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Maintaining the Internal Environment

Concept Outline

58.1 The regulatory systems of the body maintain homeostasis.

The Need to Maintain Homeostasis. Regulatory mechanisms maintain homeostasis through negative feedback loops.

Antagonistic Effectors and Positive Feedback. Antagonistic effectors cause opposite changes, while positive feedback pushes changes further in the same way.

58.2 The extracellular fluid concentration is constant in most vertebrates.

Osmolality and Osmotic Balance. Vertebrates have to cope with the osmotic gain or loss of body water.

Osmoregulatory Organs. Invertebrates have a variety of organs to regulate water balance; kidneys are the osmoregulatory organs of most vertebrates.

Evolution of the Vertebrate Kidney. Freshwater bony fish produce a dilute urine and marine bony fish produce an isotonic urine. Only birds and mammals can retain so much water that they produce a concentrated urine.

58.3 The functions of the vertebrate kidney are performed by nephrons.

The Mammalian Kidney. Each kidney contains nephrons that produce a filtrate which is modified by reabsorption and secretion to produce urine.

Transport Processes in the Mammalian Nephron. The nephron tubules of birds and mammals have loops of Henle, which function to draw water out of the tubule and back into the blood.

Ammonia, Urea, and Uric Acid. The breakdown of protein and nucleic acids yields nitrogen, which is excreted as ammonia in bony fish, as urea in mammals, and as uric acid in reptiles and birds.

58.4 The kidney is regulated by hormones.

Hormones Control Homeostatic Functions.

Antidiuretic hormone promotes water retention and the excretion of a highly concentrated urine. Aldosterone stimulates the retention of salt and water, whereas atrial natriuretic hormone promotes the excretion of salt and water.



FIGURE 58.1

Regulating body temperature with water. One of the ways an elephant can regulate its temperature is to spray water on its body. Water also cycles through the elephant's body in enormous quantities each day and helps to regulate its internal environment.

The first vertebrates evolved in seawater, and the physiology of all vertebrates reflects this origin. Approximately two-thirds of every vertebrate's body is water. If the amount of water in the body of a vertebrate falls much lower than this, the animal will die. In this chapter, we discuss the various mechanisms by which animals avoid gaining or losing too much water. As we shall see, these mechanisms are closely tied to the way animals exploit the varied environments in which they live and to the regulatory systems of the body (figure 58.1).

58.1 The regulatory systems of the body maintain homeostasis.

The Need to Maintain Homeostasis

As the animal body has evolved, specialization has increased. Each cell is a sophisticated machine, finely tuned to carry out a precise role within the body. Such specialization of cell function is possible only when extracellular conditions are kept within narrow limits. Temperature, pH, the concentrations of glucose and oxygen, and many other factors must be held fairly constant for cells to function efficiently and interact properly with one another.

Homeostasis may be defined as the dynamic constancy of the internal environment. The term *dynamic* is used because conditions are never absolutely constant, but fluctuate continuously within narrow limits. Homeostasis is essential for life, and most of the regulatory mechanisms of the vertebrate body that are not devoted to reproduction are concerned with maintaining homeostasis.

Negative Feedback Loops

To maintain internal constancy, the vertebrate body must have **sensors** that are able to measure each condition of the internal environment (figure 58.2). These constantly monitor the extracellular conditions and relay this information (usually via nerve signals) to an **integrating center**, which contains the “*set point*” (the proper value for that condition). This set point is analogous to the temperature setting on a house thermostat. In a similar manner, there are set points for body temperature, blood glucose concentration, the tension on a tendon, and so on. The integrating center is often a particular region of the brain or spinal cord, but in some cases it can also be cells of endocrine glands. It receives messages from several sensors, weighing the relative strengths of each sensor input, and then determines whether the value of the condition is deviating from the set point. When a deviation in a condition occurs (the “stimulus”), the integrating center sends a message to increase or decrease the activity of particular **effectors**. Effectors are generally muscles or glands, and can change the value of the condition in question back toward the set point value (the “response”).

To return to the idea of a home thermostat, suppose you set the thermostat at a set point of 70°F. If the temperature of the house rises sufficiently above the set point, the thermostat (equivalent to an integrating center) receives this

