of 200 m/second (450 miles per hour) have been recorded.

The intensity of a message traveling down a nerve fiber is determined by how many nerve impulses are generated within a given time span. A fiber can conduct a volley of nerve impulses because only a small number of ions are exchanged with each impulse. As soon as an action potential has moved on, the previous section undergoes a **refractory period**, during which the Na⁺ gates are unable to open. Notice, therefore, that the action potential cannot move backward and instead always moves down an axon toward its terminals.



 d. An action potential can be visualized if voltage changes are graphed over time.

Transmission Across a Synapse Every axon branches into many fine endings, each tipped by a small swelling, called an axon terminal (Fig. 37.6). Each terminal lies very close to the dendrite (or the cell body) of another neuron. This region of close proximity is called a synapse. At a synapse, the membrane of the first neuron is called the *presynaptic* membrane, and the membrane of the next neuron is called the *post*synaptic membrane.

The small gap between the neurons is called the **synaptic cleft**.

A nerve impulse cannot cross a synaptic cleft. Transmission across a synapse is carried out by molecules called **neurotransmitters**, which are stored in synaptic vesicles. When nerve impulses traveling along an axon reach an axon terminal, gated channels for calcium ions (Ca²⁺) open, and calcium enters the terminal. This sudden rise in Ca²⁺ stimulates synaptic vesicles to merge with the presynaptic membrane, and neurotransmitter molecules are released into the synaptic cleft. They diffuse across the cleft to the postsynaptic membrane, where they bind with specific receptor proteins.

cell body of

neuron

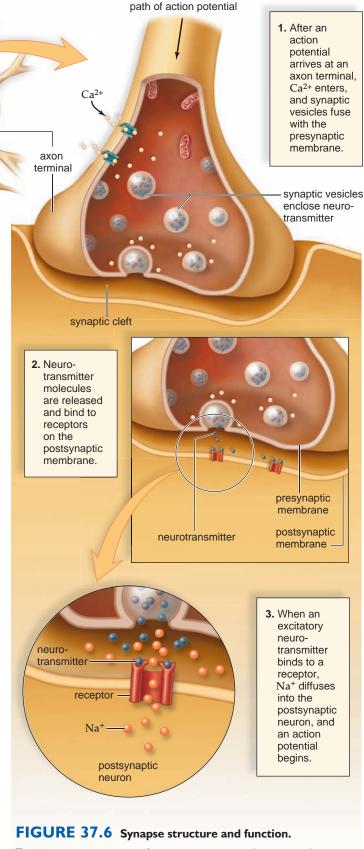
postsynaptic

Depending on the type of neurotransmitter and/or the type of receptor, the response of the postsynaptic neuron can be toward excitation or toward inhibition. Excitatory neurotransmitters that use gated ion channels are fast acting. Other neurotransmitters affect the metabolism of the postsynaptic cell and therefore are slower acting.

Neurotransmitters and Neuromodulators

Among the more than 100 substances known or suspected to be neurotransmitters are acetylcholine (ACh), norepinephrine (NE), dopamine, and serotonin, which are present in both the CNS and PNS. The effect of ACh on muscle tissue varies. It excites skeletal muscle but inhibits cardiac muscle. It has either an excitatory or inhibitory effect on smooth muscle or glands, depending on their location. In the CNS, norepinephrine is important to dreaming, waking, and mood. Dopamine is involved in emotions, learning, and attention while serotonin is involved in thermoregulation, sleeping, emotions, and perception.

Once a neurotransmitter has been released into a synaptic cleft and has initiated a response, it is removed from the cleft. In some synapses, the postsynaptic membrane contains enzymes that rapidly inactivate the neurotransmitter. For example, the enzyme acetylcholinesterase (AChE) breaks down acetylcholine. In other synapses, the presynaptic cell is responsible for reuptake, a process in which it rapidly reabsorbs the neurotransmitter, possibly for repackaging in synaptic vesicles or for molecular breakdown. The short existence of neurotransmitters at a synapse prevents continuous stimulation (or inhibition) of postsynaptic membranes.



Transmission across a synapse from one neuron to another occurs when a neurotransmitter is released at the presynaptic membrane, diffuses across a synaptic cleft, and binds to a receptor in the postsynaptic membrane. An action potential may begin.

Neurotransmitter imbalances are associated with a number of disorders. Parkinson disease is associated with a lack of dopamine in the brain. Levodopa, one of the drugs used to treat Parkinson disease, serves as a precursor in the synthesis of dopamine, thereby boosting dopamine levels in the brain.

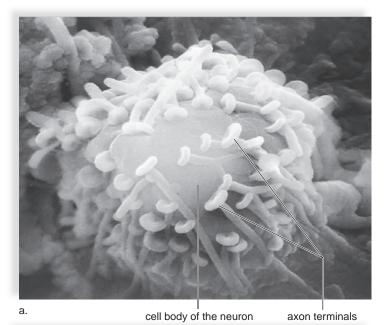
It is of interest to note here that many drugs affecting the nervous system act by interfering with or potentiating the action of neurotransmitters. Such drugs can enhance or block the release of a neurotransmitter, mimic the action of a neurotransmitter or block the receptor, or interfere with the removal of a neurotransmitter from a synaptic cleft. For instance, Alzheimer disease is associated with a deficiency of ACh; some of the drugs that slow the progression of the disease are cholinesterase inhibitors that block AChE and slow the degradation of ACh. Likewise, depression, a common mood disorder, appears to involve imbalances in norepinephrine and serotonin. Some antidepressant drugs, such as fluoxetine (Prozac), prevent the reuptake of serotonin, and others, including bupropion hydrochloride (Wellbutrin), prevent the reuptake of both serotonin and norepinephrine. Blocking reuptake prolongs the effects of these two neurotransmitters in networks of neurons within the brain that are involved in the emotional state. Several so-called "recreational drugs" (used for enjoyment rather than medical reasons) also affect neurotransmitter activity, as described in the Science Focus on pages 696–97.

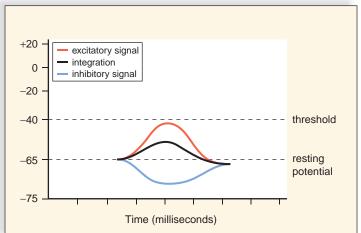
Neuromodulators are molecules that block the release of a neurotransmitter or modify a neuron's response to a neurotransmitter. Substance P and the endorphins are well-known neuromodulators. Substance P is released by sensory neurons when pain is present. Endorphins block the release of substance P and, therefore, serve as natural painkillers. They are associated with the "runner's high" of joggers because they also produce a feeling of tranquility. Endorphins are produced by the brain not only when there is physical stress but also when emotional stress is present.

Synaptic Integration

A single neuron has many dendrites plus the cell body, and both can have synapses with many other neurons. One thousand to 10,000 synapses per a single neuron is not uncommon. Therefore, a neuron is on the receiving end of many excitatory and inhibitory signals. An excitatory neurotransmitter produces a potential change called a signal that drives the neuron closer to an action potential, and an inhibitory neurotransmitter produces a signal that drives the neuron farther from an action potential. Excitatory signals have a depolarizing effect, and inhibitory signals have a hyperpolarizing effect.

Neurons integrate these incoming signals. **Integration** is the summing up of excitatory and inhibitory signals (Fig. 37.7). If a neuron receives many excitatory signals (either from different synapses or at a rapid rate from one synapse), chances are the axon will transmit a nerve impulse. On the other hand, if a neuron receives both inhibitory and





b.

FIGURE 37.7 Synaptic integration.

a. Many neurons synapse with a cell body. b. Both inhibitory signals (blue) and excitatory signals (red) are summed up in the dendrite and cell body of the postsynaptic neuron. Only if the combined signals cause the membrane potential to rise above threshold does an action potential occur. In this example, threshold was not reached.

excitatory signals, the summing up of these signals may prohibit the axon from firing.

Check Your Progress

I. Would a nerve impulse travel more quickly down an unmyelinated axon or a myelinated axon? Why?

37.2

- 2. A nerve impulse has two parts. **a.** During the first part, which ion moves where? **b.** During the second part, which ion moves where?
- 3. How are neurotransmitter molecules removed from synaptic clefts?

37.3 Central Nervous System: Brain and Spinal Cord

The central nervous system (CNS) consists of the spinal cord and the brain, where sensory information is received and motor control is initiated. The spinal cord and the brain are both protected by bone; the spinal cord is surrounded by vertebrae, and the brain is enclosed by the skull. Both the spinal cord and the brain are wrapped in three protective membranes known as **meninges**. **Meningitis** (inflammation of the meninges) is a serious disorder caused by a number of bacteria or viruses that invade the meninges. The spaces between the meninges are filled with **cerebrospinal fluid**, which cushions and protects the CNS. Cerebrospinal fluid is contained in the central canal of the spinal cord and within the **ventricles** of the brain, which are interconnecting spaces that produce and serve as reservoirs for cerebrospinal fluid.

The Spinal Cord

The **spinal cord** is a bundle of nervous tissue enclosed in the vertebral column (see Fig. 37.12); it extends from the base of the brain to the vertebrae just below the rib cage. The spinal cord has two main functions: (1) it is the center for many **reflex actions**, which are automatic responses to external stimuli, and (2) it provides a means of communication between the brain and the spinal nerves, which leave the spinal cord.

A cross section of the spinal cord reveals that it is composed of a central portion of **gray matter** and a peripheral region of white matter. The gray matter consists of cell bodies and unmyelinated fibers. It is shaped like a butterfly, or

the letter H, with two dorsal (posterior) horns and two ventral (anterior) horns surrounding a central canal. The gray matter contains portions of sensory neurons and motor neurons, as well as short interneurons that connect sensory and motor neurons.

Myelinated long fibers of interneurons that run together in bundles called **tracts** give **white matter** its color. These tracts connect the spinal cord to the brain. These tracts are like a busy superhighway, by which information continuously passes between the brain and the rest of the body. Dorsally, the tracts are primarily ascending, taking information *to* the brain; ventrally, the tracts are primarily descending, carrying information *from* the brain. Because the tracts at one point cross over, the left side of the brain controls the right side of the body, and the right side of the brain controls the left side of the body.

If the spinal cord is severed as the result of an injury, paralysis results. If the injury occurs in the cervical (neck) region, all four limbs are usually paralyzed, a condition known as quadriplegia. If the injury occurs in the thoracic region, the lower body may be paralyzed, a condition called paraplegia.

The Brain

The **brain** contains four interconnected chambers called ventricles (Fig. 37.8*a*). The two lateral ventricles are inside the cerebrum. The third ventricle is surrounded by the diencephalon, and the fourth ventricle lies between the cerebellum and the pons. Cerebrospinal fluid is continuously produced in the ventricles and circulates through them; it then flows out of the brain between the meninges.

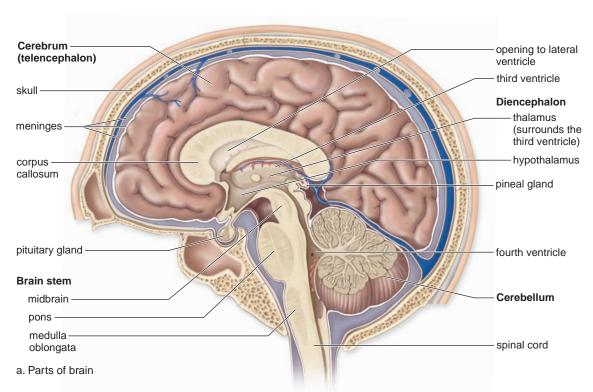


FIGURE 37.8

The human brain.

a. The right cerebral hemisphere is shown here, along with other, closely associated structures. The hemispheres are connected by the corpus callosum. b. The cerebrum is divided into the right and left cerebral hemispheres.



b. Cerebral hemispheres

The Cerebrum

The **cerebrum**, also called the telencephalon, is the largest portion of the brain in humans. The cerebrum is the last center to receive sensory input and carry out integration before commanding voluntary motor responses. It communicates with and coordinates the activities of the other parts of the brain.

Cerebral Hemispheres. The cerebrum is divided into two halves, called **cerebral hemispheres** (see Fig. 37.8*b*). A deep groove called the longitudinal fissure divides the cerebrum into the right and left hemispheres. Each hemisphere receives information from and controls the opposite side of the body. Although the hemispheres appear the same, the right hemisphere is associated with artistic and musical ability, emotion, spatial relationships, and pattern recognition. The left hemisphere is more adept at mathematics, language, and analytical reasoning. The two cerebral hemispheres are connected by a bridge of tracts within the corpus callosum.

Shallow grooves called sulci (sing., sulcus) divide each hemisphere into lobes (Fig. 37.9). The *frontal lobe* lies toward the front of the hemispheres and is associated with motor control, memory, reasoning, and judgment. For example, if a fire occurs, the frontal lobe enables you to decide whether to exit via the stairs or the window, or how to dress if the temperature plummets to subzero. The frontal lobe on the left side contains the *Broca area*, which organizes motor commands to produce speech.

The *parietal lobes* lie posterior to the frontal lobe and are concerned with sensory reception and integration, as well as taste. A *primary taste area* in the parietal lobe accounts for taste sensations.

The *temporal lobe* is located laterally. A primary auditory area in the temporal lobe receives information from

our ears. The *occipital lobe* is the most posterior lobe. A *primary visual area* in the occipital lobe receives information from our eyes.

The Cerebral Cortex. The cerebral cortex is a thin (less than 5 mm thick), but highly convoluted, outer layer of gray matter that covers the cerebral hemispheres. The convolutions increase the surface area of the cerebral cortex. The cerebral cortex contains tens of billions of neurons and is the region of the brain that accounts for sensation, voluntary movement, and all the thought processes required for learning, memory, language, and speech.

Two regions of the cerebral cortex are of particular interest. The **primary motor area** is in the frontal lobe just ventral to (before) the central sulcus. Voluntary commands to skeletal muscles begin in the primary motor area, and each part of the body is controlled by a certain section. The size of the section indicates the precision of motor control. For example, the face and hand take up a much larger portion of the primary motor area than does the entire trunk. The **primary somatosensory area** is just dorsal to the central sulcus in the parietal lobe. Sensory information from the skin and skeletal muscles arrives here, where each part of the body is sequentially represented in a manner similar to the primary motor area.

Basal Nuclei. While the bulk of the cerebrum is composed of white matter (i.e., tracts), masses of gray matter are located deep within the white matter. These so-called basal nuclei (formerly termed basal ganglia) integrate motor commands, ensuring that proper muscle groups are activated or inhibited. Huntington disease and Parkinson disease, which are both characterized by uncontrollable movements, are due to malfunctioning basal nuclei.

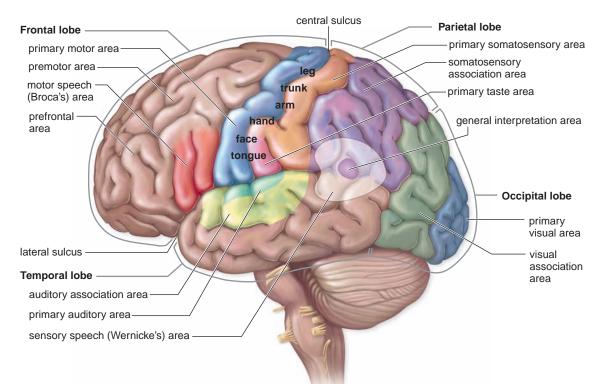


FIGURE 37.9

The lobes of a cerebral hemisphere.

Each cerebral hemisphere is divided into four lobes: frontal, parietal, temporal, and occipital. These lobes contain centers for reasoning and movement, somatic sensing, hearing, and vision, respectively.

Other Parts of the Brain

The hypothalamus and the thalamus are in the **diencephalon**, a region that encircles the third ventricle. The **hypothalamus** forms the floor of the third ventricle. It is an integrating center that helps maintain homeostasis by regulating hunger, sleep, thirst, body temperature, and water balance. The hypothalamus controls the pituitary gland and, thereby, serves as a link between the nervous and endocrine systems.

The **thalamus** consists of two masses of gray matter located in the sides and roof of the third ventricle. It is on the receiving end for all sensory input except smell. Visual, auditory, and somatosensory information arrives at the thalamus via the cranial nerves and tracts from the spinal cord. The thalamus integrates this information and sends it on to the appropriate portions of the cerebrum. For this reason, the thalamus is often referred to as the "gatekeeper" for sensory information en route to the cerebral cortex. The thalamus is involved in arousal of the cerebrum, and it also participates in higher mental functions such as memory and emotions.

The **pineal gland**, which secretes the hormone melatonin, is located in the diencephalon. Presently, there is much interest in the role of melatonin in our daily rhythms; some researchers believe it may be involved in jet lag and insomnia. Scientists are also interested in the possibility that the hormone regulates the onset of puberty.

The **cerebellum** lies under the occipital lobe of the cerebrum and is separated from the brain stem by the fourth ventricle. It is the largest part of the hindbrain. The cerebellum has two portions that are joined by a narrow central portion. Each portion is primarily composed of white matter, which in longitudinal section has a treelike pattern. Overlying the white matter is a thin layer of gray matter that forms a series of complex folds.

The cerebellum receives sensory input from the eyes, ears, joints, and muscles about the present position of body parts, and it also receives motor output from the cerebral cortex about where these parts should be located. After integrating this information, the cerebellum sends motor impulses by way of the brain stem to the skeletal muscles. In this way, the cerebellum maintains posture and balance. It also ensures that all of the muscles work together to produce smooth, coordinated voluntary movements. The cerebellum assists the learning of new motor skills such as playing the piano or hitting a baseball. New evidence indicates that the cerebellum is important in judging the passage of time.

The **brain stem** contains the midbrain, the pons, and the medulla oblongata (see Fig. 37.8). The **midbrain** acts as a relay station for tracts passing between the cerebrum and the spinal cord or cerebellum. The tracts cross in the brain stem so that the right side of the body is controlled by the left portion of the brain, and the left portion of the body is controlled by the right portion of the brain.

The brain stem also has reflex centers for visual, auditory, and tactile responses. The word **pons** means "bridge" in Latin, and true to its name, the pons contains bundles

of axons traveling between the cerebellum and the rest of the CNS. In addition, the pons functions with the medulla oblongata to regulate breathing rate, and has reflex centers concerned with head movements in response to visual and auditory stimuli.

The **medulla oblongata** contains a number of reflex centers for regulating heartbeat, breathing, and blood pressure. It also contains the reflex centers for vomiting, coughing, sneezing, hiccuping, and swallowing. The medulla oblongata lies just superior to the spinal cord, and it contains tracts that ascend or descend between the spinal cord and higher brain centers.

The Reticular Activating System. The reticular formation is a complex network of nuclei (masses of gray matter) and nerve fibers that extend the length of the brain stem (Fig. 37.10). The reticular formation is a major component of the reticular activating system (RAS), which receives sensory signals that it sends up to higher centers, and motor signals that it sends to the spinal cord.

The RAS arouses the cerebrum via the thalamus and causes a person to be alert. Apparently, the RAS can filter out unnecessary sensory stimuli, explaining why you can study with the TV on. If you want to awaken the RAS, surprise it with a sudden stimulus, like splashing your face with cold water; if you want to deactivate it, remove visual and auditory stimuli. General anesthetics function by artificially suppressing the RAS. A severe injury to the RAS can cause a person to be comatose, from which recovery may be impossible.

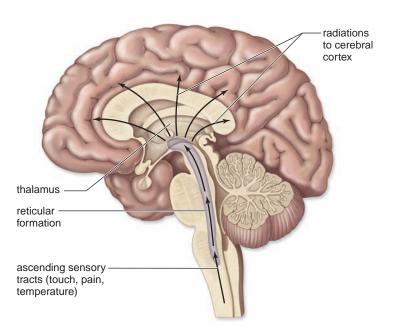


FIGURE 37.10 The reticular activating system.

The reticular formation receives and sends on motor and sensory information to various parts of the CNS. One portion, the reticular activating system (RAS; see arrows), arouses the cerebrum and, in this way, controls alertness versus sleep.

The Limbic System

The **limbic system** is a complex network of tracts and nuclei that incorporates medial portions of the cerebral lobes, the basal nuclei, and the diencephalon (Fig. 37.11). The limbic system blends higher mental functions and primitive emotions into a united whole. It accounts for why activities like sexual behavior and eating seem pleasurable and also why, say, mental stress can cause high blood pressure.

Two significant structures within the limbic system are the hippocampus and the amygdala, which are essential for learning and memory. The hippocampus, a seahorse-shaped structure that lies deep in the temporal lobe, is well situated in the brain to make the prefrontal area aware of past experiences stored in sensory association areas. The amygdala, in particular, can cause these experiences to have emotional overtones. For example, the smell of smoke may serve as an alarm to search for fire in the house. The inclusion of the frontal lobe in the limbic system means that reason can keep us from acting out strong feelings.

Learning and Memory. Memory is the ability to hold a thought in mind or recall events from the past, ranging from a word we learned only yesterday to an early emotional experience that has shaped our lives. Learning takes place when we retain and use past memories.

The prefrontal area in the frontal lobe is active during short-term memory as when we temporarily recall a telephone number. Some telephone numbers go into long-term memory. Think of a telephone number you know by heart, and see if you can bring it to mind without also thinking about the place or person associated with that number. Most likely you cannot, because typically long-term memory is a mixture of what is called semantic memory (numbers, words, etc.) and episodic memory (persons, events, etc.). Skill memory is a type of memory that can exist independent of episodic memory. Skill memory is being able to perform motor activities like riding a bike or playing ice hockey.

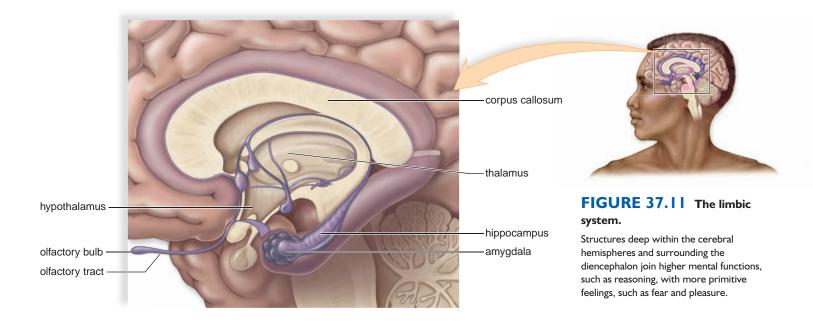
What parts of the brain are functioning when you remember something from long ago? The hippocampus gathers our long-term memories, which are stored in bits and pieces throughout the sensory association areas, and makes them available to the frontal lobe. Why are some memories so emotionally charged? The amygdala is responsible for fear conditioning and associating danger with sensory information received from the thalamus and the cortical sensory areas.

Long-term potentiation (LTP) is an enhanced response at synapses seen particularly within the hippocampus. During LTP, glutamate binds to the postsynaptic membrane, and calcium may rush in too fast due to a malformed receptor. The apoptosis that follows may contribute to Alzheimer disease (AD). AD neurons have neurofibrillary tangles (bundles of fibrous protein) surrounding the nucleus and protein-rich accumulations called amyloid plaques enveloping the axon branches. Although it is not yet known how excitotoxicity is related to structural abnormalities of AD neurons, some researchers are trying to develop neuroprotective drugs that can possibly guard brain cells against damage due to glutamate.