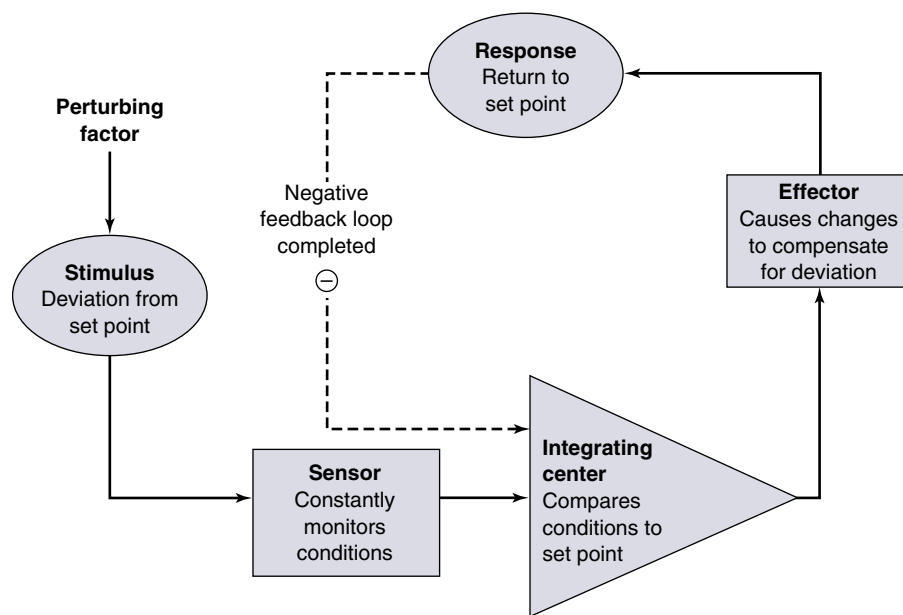


FIGURE 58.2

A generalized diagram of a negative feedback loop. Negative feedback loops maintain a state of homeostasis, or dynamic constancy of the internal environment, by correcting deviations from a set point.

input from a temperature sensor, like a thermometer (a sensor) within the wall unit. It compares the actual temperature to its set point. When these are different, it sends a signal to an effector. The effector in this case may be an air conditioner, which acts to reverse the deviation from the set point.

In a human, if the body temperature exceeds the set point of 37°C, sensors in a part of the brain detect this deviation. Acting via an integrating center (also in the brain), these sensors stimulate effectors (including sweat glands) that lower the temperature (figure 58.3). One can think of the effectors as “defending” the set points of the body against deviations. Because the activity of the effectors is influenced by the effects they produce, and because this regulation is in a negative, or reverse, direction, this type of control system is known as a *negative feedback loop*.

The nature of the negative feedback loop becomes clear when we again refer to the analogy of the thermostat and air conditioner. After the air conditioner has been on for some time, the room temperature may fall significantly below the set point of the thermostat. When this occurs, the air conditioner will be turned off. The effector (air conditioner) is turned on by a high temperature; and, when activated, it produces a negative change (lowering of the temperature) that ultimately causes the effector to be turned off. In this way, constancy is maintained.