Check Your Progress

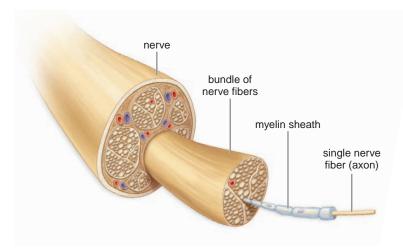
37.3

- 1. The brain is very dependent on the spinal cord. Explain.
- The hypothalamus, which has sleep centers, communicates with the RAS. What might cause narcolepsy, the disorder characterized by brief periods of unexpected sleep?
- 3. Brain injury can cause a disconnect between the amygdala and the portion of the cortex devoted to recognizing faces. People with this ailment can identify the faces of family members, but have no feelings for them. This is so disturbing that sufferers come to believe their "real" families have been replaced with "imposters." Explain.



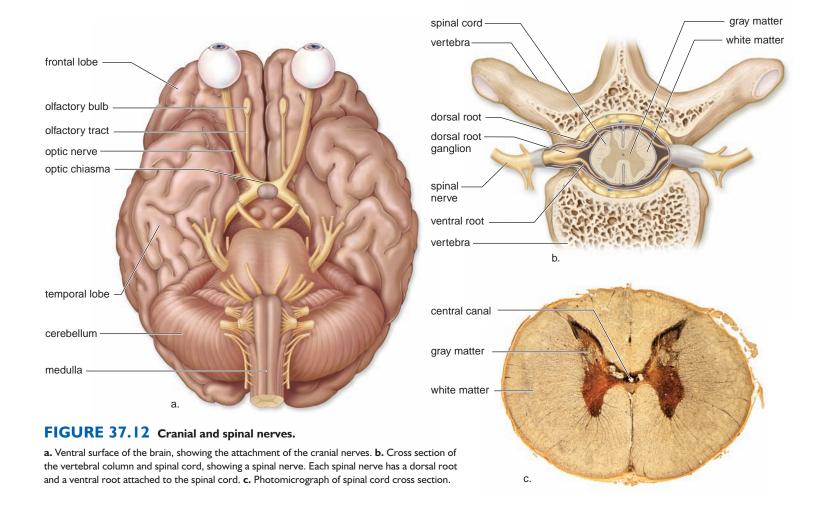
37.4 Peripheral Nervous System

The peripheral nervous system (PNS) lies outside the central nervous system and contains **nerves**, which are bundles of axons. Axons that occur in nerves are also called *nerve fibers*. The cell bodies of neurons are found in the CNS and in ganglia, collections of cell bodies outside the CNS.



Humans have 12 pairs of **cranial nerves** attached to the brain (Fig. 37.12*a*). Some of these are sensory nerves; that is, they contain only sensory nerve fibers. Some are motor nerves that contain only motor fibers, and others are mixed nerves that contain both sensory and motor fibers. Cranial nerves are largely concerned with the head, neck, and facial regions of the body. However, the vagus nerve has branches not only to the pharynx and larynx but also to most of the internal organs.

Humans have 31 pairs of **spinal nerves** (Figs. 37.12*b* and 37.13). The paired spinal nerves emerge from the spinal cord by two short branches, or roots. The dorsal root contains the axons of sensory neurons, which conduct impulses to the spinal cord from sensory receptors. The cell body of a sensory neuron is in the **dorsal root ganglion**. The ventral root contains the axons of motor neurons, which conduct impulses away from the spinal cord to effectors. These two roots join to form a spinal nerve. All spinal nerves are mixed nerves that contain many sensory and motor fibers. Each spinal nerve serves the particular region of the body in which it is located.



Somatic System

The PNS has two divisions—somatic and autonomic—and we are going to consider the somatic system first. The nerves in the **somatic system** serve the skin, joints, and skeletal muscles. Therefore, the somatic system includes nerves that take (1) sensory information from external sensory receptors in the skin and joints to the CNS, and (2) motor commands away from the CNS to the skeletal muscles. The neurotransmitter acetylcholine (ACh) is active in the somatic system.

Voluntary control of skeletal muscles always originates in the brain. Involuntary responses to stimuli, called reflex actions, can involve either the brain or just the spinal cord. Reflexes enable the body to react swiftly to stimuli that could disrupt homeostasis. Flying objects cause our eyes to blink, and sharp pins cause our hands to jerk away, even without us having to think about it.

The Reflex Arc. Figure 37.13 illustrates the path of a reflex that involves only the spinal cord. If your hand touches a sharp pin, **sensory receptors** generate nerve impulses that

move along sensory axons through a dorsal root ganglion toward the spinal cord. Sensory neurons that enter the cord dorsally pass signals on to many interneurons in the gray matter of the spinal cord. Some of these interneurons synapse with motor neurons. The short dendrites and the cell bodies of motor neurons are also in the spinal cord, but their axons leave the cord ventrally. Nerve impulses travel along motor axons to an effector, which brings about a response to the stimulus. In this case, a muscle contracts so that you withdraw your hand from the pin. (Sometimes an effector is a gland.) Various other reactions are possible—you will most likely look at the pin, wince, and cry out in pain. This whole series of responses is explained by the fact that some of the interneurons in the white matter of the cord carry nerve impulses in tracts to the brain. The brain makes you aware of the stimulus and directs subsequent reactions to the situation. You don't feel pain until the brain receives the information and interprets it! Visual information received directly by way of a cranial nerve may make you aware that your finger is bleeding. Then you might decide to look for a Band-Aid.

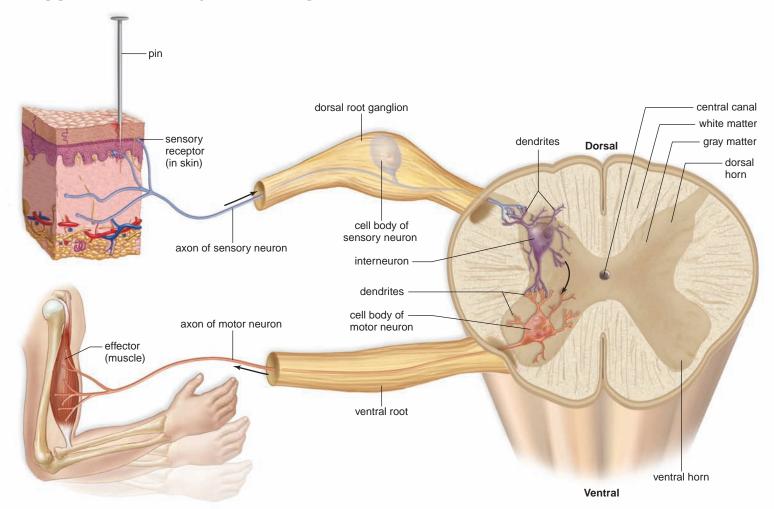
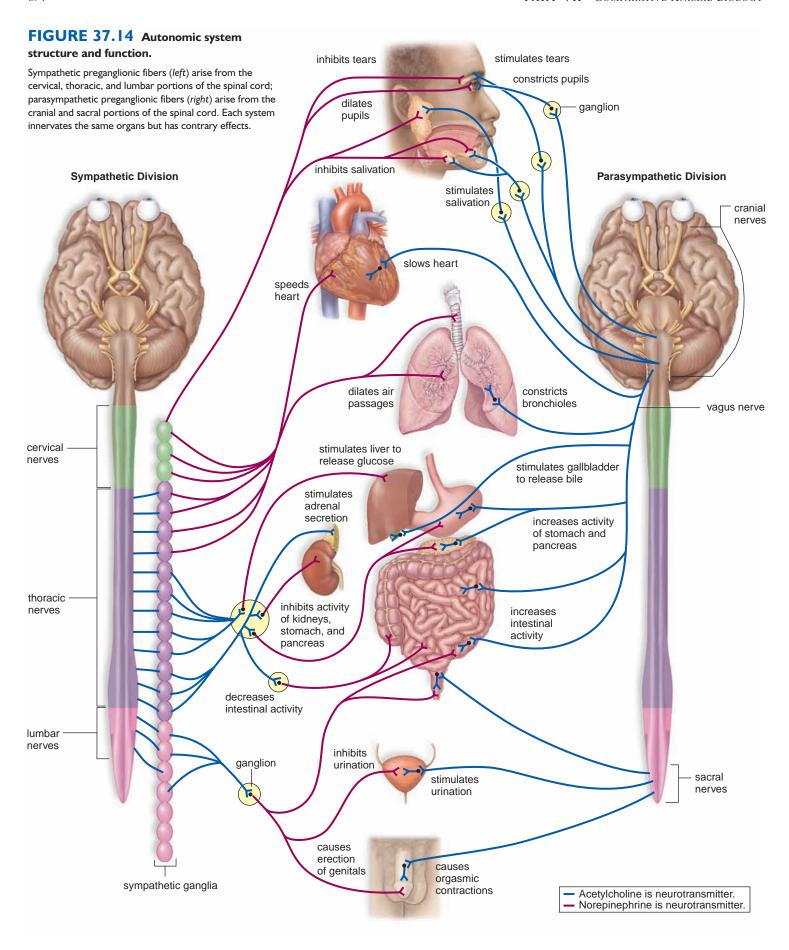


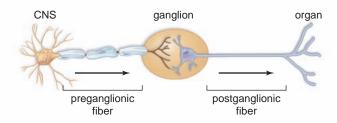
FIGURE 37.13 A reflex arc showing the path of a spinal reflex.

A stimulus (e.g., sharp pin) causes sensory receptors in the skin to generate nerve impulses that travel in sensory axons to the spinal cord. Interneurons integrate data from sensory neurons and then relay signals to motor axons. Motor axons convey nerve impulses from the spinal cord to a skeletal muscle, which contracts. Movement of the hand away from the pin is the response to the stimulus.



Autonomic System

The **autonomic system** of the PNS regulates the activity of cardiac and smooth muscle and glands. It carries out its duties without our awareness or intent. The system is divided into the sympathetic and parasympathetic divisions (Fig. 37.14 and Table 37.1). Both of these divisions (1) function automatically and usually in an involuntary manner; (2) innervate all internal organs; and (3) use two neurons and one ganglion for each impulse. The first neuron has a cell body within the CNS and a preganglionic fiber. The second neuron has a cell body within the ganglion and a postganglionic fiber.



Reflex actions, such as those that regulate blood pressure and breathing rate, are especially important to the maintenance of homeostasis. These reflexes begin when the sensory neurons in contact with internal organs send information to the CNS. They are completed by motor neurons within the autonomic system.

Sympathetic Division

Most preganglionic fibers of the **sympathetic division** arise from the middle, or thoracolumbar, portion of the spinal cord and almost immediately terminate in ganglia that lie near the cord. Therefore, in this division, the preganglionic fiber is short, but the postganglionic fiber that makes contact with an organ is long.

The sympathetic division is especially important during emergency situations and is associated with "fight or flight." If you need to fend off a foe or flee from danger, active muscles require a ready supply of glucose and oxygen. The sympathetic division accelerates the heartbeat and dilates the bronchi. On the other hand, the sympathetic division inhibits the digestive tract, since digestion is not an immediate necessity if you are under attack. The neurotransmitter released by the postganglionic axon is primarily norepinephrine (NE). The structure of NE is like that of epinephrine (adrenaline), an adrenal medulla hormone that usually increases heart rate and contractility.

Parasympathetic Division

The parasympathetic division includes a few cranial nerves (e.g., the vagus nerve) and also fibers that arise from the sacral (bottom) portion of the spinal cord. Therefore, this division often is referred to as the craniosacral portion of the autonomic system. In the parasympathetic division, the preganglionic fiber is long, and the postganglionic fiber is short because the ganglia lie near or within the organ.

The parasympathetic division, sometimes called the "housekeeper" or "rest and digest division," promotes all the internal responses we associate with a relaxed state; for example, it causes the pupil of the eye to contract, promotes digestion of food, and slows the heartbeat. The neurotransmitter used by the parasympathetic division is acetylcholine (ACh).

Check Your Progress

37.4

- I. What are two ways in which cranial nerves and spinal nerves differ from one another?
- 2. a. What part of the CNS is active when a reflex action involving the limbs occurs? b. What part of the CNS is active when we override a reflex action and do not react automatically?
- You are sitting quietly, enjoying a slice of pizza and a soft drink. Your mischievous best friend sneaks up behind you, then dumps ice down the back of your shirt. Describe the shift in autonomic system activity that ensues.

TABLE 37. I Comparison of Somatic Motor and Autonomic N

Comparison of Somatic Motor and Autonomic Motor Pathways Somatic Motor Pathway **Autonomic Motor Pathways** Sympathetic **Parasympathetic** Type of control Voluntary/involuntary Involuntary Involuntary **Number of neurons** One Two (preganglionic shorter Two (preganglionic than postganglionic) per message longer than postganglionic) Most cranial nerves Location of motor fiber Thoracolumbar spinal nerves Cranial (e.g., vagus) and and all spinal nerves sacral spinal nerves Neurotransmitter Acetylcholine Norepinephrine Acetylcholine Effectors Skeletal muscles Smooth and cardiac muscle, Smooth and cardiac glands muscle, glands

science focus

Drugs of Abuse

rug abuse is apparent when a person takes a drug at a dose level and under circumstances that increase the potential for a harmful effect. Addiction is present when more of the drug is needed to get the same effect, and withdrawal symptoms occur when the user stops taking the drug. This is true not only for teenagers and adults, but also for newborn babies of mothers who abuse and are addicted to drugs. Alcohol, drugs, and tobacco can all adversely affect the developing embryo, fetus, or newborn.

Alcohol

Alcohol consumption is the most socially accepted form of drug use worldwide. The approximate number of adults who consume alcohol in the United States on a regular basis is 65%. Of those, 5% say they are "heavy drinkers." Notably, 80% of college-age young adults drink. Unfortunately, so-called binge drinking has resulted in the deaths of many college students.

Alcohol (ethanol) acts as a depressant on many parts of the brain where it affects neurotransmitter release or uptake. For example, alcohol increases the action of GABA, which inhibits motor neurons, and it also increases the release of endorphins, which are natural painkillers. Depending on the amount consumed, the effects of alcohol on the brain can lead to a feeling of relaxation, lowered inhibitions, impaired concentration and coordination, slurred speech, and vomiting. If the blood level of alcohol becomes too high, coma or death can occur.

Chronic alcohol consumption can damage the frontal lobes, decrease overall brain size, and increase the size of the ventricles. Brain damage is manifested by permanent memory loss, amnesia, confusion, apathy, disorientation, or lack of motor coordination. Prolonged alcohol use can also permanently damage the liver, the major detoxification organ of the body, to the point that a liver transplant may be required.

Nicotine

When tobacco is smoked, nicotine is rapidly delivered to the CNS, especially the midbrain.

There it binds to neurons, causing the release of dopamine, the neurotransmitter that promotes a sense of pleasure and is involved in motor control. In the PNS, nicotine also acts as a *stimulant* by mimicking acetylcholine and increasing heart rate, blood pressure, and muscle activity. Fingers and toes become cold because blood vessels have constricted. Increased digestive tract motility may account for the weight loss sometimes seen in smokers.

The physiologically and psychologically addictive nature of nicotine is well known. The addiction rate of smokers is about 70%. The failure rate in those who try to guit smoking is about 80-90% of smokers. Withdrawal symptoms include irritability, headache, insomnia, poor cognitive performance, the urge to smoke, and weight gain. Ways to quit smoking include applying nicotine skin patches, chewing nicotine gum, or taking oral drugs that block the actions of acetylcholine. The effectiveness of these therapies is variable. An experimental therapy involves "immunizing" the brain of smokers against nicotine. Injections cause the production of antibodies that bind to nicotine and prevent it from entering the brain. The effectiveness of this new therapy is not yet known.

Club and Date Rape Drugs

Methamphetamine and Ecstasy are considered club or party drugs. Methamphetamine (commonly called meth or speed) is a synthetic drug made by the addition of a methyl group to amphetamine. Because the addition of the methyl group is fairly simple, methamphetamine is often produced from amphetamine in clandestine, makeshift laboratories in homes, motel rooms, or campers. The number of toxic chemicals used to prepare the drug makes a former meth lab site hazardous to humans and to the environment. Over 9 million people in the United States have used methamphetamine at least once in their lifetime. It is available as a powder or as crystals (crystal meth or ice).

The structure of methamphetamine is similar to that of dopamine, and its *stimulatory* effect mimics that of cocaine. It reverses the effects of fatigue, maintains wakefulness, and temporarily elevates the user's mood. The initial rush is

typically followed by a state of high agitation that, in some individuals, leads to violent behavior. Chronic use can result in what is called an amphetamine psychosis, characterized by paranoia, auditory and visual hallucinations, self-absorption, irritability, and aggressive, erratic behavior. Excessive intake can lead to hyperthermia, convulsions, and death.

Ecstasy is the street name for MDMA (methylenedioxymethamphetamine), a drug with effects similar to those of methamphetamine. Also referred to as E, X, or the love drug, it is taken as a pill that looks like an aspirin or candy. Many people using Ecstasy believe that it is totally safe if used with lots of water to counter its effect on body temperature. A British teen, Lorna Spinks, died after taking two high-strength Ecstasy pills, which caused her body temperature to rise to a fatal level. Also, Ecstasy has an overstimulatory effect on neurons that produce serotonin, which, like dopamine, elevates our mood. Most of the damage to these neurons can be repaired when the use of Ecstasy is discontinued, but some damage appears to be permanent.

Drugs with sedative effects, known as date rape or predatory drugs, include Rohypnol (roofies), gamma-hydroxybutyric acid (GHB), and ketamine (special K). These drugs can be given to an unsuspecting person, who then becomes vulnerable to sexual assault after the drug takes effect. Relaxation, amnesia, and disorientation occur after taking these drugs, which are popular at clubs or raves because they enhance the effect of heroin and Ecstasy.

Cocaine

Cocaine is an alkaloid derived from the shrub Erythroxylon coca. Approximately 35 million Americans have used cocaine by sniffing/snorting, injecting, or smoking. Cocaine is a powerful stimulant in the CNS that interferes with the re-uptake of dopamine at synapses. The result is a rush of well-being that lasts from 5 to 30 minutes. People on cocaine sprees (or binges) take the drug repeatedly and at everhigher doses. The result is sleeplessness, lack of appetite, increased sex drive, tremors, and "cocaine psychosis," a condition that resembles paranoid schizophrenia. During the crash period, fatigue, depression, and irritability are

common, along with memory loss and confused thinking.

"Crack" is the street name given to cocaine that is processed to a free base for smoking. The term *crack* refers to the crackling sound heard when smoking. Smoking allows extremely high doses of the drug to reach the brain rapidly, providing an intense and immediate high, or "rush." Approximately 8 million Americans use crack. Long-term use is expected to cause brain damage (Fig. 37A).

Cocaine is highly addictive; related deaths are usually due to cardiac and/or respiratory arrest. The combination of cocaine and alcohol dramatically increases the risk of sudden death.

Heroin

Heroin is derived from the resin or sap of the opium poppy plant, which is widely grown—from Turkey to Southeast Asia and in parts of Latin America. Heroin is a highly addictive drug that acts as a *depressant* in the nervous system. Drugs derived from opium are called opiates, a class that also includes morphine and codeine, both of which have painkilling effects.

Heroin is the most abused opiate—it travels rapidly to the brain, where it is converted to morphine, and the result is a rush sensation and a feeling of euphoria. Opiates depress breathing, block pain pathways, cloud mental function, and sometimes cause nausea and vomiting. Long-term effects of heroin use are addiction, hepatitis, HIV/AIDS, and various bacterial infections due to the use of shared needles. As with other drugs of abuse, addiction is common, and heavy users may experience convulsions and death by respiratory arrest.

Heroin can be injected, snorted, or smoked. Abusers typically inject heroin up to four times a day. It is estimated that 4 million Americans have used heroin some time in their lives, and over 300,000 people use heroin annually.

Marijuana

The dried flowering tops, leaves, and stems of the Indian hemp plant, *Cannabis sativa*, contain and are covered by a resin that is rich in THC (tetrahydrocannabinol). The names *cannabis* and *marijuana* apply to either the plant or THC. Mari-

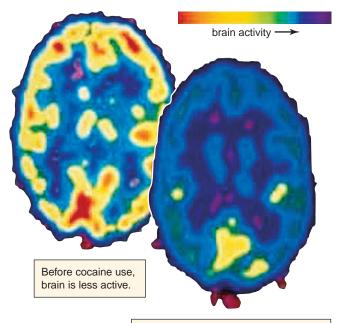


FIGURE 37A

Drug use.

Brain activity before and after the use of cocaine.

After cocaine use, brain is more active.

juana can be consumed, but usually it is smoked in a cigarette called a "joint." An estimated 22 million Americans use marijuana. Although the drug was banned in the United States in 1937, several states have legalized its use for medical purposes, such as lessening the effects of chemotherapy.

It seems that THC may mimic the actions of anandamide, a neurotransmitter that was recently discovered. Both THC and anandamide belong to a class of chemicals called cannabinoids. Receptors that bind cannabinoids are located in the hippocampus, cerebellum, basal nuclei, and cerebral cortex, brain areas that are important for memory, orientation, balance, motor coordination, and perception.

When THC reaches the CNS, the person experiences mild euphoria, along with alterations in vision and judgment. Distortions of space and time can also occur in occasional users. In heavy users, hallucinations, anxiety, depression, rapid flow of ideas, body image distortions, paranoia, and psychotic symptoms can result. The terms cannabis psychosis and

cannabis delirium describe such reactions to marijuana's influence on the brain. Regular usage of marijuana can cause cravings that make it difficult to stop.

Treatment for Addictive Drugs

Presently, treatment for addiction to drugs consists mainly of behavior modification. Heroin addiction can be treated with synthetic opiate compounds, such as methadone or suboxone, that decrease withdrawal symptoms and block heroin's effects. Unfortunately, inappropriate methadone use can be dangerous, as demonstrated by celebrity deaths associated with methadone overdose or taking methadone along with other drugs.

New treatment techniques include the administration of antibodies to block the effects of cocaine and methamphetamine. These antibodies would make relapses by former drug abusers impossible and could be used to treat overdoses. A vaccine for cocaine that would stimulate antibody production is being tested.

Connecting the Concepts

Like the wiring of a modern office building, the peripheral nervous system of humans contains nerves that reach to all parts of the body. There is a division of labor among the nerves. The cranial nerves serve the head region, with the exception of the vagus nerve. All body movements are controlled by spinal nerves, and this is why paralysis may follow a spinal injury. Except for the vagus nerve, only spinal nerves make up the autonomic system, which controls the internal organs. As in most other animals, much of the work of the

nervous system in humans is below the level of consciousness.

The nervous system has just three functions: sensory input, integration, and motor output. Sensory input would be impossible without sensory receptors, which are sensitive to external and internal stimuli. You might even argue that sense organs like the eyes and ears should be considered a part of the nervous system, since there would be no sensory nerve impulses without their ability to generate them.

Nerve impulses are the same in all neurons, so how is it that stimulation of eyes

causes us to see, and stimulation of ears causes us to hear? Essentially, the central nervous system carries out the function of integrating incoming data. The brain allows us to perceive our environment, reason, and remember. After sensory data have been processed by the CNS, motor output occurs. Muscles and glands are the effectors that allow us to respond to the original stimuli. Without the musculoskeletal system, we would never be able to respond to a danger detected by our eyes and ears.

summary

37.1 Evolution of the Nervous System

A comparative study of the invertebrates shows a gradual increase in the complexity of the nervous system. The vertebrate nervous system, like that of the earthworm, is divided into the central and peripheral nervous systems.

37.2 Nervous Tissue

The anatomical unit of the nervous system is the neuron, of which there are three types: sensory, motor, and interneuron. Each of these is made up of a cell body, an axon, and dendrites.