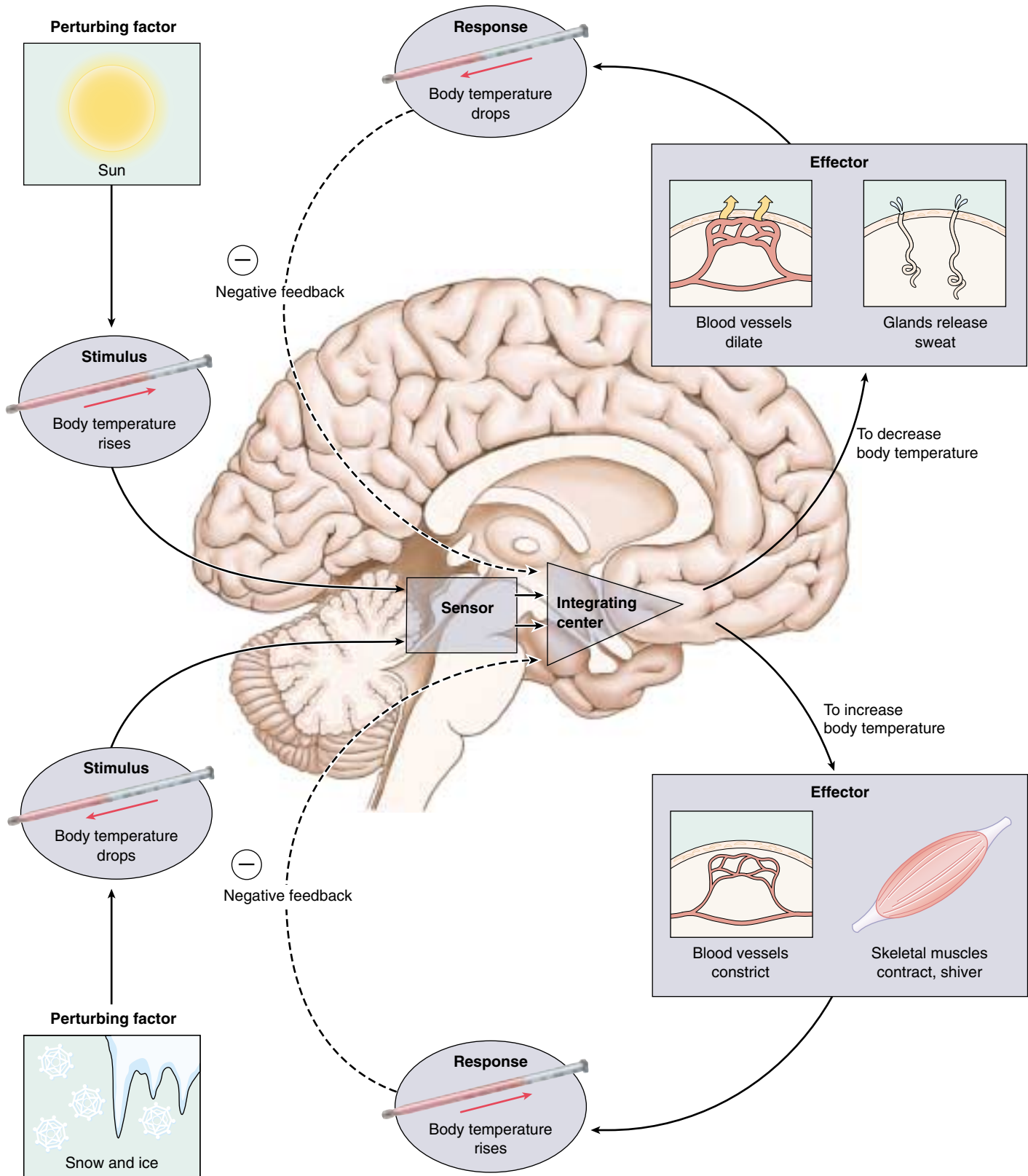


FIGURE 58.3

Negative feedback loops keep the body temperature within a normal range. An increase (*top*) or decrease (*bottom*) in body temperature is sensed by the brain. The integrating center in the brain then processes the information and activates effectors, such as surface blood vessels, sweat glands, and skeletal muscles. When the body temperature returns to normal, negative feedback prevents further stimulation of the effectors by the integrating center.

Regulating Body Temperature

Humans, together with other mammals and with birds, are *endothermic*; they can maintain relatively constant body temperatures independent of the environmental temperature. When the temperature of your blood exceeds 37°C (98.6°F), neurons in a part of the brain called the hypothalamus detect the temperature change. Acting through the control of motor neurons, the hypothalamus responds by promoting the dissipation of heat through sweating, dilation of blood vessels in the skin, and other mechanisms. These responses tend to counteract the rise in body temperature. When body temperature falls, the hypothalamus coordinates a different set of responses, such as shivering and the constriction of blood vessels in the skin, which help to raise body temperature and correct the initial challenge to homeostasis.

Vertebrates other than mammals and birds are *ectothermic*; their body temperatures are more or less dependent on the environmental temperature. However, to the extent that it is possible, many ectothermic vertebrates attempt to maintain some degree of temperature homeostasis. Certain large fish, including tuna, swordfish, and some sharks, for example, can maintain parts of their body at a significantly higher temperature than that of the water. Reptiles attempt to maintain a constant body temperature through behavioral means—by placing themselves in varying locations of sun and shade (see chapter 29). That’s why you frequently see lizards basking in the sun. Sick lizards even give themselves a “fever” by seeking warmer locations!

Most invertebrates do not employ feedback regulation to physiologically control their body temperature. Instead, they use behavior to adjust their temperature. Many butterflies, for example, must reach a certain body temperature before they can fly. In the cool of the morning they orient so as to maximize their absorption of sunlight. Moths and many other insects use a shivering reflex to warm their thoracic flight muscles (figure 58.4).

Regulating Blood Glucose

When you digest a carbohydrate-containing meal, you absorb glucose into your blood. This causes a temporary rise in the blood glucose concentration, which is brought back down in a few hours. What counteracts the rise in blood glucose following a meal?

Glucose levels within the blood are constantly monitored by a sensor, the islets of Langerhans in the pancreas. When levels increase, the islets secrete the hormone *insulin*, which stimulates the uptake of blood glucose into muscles, liver, and adipose tissue. The islets are, in this case, the sensor and the integrating center. The muscles, liver, and adipose cells are the effectors, taking up glucose to control the levels. The muscles and liver can convert the glucose into the polysaccharide glycogen; adipose cells can convert glucose into fat. These actions lower the blood glucose (figure 58.5) and help to store energy in forms that the body can use later.

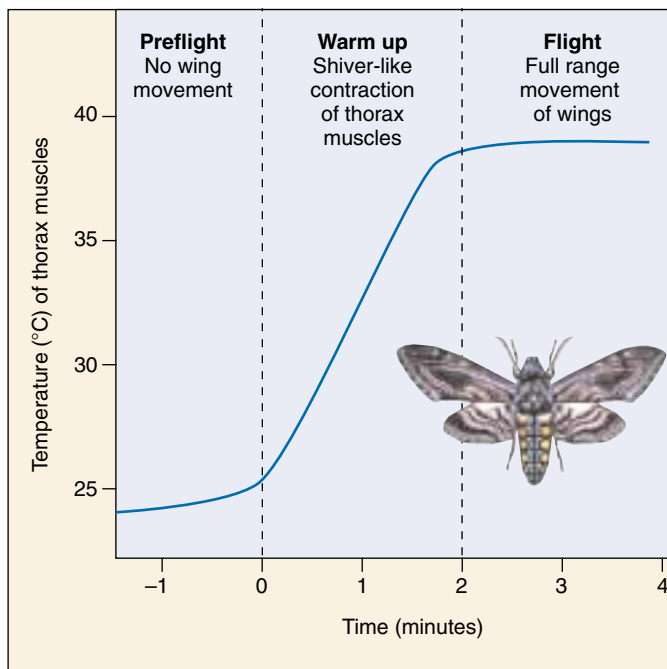


FIGURE 58.4
Thermoregulation in insects. Some insects, such as the sphinx moth, contract their thoracic muscles to warm up for flight.

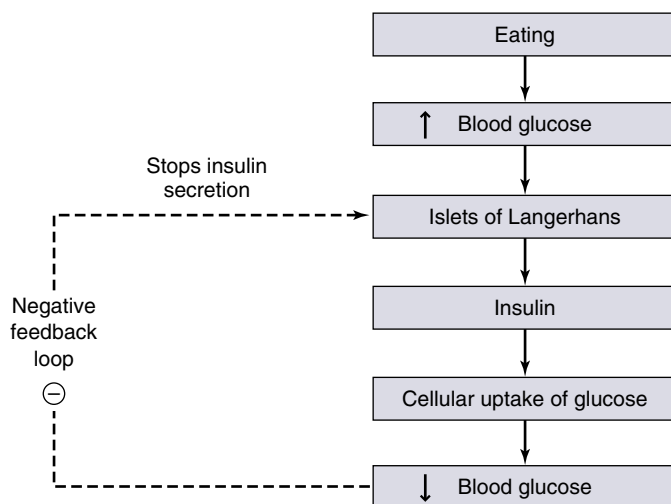


FIGURE 58.5
The negative feedback control of blood glucose. The rise in blood glucose concentration following a meal stimulates the secretion of insulin from the islets of Langerhans in the pancreas. Insulin is a hormone that promotes the entry of glucose in skeletal muscle and other tissue, thereby lowering the blood glucose and compensating for the initial rise.

Negative feedback mechanisms correct deviations from a set point for different internal variables. In this way, body temperature and blood glucose, for example, are kept within normal limits.

Antagonistic Effectors and Positive Feedback

The negative feedback mechanisms that maintain homeostasis often oppose each other to produce a finer degree of control. In a few cases positive feedback mechanisms, which push a change further in the same direction, are used by the body.

Antagonistic Effectors

Most factors in the internal environment are controlled by several effectors, which often have antagonistic actions. Control by antagonistic effectors is sometimes described as “push-pull,” in which the increasing activity of one effector is accompanied by decreasing activity of an antagonistic effector. This affords a finer degree of control than could be achieved by simply switching one effector on and off.

Room temperature can be maintained, for example, by simply turning an air conditioner on and off, or by just turning a heater on and off. A much more stable temperature, however, can be achieved if the air conditioner and heater are both controlled by a thermostat (figure 58.6). Then the heater is turned on when the air conditioner shuts off, and vice versa. Antagonistic effectors are similarly involved in the control of body temperature and blood glucose. Whereas insulin, for example, lowers blood glucose following a meal, other hormones act to raise the blood glucose concentration between meals, especially when a person is exercising. The heart rate is similarly controlled by antagonistic effectors. Stimulation of one group of nerve fibers increases the heart rate, while stimulation of another group slows the heart rate.

Positive Feedback Loops

Feedback loops that accentuate a disturbance are called positive feedback loops. In a positive feedback loop, perturbations cause the effector to drive the value of the controlled variable even *farther* from the set point. Hence, systems in which there is positive feedback are highly unstable, analogous to a spark that ignites an explosion. They do not help to maintain homeostasis. Nevertheless, such systems are important components of some physiological mechanisms. For example, positive feedback occurs in blood clotting, where one clotting factor activates another in a cascade that leads quickly to the formation of a clot. Positive feedback also plays a role in the contractions of the uterus during childbirth (figure 58.7). In this case, stretching of the uterus by the fetus stimulates contraction, and contraction causes further stretching; the cycle continues until the fetus is expelled from the uterus. In the body, most positive feedback systems act as part of some larger mechanism that maintains homeostasis. In the examples we’ve described, formation of a blood clot stops bleeding and hence tends to keep blood volume constant, and expulsion of the fetus reduces the contractions of the uterus.

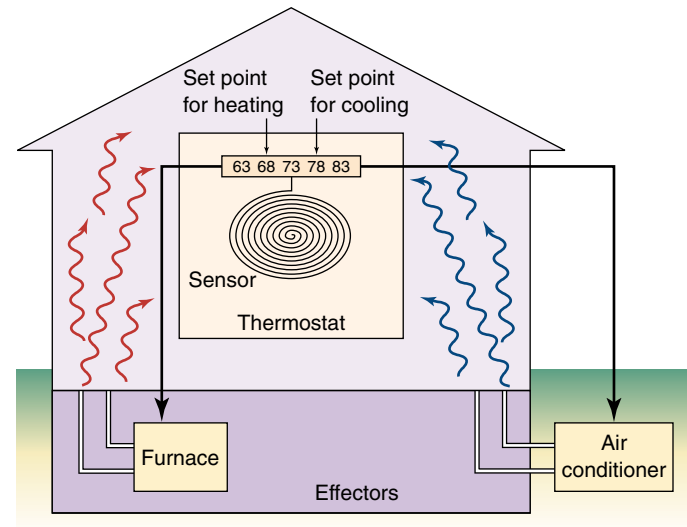


FIGURE 58.6
Room temperature is maintained by antagonistic effectors. If a thermostat senses a low temperature, the heater is turned on and the air conditioner is turned off. If the temperature is too high, the air conditioner is activated, and the heater is turned off.