When an axon is not conducting an action potential (nerve impulse), the resting potential indicates that the inside of the fiber is negative compared to the outside. The sodium-potassium pump helps maintain a concentration of Na^+ outside the fiber and K^+ inside the fiber. When the axon is conducting a nerve impulse, an action potential (i.e., a change in membrane potential) travels along the fiber. Depolarization occurs (inside becomes positive) due to the movement of Na^+ to the inside, and then repolarization occurs (inside becomes negative again) due to the movement of K^+ to the outside of the fiber.

Transmission of the nerve impulse from one neuron to another takes place across a synapse. In humans, synaptic vesicles release a chemical, known as a neurotransmitter, into the synaptic cleft. The binding of neurotransmitters to receptors in the postsynaptic membrane can either increase the chance of an action potential (stimulation) or decrease the chance of an action potential (inhibition) in the next neuron. A neuron usually transmits several nerve impulses, one after the other.

37.3 Central Nervous System: Brain and Spinal Cord

The CNS consists of the spinal cord and brain, which are both protected by bone. The CNS receives and integrates sensory input and formulates motor output. The gray matter of the spinal cord contains neuron cell bodies; the white matter consists of myelinated axons that occur in bundles called tracts. The spinal cord sends sensory information to the brain, receives motor output from the brain, and carries out reflex actions.

In the brain, the cerebrum has two cerebral hemispheres connected by the corpus callosum. Sensation, reasoning, learning and memory, and language and speech take place in the cerebrum. The cerebral cortex is a thin layer of gray matter covering the cerebrum. The cerebral cortex of each cerebral hemisphere has four

lobes: a frontal, parietal, occipital, and temporal lobe. The primary motor area in the frontal lobe sends out motor commands to lower brain centers, which pass them on to motor neurons. The primary somatosensory area in the parietal lobe receives sensory information from lower brain centers in communication with sensory neurons. Association areas for vision are in the occipital lobe, and those for hearing are in the temporal lobe.

The brain has a number of other regions. The hypothalamus controls homeostasis, and the thalamus specializes in sending sensory input on to the cerebrum. The cerebellum primarily coordinates skeletal muscle contractions. The medulla oblongata and the pons have centers for vital functions such as breathing and the heartbeat.

37.4 Peripheral Nervous System

The peripheral nervous system contains the somatic system and the autonomic system. Reflexes are automatic, and some do not require involvement of the brain. A simple reflex requires the use of neurons that make up a reflex arc. In the somatic system, a sensory neuron conducts nerve impulses from a sensory receptor to an interneuron, which in turn transmits impulses to a motor neuron, which stimulates an effector to react.

While the motor portion of the somatic system of the PNS controls skeletal muscle, the motor portion of the autonomic system controls smooth muscle of the internal organs and glands. The sympathetic division, which is often associated with reactions that occur during times of stress, and the parasympathetic division, which is often associated with activities that occur during times of relaxation, are both parts of the autonomic system.

understanding the terms

acetylcholine (ACh) 686
acetylcholinesterase
(AChE) 686
action potential 685
autonomic system 695
axon 683
basal nuclei 689
brain 688
brain stem 690
cell body 683
central nervous system

(CNS) 681 cephalization 680

cerebellum 690
cerebral cortex 689
cerebral hemisphere 689
cerebrospinal fluid 688
cerebrum 689
cranial nerve 692
dendrite 683
diencephalon 690
dopamine 686
dorsal root ganglion 692
effector 693
ganglion 680
gray matter 688

Huntington disease 689 hypothalamus 690 integration 687 interneuron 683 ladderlike nervous system 680 limbic system 691 medulla oblongata 690 memory 691 meninges 688 meningitis 688 midbrain 690 motor (efferent) neuron 683 myelin sheath 683 nerve 692 nerve fiber 683 nerve net 680 neuroglia 683 687 neuromodulator neuron 683 neurotransmitter 686 nodes of Ranvier 683

peripheral nervous system (PNS) 682 pineal gland 690 pons 690 primary motor area 689 primary somatosensory area 689 reflex action 688 refractory period 685 resting potential 684 saltatory conduction 685 Schwann cell 683 sensory (afferent) neuron 683 sensory receptor 693 serotonin 686 somatic system 693 spinal cord 688 spinal nerve 692 sympathetic division 695 synapse 686 synaptic cleft 686 thalamus 690 tract 688 ventricle 688 white matter 688

Match the terms to these definitions:

norepinephrine (NE) 686

parasympathetic division 695

oligodendrocyte 683

Parkinson disease 689

organism to a stimulus.

b. _____ Chemical stored at the ends of axons that is responsible for transmission across a synapse.

c. _____ System within the peripheral nervous system that regulates internal organs.

d. _____ Collection of neuron cell bodies usually outside the central nervous system.

e. ____ Neurotransmitter active in the somatic system of the peripheral nervous system.

_ Automatic, involuntary responses of an

reviewing this chapter

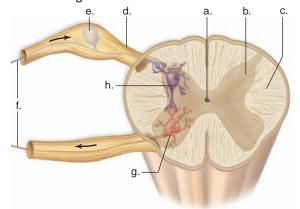
- Trace the evolution of the nervous system by contrasting its organization in hydras, planarians, earthworms, and humans. 680–82
- Describe the structure of a neuron, and give a function for each part mentioned. Name three types of neurons, and give a function for each. 683
- 3. What are the major events of an action potential, and what ion changes are associated with each event? 685
- 4. Describe the mode of action of a neurotransmitter at a synapse, including how it is stored and how it is destroyed. 686–87
- 5. Name the major parts of the human brain, and give a principal function for each part. 688–90
- 6. Describe the limbic system, and discuss its possible involvement in learning and memory. 691
- Discuss the structure and function of the peripheral nervous system. 692
- 8. Trace the path of a spinal reflex. 693
- 9. Contrast the sympathetic and parasympathetic divisions of the autonomic system. 694–95

testing yourself

Choose the best answer for each question.

- I. Which is the most complete list of animals that have a central nervous system (CNS) and a peripheral nervous system (PNS)?
 - a. hydra, planarian, earthworm, rabbit, human
 - b. planarian, earthworm, rabbit, human
 - c. earthworm, rabbit, human
 - d. rabbit, human
- 2. Which of these are the first and last elements in a spinal reflex?
 - a. axon and dendrite
 - b. sense organ and muscle effector
 - c. ventral horn and dorsal horn
 - d. motor neuron and sensory neuron
 - e. sensory receptor and the brain
- 3. A spinal nerve takes nerve impulses
 - a. to the CNS.
 - b. away from the CNS.
 - c. both to and away from the CNS.
 - d. only inside the CNS.
 - e. only from the cerebrum.
- 4. Which of these correctly describes the distribution of ions on either side of an axon when it is not conducting a nerve impulse?
 - a. more sodium ions (Na $^+$) outside and fewer potassium ions (K $^+$) inside
 - b. K⁺ outside and Na⁺ inside
 - c. charged proteins outside; Na+ and K+ inside
 - d. charged proteins inside
 - e. Both a and d are correct.
- 5. When the action potential begins, sodium gates open, allowing Na⁺ to cross the membrane. Now the polarity changes to
 - a. negative outside and positive inside.
 - b. positive outside and negative inside.
 - c. There is no difference in charge between outside and inside.
 - d. Any one of these could be correct.
- Transmission of the nerve impulse across a synapse is accomplished by
 - a. the release of Na⁺ at the presynaptic membrane.
 - b. the release of neurotransmitters at the postsynaptic membrane
 - c. the reception of neurotransmitters at the postsynaptic membrane.
 - d. Only a and c are correct.
- 7. The autonomic system has two divisions, called the
 - a. CNS and PNS.
 - b. somatic and skeletal systems.
 - c. efferent and afferent systems.
 - d. sympathetic and parasympathetic divisions.
- 8. Synaptic vesicles are
 - a. at the ends of dendrites and axons.
 - b. at the ends of axons only.
 - c. along the length of all long fibers.
 - d. at the ends of interneurons only.
 - e. Both b and d are correct.
- 9. Which of these pairs is mismatched?
 - a. cerebrum—thinking and memory
 - b. thalamus-motor and sensory centers
 - c. hypothalamus—internal environment regulator
 - d. cerebellum-motor coordination
 - e. medulla oblongata-fourth ventricle

- 10. Repolarization of an axon during an action potential is produced by
 - a. inward diffusion of Na⁺.
 - b. active extrusion of K⁺.
 - c. outward diffusion of K+
 - d. inward active transport of Na⁺.
- 11. Which two parts of the brain are least likely to work directly together?
 - a. thalamus and cerebrum
 - b. cerebrum and cerebellum
 - c. hypothalamus and medulla oblongata
 - d. cerebellum and medulla oblongata
- 12. Which of the following is not part of the spinal cord?
 - a. central canal
- d. tracts
- b. dorsal horn
- e. ventral horn
- c. association areas
- 13. A drug that inactivates acetylcholinesterase
 - a. stops the release of ACh from presynaptic endings.
 - b. prevents the attachment of ACh to its receptor.
 - c. increases the ability of ACh to stimulate postsynaptic cells.
 - d. All of these are correct.
- 14. Which of these statements about autonomic neurons is correct?
 - a. They are motor neurons.
 - b. Preganglionic neurons have cell bodies in the CNS.
 - Postganglionic neurons innervate smooth muscles, cardiac muscle, and glands.
 - d. All of these are correct.
- 15. Which of these fibers release norepinephrine?
 - a. preganglionic sympathetic axons
 - b. postganglionic sympathetic axons
 - c. preganglionic parasympathetic axons
 - d. postganglionic parasympathetic axons
- 16. Sympathetic nerve stimulation does not cause
 - a. the liver to release glycogen.
 - b. dilation of bronchioles.
 - c. the gastrointestinal tract to digest food.
 - d. an increase in the heart rate.
- 17. The limbic system
 - a. involves portions of the cerebral lobes, basal nuclei, and the diencephalon.
 - is responsible for our deepest emotions, including pleasure, rage, and fear.
 - c. is not responsible for reason and self-control.
 - d. All of these are correct.
- 18. Which of these would be covered by a myelin sheath?
 - a. short dendrites
- d. interneurons
- b. globular cell bodies
- e. All of these are correct.
- c. long axons
- 19. Label this diagram of a reflex arc.



thinking scientifically

- I. In individuals with panic disorder, the fight-or-flight response is activated by inappropriate stimuli. How might it be possible to directly control this response in order to treat panic disorder? Why is such control often impractical?
- 2. A man who lost his leg several years ago continues to experience pain as though it were coming from the missing limb. What hypothesis could explain the neurological basis of this pain?

bioethical issue

The Terri Schiavo Case

On March 31, 2005, news outlets across the country were dominated by the death of a 41-year-old Florida woman named Terri Schiavo. Mrs. Schiavo had required a feeding tube to provide her with fluid and nutrients for 15 years, ever since cardiac arrest deprived her brain of oxygen, causing what doctors diagnosed as a permanent vegetative state (PVS). She died about two weeks after her feeding tube was withdrawn under court order.

PVS is different from brain death, in which all brain function is destroyed. A brain-dead patient lacks the reflexes needed to breathe and maintain blood pressure, and therefore needs more extensive life-support than a PVS patient. A person in a PVS is not aware of his or her surroundings and is unable to communicate or respond to commands. However, the individual can usually breathe without a ventilator, make spontaneous movements, respond to stimuli with involuntary reflexes, open and close his or her eyes, and sometimes even laugh or cry. PVS is caused by prolonged oxygen deprivation of the brain, and is diagnosed if a completely unconscious individual remains so for several months. The longer a person is in a vegetative state, the less likely it is that he or she will ever recover.

The decision to remove Terri Schiavo's feeding tube was sought by Mrs. Schiavo's husband, who stated that his wife would not choose to exist in such a condition. However, his decision met with strong opposition from her parents, who insisted their daughter could be in an ongoing, minimally conscious state (MCS). There is evidence that individuals in a MCS may be aware, but are severely limited in their ability to respond to stimuli and communicate. Even if Mrs. Schiavo could never regain full consciousness, her parents maintained their desire to continue care and support for her.

Although an autopsy following Terri Schiavo's death showed that her brain was less than half the mass that it should have been, it was impossible to determine if she was in a PVS or MCS state. The Terri Schiavo case raises a multitude of difficult questions. What evidence should a family require before making the decision to cease all life-sustaining measures for a loved one? Does it make a difference if the patient is in a MCS versus a PVS? Who should bear the cost of diagnosing and caring for patients with long-term loss of consciousness? Should everyone sign a document or carry a card stating his or her wishes in the event of a traumatic brain injury?

Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

http://www.mhhe.com/maderbiology I 0



38

Sense Organs

ogs, especially bloodhounds, have an astonishing sense of smell and can detect drugs, explosives, human remains, termites, gas leaks, and much more. Dogs have a better sense of smell than humans because they have approximately 40 times more olfactory cells in their nasal cavities. Upon stimulation, olfactory cells generate nerve impulses that travel to the brain where they are interpreted. Impulses arriving at a particular sensory area of the brain can be interpreted in only one way; for example, those arriving at the olfactory area only result in smell sensations.

Dogs and other animals, including humans, have a variety of sensory receptors. Chemoreceptors are sensitive to the presence of particular molecules, photoreceptors are sensitive to light, and mechanoreceptors detect touch and pressure. Sensory receptors play a significant role in homeostasis because they gather the information that allows the brain to make decisions about finding prey, escaping a predator, and any number of other adaptative behaviors. In this chapter, you will learn how sense organs work, and how they enable animals to survive in changing environments.



concepts

38.1 CHEMICAL SENSES

- Chemoreceptors are almost universally found in animals for sensing chemical substances in food and air. 702
- Human taste buds and olfactory cells are chemoreceptors that respond to chemicals in food and air, respectively. 702–3

38.2 SENSE OF VISION

The eye of arthropods is a compound eye made up of many individual units; the human eye is a camera-type eye with a single lens. Photoreceptors contain visual pigments that respond to light rays. In humans, synaptic integration and processing begin in the retina before nerve impulses are sent to the brain. 704–8

38.3 SENSES OF HEARING AND BALANCE

■ The inner ear of humans contains mechanoreceptors for hearing and for a sense of balance. The mechanoreceptors for hearing are hair cells in the cochlea, and the mechanoreceptors for balance are hair cells in the vestibule and semicircular canals. 709–13

38.1 Chemical Senses

The sensory receptors responsible for taste and smell are termed **chemoreceptors** [Gk. *chemo*, pertaining to chemicals; L. *receptor*, receiver] because they are sensitive to certain chemical substances in food, including liquids, and air. Chemoreception is found almost universally in animals and is, therefore, believed to be the most primitive sense.

The location and sensitivity of chemoreceptors vary throughout the animal kingdom. They are important in finding food, locating a mate, and detecting potentially dangerous chemicals in the environment. Although chemoreceptors are present throughout the body of planarians, they are concentrated in the auricles located on the sides of the head. Insects, crustaceans, and other arthropods possess a number of chemoreceptors. In the housefly, chemoreceptors are located primarily on the feet. A fly literally tastes with its feet instead of its mouth. Insects also detect airborne pheromones, which are chemical messages passed between individuals. In crustaceans such as lobsters and crabs, chemoreceptors are widely distributed in their appendages and antennae. In vertebrates such as amphibians, chemoreceptors are located in the nose, mouth, and skin. Snakes possess Jacobsen's organs, a pair of sensory pitlike organs located in the roof of the mouth. When a snake flicks its forked tongue, scent molecules are carried to the Jacobsen's organs and sensory information is transmitted to the brain for interpretation. In mammals, the receptors for taste are located in the mouth, and the receptors for smell are located in the nose.

Sense of Taste

In adult humans, approximately 3,000 **taste buds** are located primarily on the tongue (Fig. 38.1). Many taste buds lie along the walls of the papillae, the small elevations on the tongue

that are visible to the unaided eye. Isolated taste buds are also present on the hard palate, the pharynx, and the epiglottis.

Taste buds open at a taste pore. Taste buds have supporting cells and a number of elongated taste cells that end in microvilli. The microvilli, which project into the taste pore, bear receptor proteins for certain molecules. When molecules bind to receptor proteins, nerve impulses are generated in associated sensory nerve fibers. These nerve impulses go to the brain, including cortical areas that interpret them as tastes.

There are five primary types of taste: sweet, sour, salty, bitter, and umami (Japanese savory, delicious). Foods rich in certain amino acids, such as the common seasoning monosodium glutamate (MSG), as well as certain flavors of cheese, beef broth, and some seafood, produce the taste of umami. Taste buds for each of these tastes are located throughout the tongue, although certain regions may be slightly more sensitive to particular tastes. A particular food can stimulate more than one of these types of taste buds. In this way, the response of taste buds can result in a range of sweet, sour, salty, bitter, and umami tastes. The brain appears to survey the overall pattern of incoming sensory impulses and to take a "weighted average" of their taste messages as the perceived taste.

Sense of Smell

In humans, the sense of smell, or olfaction, is dependent on between 10 and 20 million **olfactory cells**. These structures are located within olfactory epithelium high in the roof of the nasal cavity (Fig. 38.2). Olfactory cells are modified neurons. Each cell ends in a tuft of about five olfactory cilia that bear receptor proteins for odor molecules. Each olfactory cell has only 1 out of 1,000 different types of receptor proteins. Nerve fibers from like olfactory cells lead to the same neuron in the olfactory

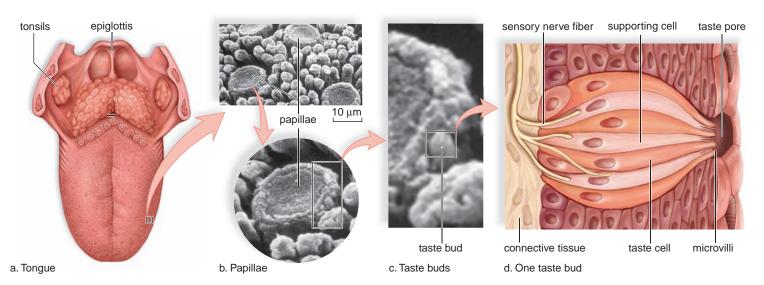
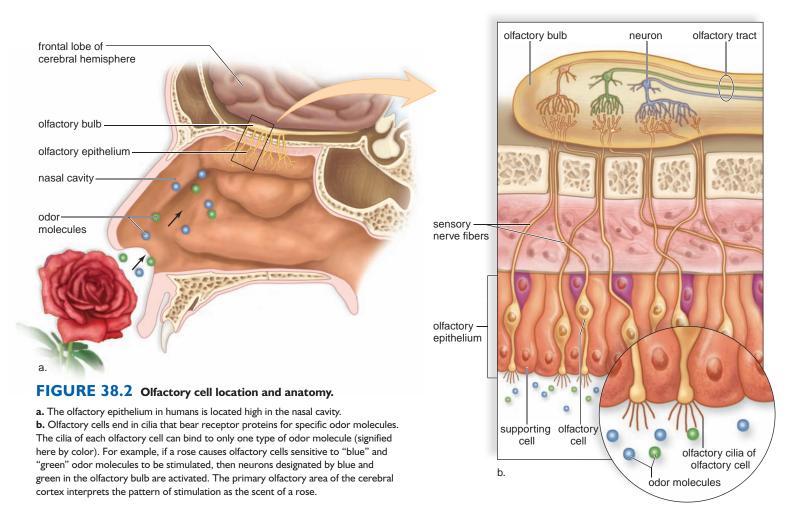


FIGURE 38.1 Taste buds in humans.

a. Papillae on the tongue contain taste buds that are sensitive to sweet, sour, salty, bitter, and umami. b. Photomicrograph and enlargement of papillae. c. Taste buds occur along the walls of the papillae. d. Taste cells end in microvilli that bear receptor proteins for certain molecules. When molecules bind to the receptor proteins, nerve impulses are generated and go to the brain, where the sensation of taste occurs.

CHAPTER 38 Sense Organs 703



bulb, an extension of the brain. An odor contains many odor molecules that activate a characteristic combination of receptor proteins. A rose might stimulate olfactory cells, designated by blue and green in Figure 38.2, while a gardenia might stimulate a different combination. An odor's signature in the olfactory bulb is determined by which neurons are stimulated. When the neurons communicate this information via the olfactory tract to the olfactory areas of the cerebral cortex, we know we have smelled a rose or a gardenia.

Have you ever noticed that a certain aroma vividly brings to mind a certain person or place? A whiff of perfume may remind you of a specific person, or the smell of boxwood may remind you of your grandfather's farm. The olfactory bulbs have direct connections with the limbic system and its centers for emotions and memory. One investigator showed that when subjects smelled an orange while viewing a painting, they not only remembered the painting when asked about it later, they had many deep feelings about the painting.

The number of olfactory cells declines with age and the remaining population of receptors becomes less sensitive. Thus, older people tend to apply excessive amounts of perfume or aftershave to detect its smell. The ability to smell can also be lost as the result of head trauma, respiratory infection, or brain disease. This can become dangerous if these individuals cannot smell spoiled food, smoke, or a gas leak.

Usually, the sense of taste and the sense of smell work together to create a combined effect when interpreted by the cerebral cortex. For example, when you have a cold, you think food has lost its taste, but most likely you have lost the ability to sense its smell. This method works in reverse also. When you smell something, some of the molecules move from the nose down into the mouth region and stimulate the taste buds there. Therefore, part of what we refer to as smell may in fact be taste.

Check Your Progress

38.1

- I. How are the senses of smell and taste similar to one another?
- 2. List the five types of taste.
- The sense of smell has been called the most direct of the senses. Examine Figure 38.2 again, and explain the reason why.

38.2 Sense of Vision

Photoreceptors [Gk. *photos*, light; L. *receptor*, receiver] are sensory receptors that are sensitive to light. Some animals lack photoreceptors and depend on senses such as smelling and hearing instead; other animals have photoreceptors but live in environments that do not require them. For example, moles live underground and use their senses of smell and touch rather than eyesight.

Not all photoreceptors form images. The "eyespots" of planarians allow these animals to determine the direction of light. Image-forming eyes are found among four invertebrate groups: cnidarians, annelids, molluscs, and arthropods. Arthropods have compound eyes composed of many independent visual units called ommatidia [Gk. ommation, dim. of omma, eye], each possessing all the elements needed for light reception (Fig. 38.3). Both the cornea and crystalline cone function as lenses to direct light rays toward the photoreceptors. The photoreceptors generate nerve impulses, which pass to the brain by way of optic nerve fibers. The outer pigment cells absorb stray light rays so that the rays do not pass from one visual unit to the other. The image that results from all the stimulated visual units is crude because the small size of compound eyes limits the number of visual units, which still might number as many as 28,000. How arthropod brains integrate images from the compound eye to perceive objects is not known.

Insects have color vision, but they make use of a slightly shorter range of the electromagnetic spectrum compared to humans. However, they can see the longest of the ultraviolet rays, and this enables them to be especially sensitive to the particular parts of flowers such as nectar guides that have particular ultraviolet patterns (Fig. 38.4). Some fishes, all reptiles, and most birds are believed to have color vision, but among mammals, only humans and other primates have color vision. It would seem, then, that this trait was adaptive for a diurnal habit (active during the day), which accounts for its retention in a few mammals.

Vertebrates (including humans) and certain molluscs, such as the squid and the octopus, have a **camera-type eye**. Since molluscs and vertebrates are not closely related, this similarity is an example of convergent evolution. A single lens focuses an image of the visual field on photoreceptors,



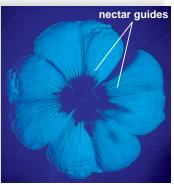


FIGURE 38.4 Nectar guides.