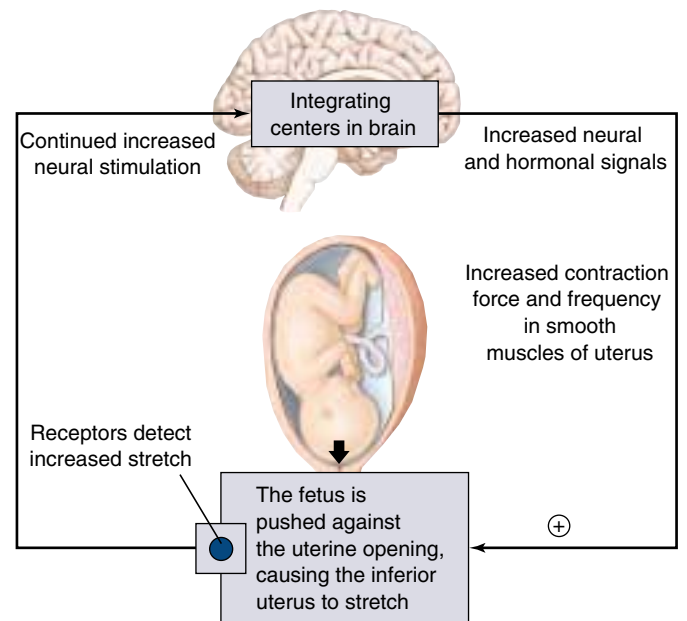


FIGURE 58.7
An example of positive feedback during childbirth. This is one of the few examples of positive feedback that operate in the vertebrate body.

Antagonistic effectors that act antagonistically to each other are more effective than effectors that act alone. Positive feedback mechanisms accentuate changes and have limited functions in the body.

58.2 The extracellular fluid concentration is constant in most vertebrates.

Osmolality and Osmotic Balance

Water in an animal's body is distributed between the intracellular and extracellular compartments (figure 58.8). In order to maintain osmotic balance, the extracellular compartment of an animal's body (including its blood plasma) must be able to take water from its environment or to excrete excess water into its environment. Inorganic ions must also be exchanged between the extracellular body fluids and the external environment to maintain homeostasis. Such exchanges of water and electrolytes between the body and the external environment occur across specialized epithelial cells and, in most vertebrates, through a filtration process in the kidneys.

Most vertebrates maintain homeostasis in regard to the total solute concentration of their extracellular fluids and in regard to the concentration of specific inorganic ions. Sodium (Na^+) is the major cation in extracellular fluids, and chloride (Cl^-) is the major anion. The divalent cations, calcium (Ca^{++}) and magnesium (Mg^{++}), as well as other ions, also have important functions and must be maintained at their proper concentrations.

Osmolality and Osmotic Pressure

Osmosis is the diffusion of water across a membrane, and it always occurs from a more dilute solution (with a lower solute concentration) to a less dilute solution (with a higher solute concentration). Because the total solute concentration of a solution determines its osmotic behavior, the total moles of solute per kilogram of water is expressed as the **osmolality** of the solution. Solutions that have the same osmolality are *isosmotic*. A solution with a lower or higher osmolality than another is called *hypoosmotic* or *hyperosmotic*, respectively.

If one solution is hyperosmotic compared with another, and if the two solutions are separated by a semi-permeable membrane, water may move by osmosis from the more dilute solution to the hyperosmotic one. In this case, the hyperosmotic solution is also **hypertonic** ("higher strength") compared with the other solution, and it has a higher osmotic pressure. The **osmotic pressure** of a solution is a measure of its tendency to take in water by osmosis. A cell placed in a hypertonic solution, which has a higher osmotic pressure than the cell cytoplasm, will lose water to the surrounding solution and shrink. A cell placed in a **hypotonic** solution, in contrast, will gain water and expand.

If a cell is placed in an isosmotic solution, there may be no net water movement. In this case, the isosmotic solution can also be said to be **isotonic**. Isotonic solutions such as normal saline and 5% dextrose are used in medical care to bathe exposed tissues and to be given as intravenous fluids.

Osmoconformers and Osmoregulators

Most marine invertebrates are **osmoconformers**; the osmolality of their body fluids is the same as that of seawater (although the concentrations of particular solutes, such as magnesium ion, are not equal). Because the extracellular fluids are isotonic to seawater, there is no osmotic gradient and no tendency for water to leave or enter the body. Therefore, osmoconformers are in osmotic equilibrium with their environment. Among the vertebrates, only the primitive hagfish are strict osmoconformers. The sharks and their relatives in the class Chondrichthyes (cartilaginous fish) are also isotonic to seawater, even though their blood level of NaCl is lower than that of seawater; the difference in total osmolality is made up by retaining urea at a high concentration in their blood plasma.

All other vertebrates are osmoregulators—that is, animals that maintain a relatively constant blood osmolality despite the different concentration in the surrounding environment. The maintenance of a relatively constant body fluid osmolality has permitted vertebrates to exploit a wide variety of ecological niches. Achieving this constancy, however, requires continuous regulation.

Freshwater vertebrates have a much higher solute concentration in their body fluids than that of the surrounding water. In other words, they are hypertonic to their environment. Because of their higher osmotic pressure, water tends to enter their bodies. Consequently, they must prevent water from entering their bodies as much as possible and eliminate the excess water that does enter. In addition, they tend to lose inorganic ions to their environment and so must actively transport these ions back into their bodies.

In contrast, most marine vertebrates are hypotonic to their environment; their body fluids have only about one-third the osmolality of the surrounding seawater. These animals are therefore in danger of losing water by osmosis and must retain water to prevent dehydration. They do this by drinking seawater and eliminating the excess ions through their kidneys and gills.

The body fluids of terrestrial vertebrates have a higher concentration of water than does the air surrounding them. Therefore, they tend to lose water to the air by evaporation from the skin and lungs. All reptiles, birds, and mammals, as well as amphibians during the time when they live on land, face this problem. These vertebrates have evolved excretory systems that help them retain water.

Marine invertebrates are isotonic with their environment, but most vertebrates are either hypertonic or hypotonic to their environment and thus tend to gain or lose water. Physiological mechanisms help most vertebrates to maintain a constant blood osmolality and constant concentrations of individual ions.

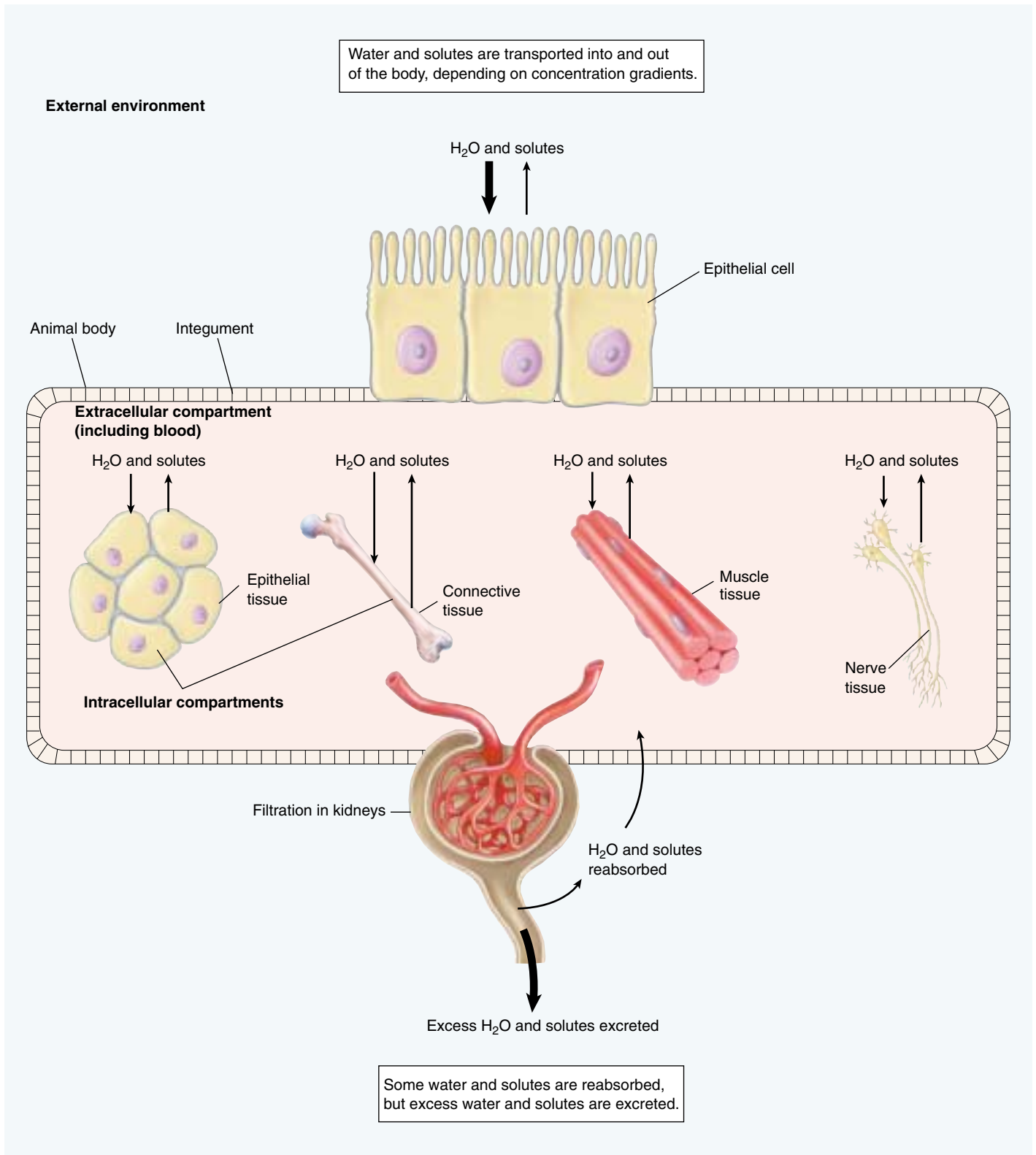


FIGURE 58.8

The interaction between intracellular and extracellular compartments of the body and the external environment. Water can be taken in from the environment or lost to the environment. Exchanges of water and solutes between the extracellular fluids of the body and the environment occur across transport epithelia, and water and solutes can be filtered out of the blood by the kidneys. Overall, the amount of water and solutes that enters and leaves the body must be balanced in order to maintain homeostasis.