Evening primrose, *Oenothera*, as seen by humans (*left*) and insects (*right*). Humans see no markings, but insects see distinct blotches because their eyes respond to ultraviolet rays. These types of markings, known as nectar guides, often highlight the reproductive parts of flowers, where insects feed on nectar and pick up pollen at the same time.

which are closely packed together. In vertebrates, the lens changes shape to aid focusing, but in molluscs the lens moves back and forth. All of the photoreceptors taken together can be compared to a piece of film in a camera. The human eye is more complex than a camera, however, as we shall see.

Animals with two eyes facing forward have threedimensional, or **stereoscopic**, **vision**. The visual fields overlap and each eye is able to view an object from a different angle. Predators tend to have stereoscopic vision and so do humans. Animals with eyes facing sideways, such as rabbits, don't have stereoscopic vision, but they do have **panoramic vision**, meaning that the visual field is very wide. Panoramic vision is useful to prey animals because it makes it more difficult for a predator to sneak up on them.

The Human Eye

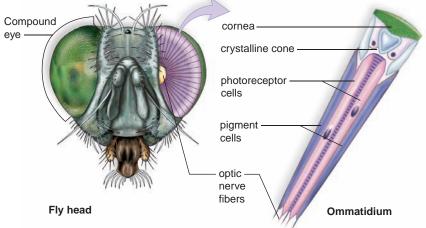
The most important parts of the human eye and their functions are listed in Table 38.1. The human eye, which is an elongated sphere about 2.5 cm in diameter, has three layers, or coats: the sclera, the choroid, and the retina (Fig. 38.5). The outer layer, the **sclera** [Gk. *skleros*, hard], is an opaque, white, fibrous layer that covers most of the eye; in front of the

FIGURE 38.3

Compound eye.

Each visual unit of a compound eye has a cornea and a lens that focus light onto photoreceptors. The photoreceptors generate nerve impulses that are transmitted to the brain, where interpretation produces a mosaic image.





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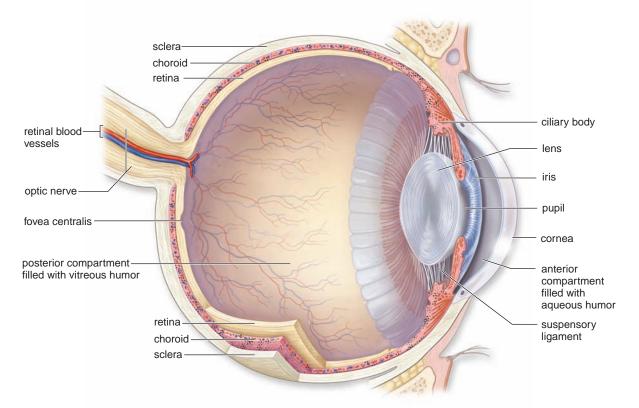


FIGURE 38.5

Anatomy of the human eye.

Notice that the sclera, the outer layer of the eye, becomes the cornea and that the choroid, the middle layer, is continuous with the ciliary body and the iris. The retina, the inner layer, contains the photoreceptors for vision. The fovea centralis is the region where vision is most acute.

eye, the sclera becomes the transparent **cornea**, the window of the eye. A thin layer of epithelial cells forms a mucous membrane called the **conjunctiva** that covers the surface of the sclera and keeps the eyes moist. The middle, thin, darkbrown layer, the **choroid** [Gk. *chorion*, membrane], contains many blood vessels and a brown pigment that absorbs stray

TABLE 38.1		
Functions of the Parts of the Eye		
Part	Function	
Sclera	Protects and supports eyeball	
Conjunctiva	Moistens eye surface	
Cornea	Refracts light rays	
Pupil	Admits light	
Choroid	Absorbs stray light	
Ciliary body	Holds lens in place, accommodation	
Iris	Regulates light entrance	
Retina	Contains sensory receptors for sight	
Rods	Make black-and-white vision possible	
Cones	Make color vision possible	
Fovea centralis	Makes acute vision possible	
Other		
Lens	Refracts and focuses light rays	
Humors	Transmit light rays and support eyeball	
Optic nerve	Transmits impulse to brain	

light rays. Toward the front of the eye, the choroid thickens and forms the ring-shaped ciliary body and a thin, circular, muscular diaphragm, the iris. The iris is the colored portion of the eye and regulates the size of an opening called the pupil. The pupil, like the aperture of a camera lens, regulates light entering the eye. The lens, which is attached to the ciliary body by ligaments, divides the cavity of the eye into two portions and helps form images. A basic, watery solution called aqueous humor fills the anterior compartment between the cornea and the lens. The aqueous humor provides a fluid cushion and nutrient and waste transport for the eye. Glaucoma results when aqueous humor builds up and increases intraocular pressure. A viscous, gelatinous material, the vitreous humor, fills the large posterior compartment behind the lens. The vitreous humor helps stabilize the shape of the eye and supports the retina.

The inner layer of the eye, the **retina** [L. *rete*, net], is located in the posterior compartment. The retina contains photoreceptors called rod cells and cone cells. The rods are very sensitive to light, but they do not see color; therefore, at night or in a darkened room, we see only shades of gray. The cones, which require bright light, are sensitive to different wavelengths of light, and therefore, we have the ability to distinguish colors. The retina has a very special region called the **fovea centralis**, where cone cells are densely packed. Light is normally focused on the fovea when we look directly at an object. This is helpful because vision is most acute in the fovea centralis. Rods are distributed in the peripheral regions of the retina. Sensory fibers form the optic nerve, which takes nerve impulses to the brain.

Focusing of the Eye

When we look at an object, light rays pass through the pupil and are focused on the retina. The image produced is much smaller than the object because light rays are bent (refracted) when they are brought into focus. Focusing starts at the cornea and continues as the rays pass through the lens and the humors. The image on the retina is inverted (it is upside down) and reversed from left to right. When information from the retina reaches the brain, it is processed so that we perceive our surroundings in the correct orientation.

The lens provides additional focusing power as **visual accommodation** occurs for close vision. The shape of the lens is controlled by the **ciliary muscle** within the ciliary body. When we view a distant object, the ciliary muscle is relaxed, causing the suspensory ligaments attached to the ciliary body to be taut; therefore, the lens remains relatively flat (Fig. 38.6a). When we view a near object, the ciliary muscle contracts, releasing the tension on the suspensory ligaments, and the lens becomes more round due to its natural elasticity (Fig. 38.6b). Because close work requires contraction of the ciliary muscle, it very often causes muscle fatigue known as eyestrain. With normal aging, the lens loses its ability to accommodate for near objects (Fig. 38.6b); therefore, people frequently need reading glasses once they reach middle age.

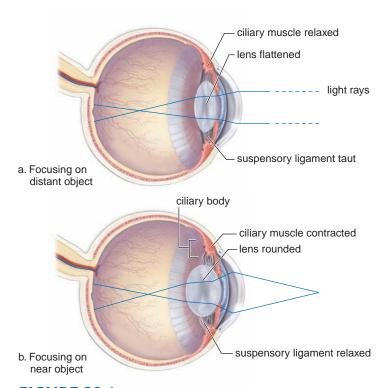


FIGURE 38.6 Focusing of the human eye.

Light rays from each point on an object are bent by the cornea and the lens in such a way that an inverted and reversed image of the object forms on the retina. **a.** When focusing on a distant object, the lens is flat because the ciliary muscle is relaxed and the suspensory ligament is taut. **b.** When focusing on a near object, the lens accommodates; that is, it becomes rounded because the ciliary muscle contracts, causing the suspensory ligament to relax.

Aging, or possibly exposure to the sun, also makes the lens subject to cataracts; the lens can become opaque and therefore incapable of transmitting light rays. Currently, surgery is the only viable treatment for cataracts. First, a surgeon opens the eye near the rim of the cornea. The protein-digesting enzyme zonulysin may be used to dissolve the ligaments holding the lens in place. Most surgeons then use a cryoprobe, which freezes the lens for easy removal. An intraocular lens attached to the iris can then be implanted so that the patient does not need to wear thick glasses or contact lenses.

Distance Vision. Those who can easily see a near object but have trouble seeing what is designated as a size 20 letter 20 ft away on an optometrist's chart are said to be *nearsighted* (myopic). These individuals often have an elongated eyeball, and when they attempt to look at a distant object, the image is brought to focus in front of the retina. These people can wear concave lenses, which diverge the light rays so that the image can be focused on the retina (Fig. 38.7a). Rather

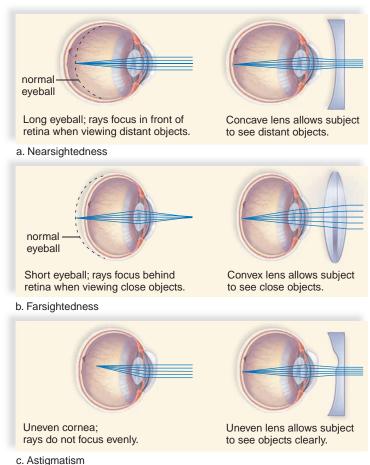


FIGURE 38.7 Common abnormalities of the eye with possible corrective lenses.

a. A concave lens in nearsighted persons focuses light rays on the retina. **b.** A convex lens in farsighted persons focuses light rays on the retina. **c.** An uneven lens in persons with astigmatism focuses light rays on the retina.

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than wear glasses or contact lenses, many nearsighted people are now choosing to undergo laser surgery. First, specialists determine how much the cornea needs to be flattened to achieve visual acuity. Controlled by a computer, the laser then removes this amount of the cornea. Most patients achieve at least 20/40 vision, but a few complain of glare and varying visual acuity.

Those who can easily see the optometrist's chart but cannot easily see near objects are *farsighted* (hyperopic). They often have a shortened eyeball, and when they try to see near objects, the image is focused behind the retina. These individuals must wear a convex lens to increase the bending of light rays so that the image can be focused on the retina (Fig. 38.7b). When the cornea or lens is uneven, the image is fuzzy. This condition, called astigmatism, can be corrected by an unevenly ground lens to compensate for the uneven cornea (Fig. 38.7c).

Photoreceptors of the Eye

Vision begins once light has been focused on the photoreceptors in the retina. Figure 38.8 illustrates the structure of the photoreceptors called **rod cells** and **cone cells**. Both rods and cones have an outer segment joined to an inner segment by a stalk. Pigment molecules are embedded in the membrane of the many disks present in the outer segment. Synaptic vesicles are located at the synaptic endings of the inner segment.

The visual pigment in rods is a deep-purple pigment called rhodopsin. **Rhodopsin** is a complex molecule made

up of the protein opsin and a light-absorbing molecule called *retinal*, which is a derivative of vitamin A. When a rod absorbs light, rhodopsin splits into opsin and retinal, leading to a cascade of reactions and the closure of ion channels in the rod cell's plasma membrane. The release of inhibitory transmitter molecules from the rod's synaptic vesicles ceases. Thereafter, nerve impulses go to the visual areas of the cerebral cortex. Rods are very sensitive to light and, therefore, are suited to night vision. (Since carrots are rich in vitamin A, it is true that eating carrots can improve your night vision.) Rod cells are plentiful in the peripheral region of the retina; therefore, they also provide us with peripheral vision and perception of motion.

The cones, on the other hand, are located primarily in the fovea centralis and are activated by bright light. They allow us to detect the fine detail and the color of an object. Color vision depends on three different kinds of cones, which contain pigments called the B (blue), G (green), and R (red) pigments. Each pigment is made up of retinal and opsin, but there is a slight difference in the opsin structure of each, which accounts for their individual absorption patterns. Various combinations of cones are believed to be stimulated by in-between shades of color. For example, the color yellow is perceived when green cones are highly stimulated, red cones are partially stimulated, and blue cones are not stimulated. In color blindness, an individual lacks certain visual pigments. As indicated in Chapter 11, color blindness is a hereditary disorder.