Osmoregulatory Organs

Animals have evolved a variety of mechanisms to cope with problems of water balance. In many animals, the removal of water or salts from the body is coupled with the removal of metabolic wastes through the excretory system. Protists employ contractile vacuoles for this purpose, as do sponges. Other multicellular animals have a system of excretory tubules (little tubes) that expel fluid and wastes from the body.

In flatworms, these tubules are called *protonephridia*, and they branch throughout the body into bulblike **flame cells** (figure 58.9). While these simple excretory structures open to the outside of the body, they do not open to the inside of the body. Rather, cilia within the flame cells must draw in fluid from the body. Water and metabolites are then reabsorbed, and the substances to be excreted are expelled through excretory pores.

Other invertebrates have a system of tubules that open both to the inside and to the outside of the body. In the earthworm, these tubules are known as *metanephridia* (figure 58.10). The metanephridia obtain fluid from the body cavity through a process of filtration into funnel-shaped structures called *nephrostomes*. The term *filtration* is used because the fluid is formed under pressure and passes through small openings, so that molecules larger than a certain size are excluded. This filtered fluid is isotonic to the fluid in the coelom, but as it passes through the tubules of the metanephridia, NaCl is removed by active transport processes. A general term for transport out of the tubule and into the surrounding body fluids is *reabsorption*. Because salt is reabsorbed from the filtrate, the urine excreted is more dilute than the body fluids (is hypotonic). The kidneys of mollusks and the excretory organs of crustaceans (called *antennal glands*) also produce urine by filtration and reclaim certain ions by reabsorption.

The excretory organs in insects are the Malpighian tubules (figure 58.11), extensions of the digestive tract that branch off anterior to the hindgut. Urine is not formed by filtration in these tubules, because there is no pressure difference between the blood in the body cavity and the tubule. Instead, waste molecules and potassium (K^+) ions are secreted into the tubules by active transport. Secretion is the opposite of reabsorption—ions or molecules are transported from the body fluid into the tubule. The secretion of K^+ creates an osmotic gradient that causes water to enter the tubules by osmosis from the body's

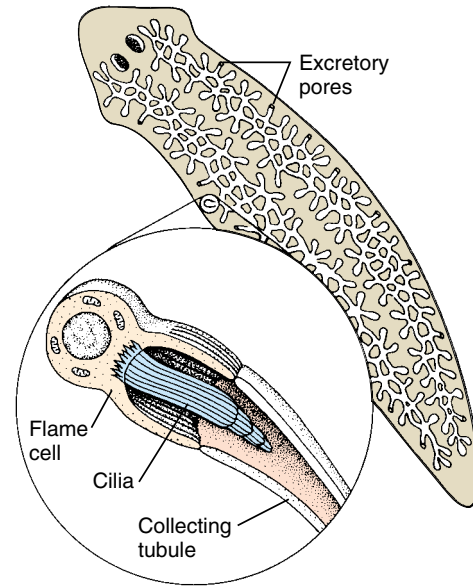


FIGURE 58.9

The protonephridia of flatworms. A branching system of tubules, bulblike flame cells, and excretory pores make up the protonephridia of flatworms. Cilia inside the flame cells draw in fluids from the body by their beating action. Substances are then expelled through pores which open to the outside of the body.

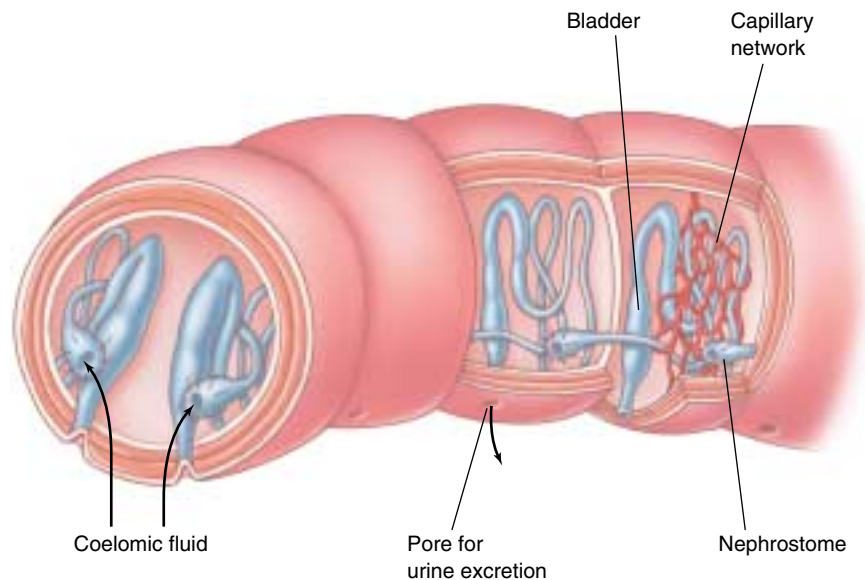


FIGURE 58.10

The metanephridia of annelids. Most invertebrates, such as the annelid shown here, have metanephridia. These consist of tubules that receive a filtrate of coelomic fluid, which enters the funnel-like nephrostomes. Salt can be reabsorbed from these tubules, and the fluid that remains, urine, is released from pores into the external environment.