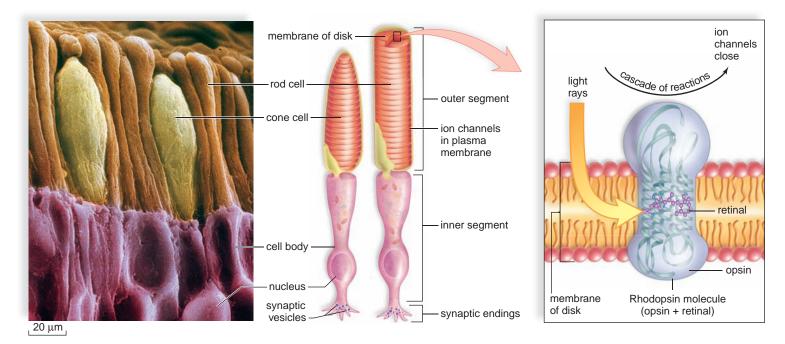


FIGURE 38.8 Photoreceptors in the eye.

The outer segment of rods and cones contains stacks of membranous disks, which contain visual pigments. In rods, the membrane of each disk contains rhodopsin, a complex molecule containing the protein opsin and the pigment retinal. When rhodopsin absorbs light energy, it splits, releasing opsin, which sets in motion a cascade of reactions that cause ion channels in the plasma membrane to close. Thereafter, nerve impulses go to the brain.

Integration of Visual Signals in the Retina

The retina has three layers of neurons (Fig. 38.9). The layer closest to the choroid contains the rod cells and cone cells; the middle layer contains bipolar cells; and the innermost layer contains ganglion cells, whose sensory fibers become the optic nerve. Only the rod cells and the cone cells are sensitive to light, and therefore light must penetrate to the back of the retina before they are stimulated.

The rod cells and the cone cells synapse with the bipolar cells, which in turn synapse with ganglion cells that initiate nerve impulses. Notice in Figure 38.9 that there are many more rod cells and cone cells than ganglion cells. In fact, the retina has as many as 150 million rod cells and 6 million cone cells but only 1 million ganglion cells. The sensitivity of cones versus rods is mirrored by how directly they connect to ganglion cells. As many as 150 rods may excite the same ganglion cell. Stimulation of rods results in vision that is blurred and indistinct. In contrast, some cone cells in the fovea centralis excite only one ganglion cell. This explains why cones, especially in the fovea, provide us with a sharper, more detailed image of an object.

As signals pass to bipolar cells and ganglion cells, integration occurs. Each ganglion cell receives signals from rod cells covering about 1 mm² of retina (about the size of a thumbtack hole). This region is the ganglion cell's receptive field. Some time ago, scientists discovered that a ganglion cell is stimulated only by messages received from the center of its receptive field; otherwise, it is inhibited. If all the rod cells in the receptive field

receive light, the ganglion cell responds in a neutral way—that is, it reacts only weakly or perhaps not at all. This supports the hypothesis that considerable processing occurs in the retina before nerve impulses are sent to the brain. Additional integration occurs in the visual areas of the cerebral cortex.

Blind Spot

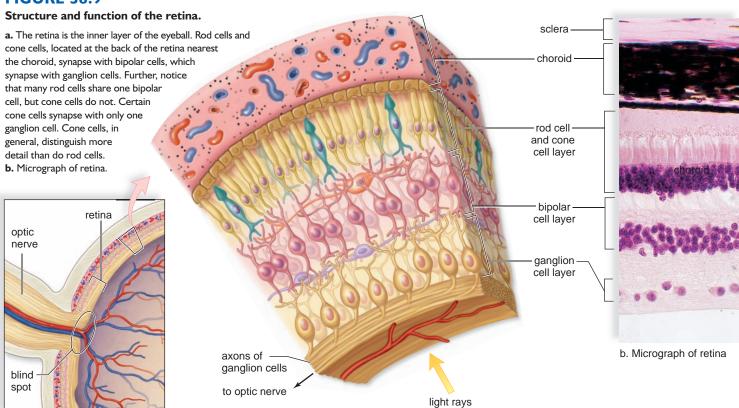
Figure 38.9 provides an opportunity to point out that there are no rods and cones where the optic nerve exits the retina. Therefore, no vision is possible in this area. You can prove this to yourself by putting a dot to the right of center on a piece of paper. Use your right hand to move the paper slowly toward your right eye while you look straight ahead. The dot will disappear at one point—this is your **blind spot**.

Check Your Progress

38.2

- Contrast rod and cone photoreceptors in terms of main functions, light conditions, and excitation of ganglion cells.
- 2. List the three layers (or coats) of the human eye, from the outside in.
- 3. List the three layers of neurons in the human retina, from the layer facing the inside of the eyeball to the layer that contacts the choroid. Why do you think the arrangement of neuron layers is sometimes described as "backwards?"





a. Location of retina

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38.3 Senses of Hearing and Balance

The ear has two sensory functions: hearing and balance (equilibrium). The sensory receptors for both of these are located in the inner ear, and each consists of *hair cells* with stereocilia (long microvilli) that are sensitive to mechanical stimulation. They are **mechanoreceptors**.

Anatomy of the Ear

The ear has three distinct divisions: the outer, inner, and middle ear (Fig. 38.10). The **outer ear** consists of the pinna (external flap) and the auditory canal. The opening of the auditory canal is lined with fine hairs and glands. Glands that secrete earwax are located in the upper wall of the auditory canal. Earwax helps guard the ear against the entrance of foreign materials, such as air pollutants and microorganisms.

The **middle ear** begins at the **tympanic membrane** (eardrum) and ends at a bony wall containing two small

openings covered by membranes. These openings are called the *oval window* and the *round window*. Three small bones are found between the tympanic membrane and the oval window. Collectively called the **ossicles**, individually they are the *malleus* (hammer), the *incus* (anvil), and the *stapes* (stirrup) because their shapes resemble these objects. The malleus adheres to the tympanic membrane, and the stapes touches the oval window. An *auditory tube* (eustachian tube), which extends from each middle ear to the nasopharynx, permits equalization of air pressure. Chewing gum, yawning, and swallowing in elevators and airplanes help move air through the auditory tubes upon ascent and descent. As this occurs, we often hear the ears "pop."

Whereas the outer ear and the middle ear contain air, the inner ear is filled with fluids. Anatomically speaking, the inner ear has three areas: the semicircular canals and the vestibule are both concerned with equilibrium; the cochlea is concerned with hearing. The cochlea resembles the shell of a snail because it spirals.

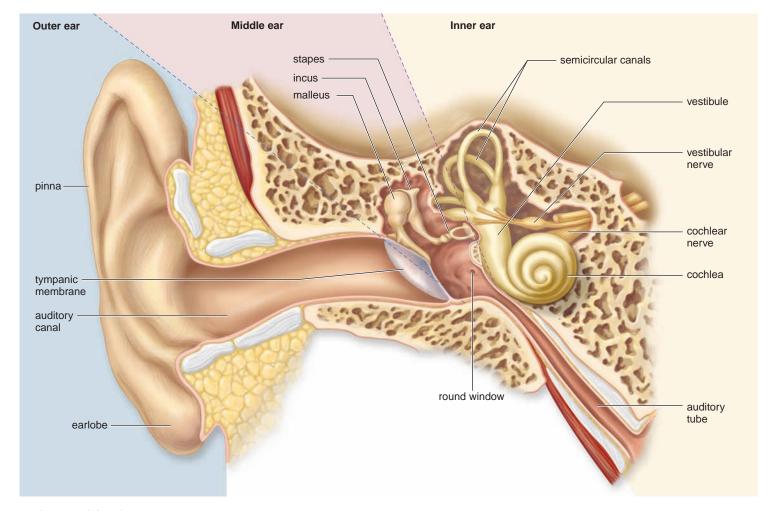


FIGURE 38.10 Anatomy of the human ear.

In the middle ear, the malleus (hammer), the incus (anvil), and the stapes (stirrup) amplify sound waves. In the inner ear, the mechanoreceptors for equilibrium are in the semicircular canals and the vestibule, and the mechanoreceptors for hearing are in the cochlea.

Process of Hearing

The sound pathway travels from the auditory canal to the inner ear.

The Auditory Canal and Middle Ear

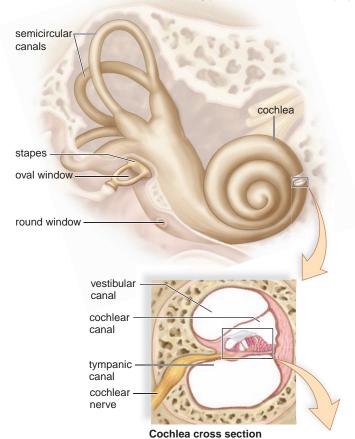
The process of hearing begins when sound waves enter the auditory canal. Just as ripples travel across the surface of a pond, sound waves travel by the successive vibrations of molecules. Ordinarily, sound waves do not carry much energy, but when a large number of waves strike the tympanic membrane, it moves back and forth (vibrates) ever so slightly. The malleus then takes the pressure from the inner surface of the tympanic membrane and passes it by means of the incus to the stapes in such a way that the pressure is multiplied about 20 times as it moves. The stapes strikes the membrane of the oval window, causing it to vibrate, and in this way, the pressure is passed to the fluid within the cochlea.

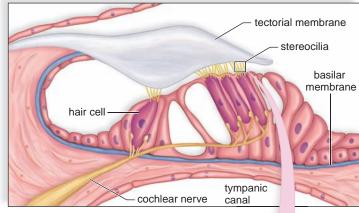
Inner Ear

When the snail-shaped cochlea is examined in cross section (Fig. 38.11), the vestibular canal, the cochlear canal, and the tympanic canal become apparent. The cochlear canal contains endolymph, which is similar in composition to tissue fluid. The vestibular and tympanic canals are filled with perilymph, which is continuous with the cerebrospinal fluid. Along the length of the basilar membrane, which forms the lower wall of the *cochlear canal*, are little hair cells whose stereocilia are embedded within a gelatinous material called the *tectorial membrane*. The hair cells of the cochlear canal, called the **organ of Corti**, or spiral organ, synapse with nerve fibers of the *cochlear nerve* (auditory nerve).

When the stapes strikes the membrane of the oval window, pressure waves move from the vestibular canal to the tympanic canal across the basilar membrane, and the round window membrane bulges. The basilar membrane moves up and down, and the stereocilia of the hair cells embedded in the tectorial membrane bend. Then nerve impulses begin in the cochlear nerve and travel to the brain stem. When they reach the auditory areas of the cerebral cortex, they are interpreted as a sound.

Each part of the organ of Corti is sensitive to different wave frequencies, or pitch. Near the tip, the organ of Corti responds to low pitches, such as a tuba, and near the base, it responds to higher pitches, such as a bell or a whistle. The nerve fibers from each region along the length of the organ of Corti lead to slightly different areas in the brain. The pitch sensation we experience depends on which region of the basilar membrane vibrates and which area of the brain is stimulated. Volume is a function of the amplitude of sound waves. Loud noises cause the fluid within the vestibular canal to exert more pressure and the basilar membrane to vibrate to a greater extent. The resulting increased stimulation is interpreted by the brain as volume. It is believed that the brain interprets the tone of a sound based on the distribution of the hair cells stimulated.





Organ of Corti

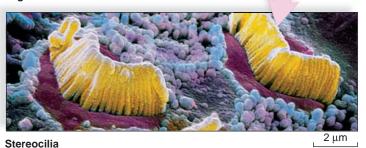


FIGURE 38.11 Mechanoreceptors for hearing.

The organ of Corti is located within the cochlea. In the uncoiled cochlea, note that the organ consists of hair cells resting on the basilar membrane, with the tectorial membrane above. Pressure waves move from the vestibular canal to the tympanic canal, causing the basilar membrane to vibrate. This causes the stereocilia (or at least a portion of the more than 20,000 hair cells) embedded in the tectorial membrane to bend. Nerve impulses traveling in the cochlear nerve result in hearing.