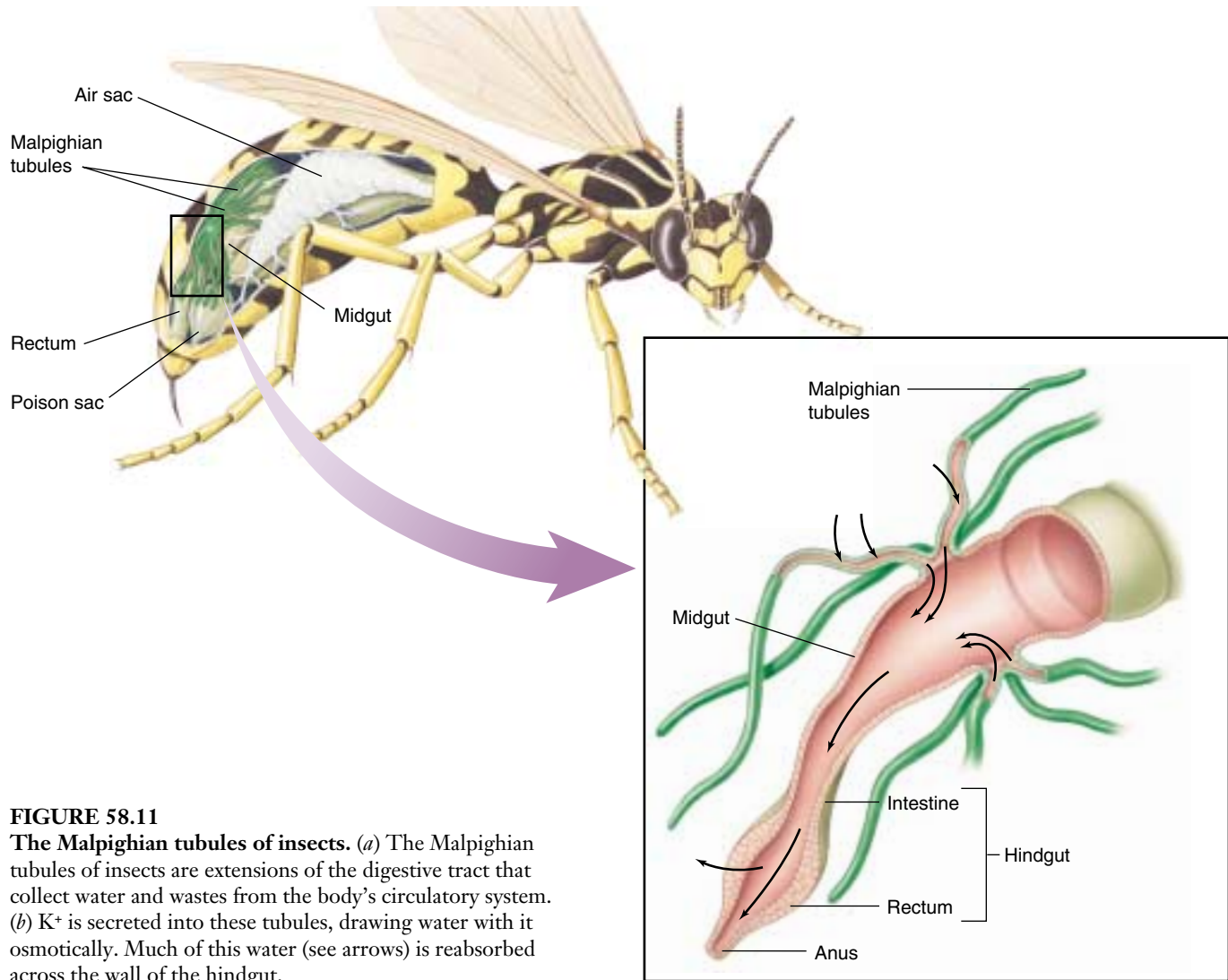


FIGURE 58.11
The Malpighian tubules of insects. (a) The Malpighian tubules of insects are extensions of the digestive tract that collect water and wastes from the body's circulatory system. (b) K^+ is secreted into these tubules, drawing water with it osmotically. Much of this water (see arrows) is reabsorbed across the wall of the hindgut.

open circulatory system. Most of the water and K^+ is then reabsorbed into the circulatory system through the epithelium of the hindgut, leaving only small molecules and waste products to be excreted from the rectum along with feces. Malpighian tubules thus provide a very efficient means of water conservation.

The kidneys of vertebrates, unlike the Malpighian tubules of insects, create a tubular fluid by filtration of the blood under pressure. In addition to containing waste products and water, the filtrate contains many small molecules that are of value to the animal, including glucose, amino acids, and vitamins. These molecules and most of the water are reabsorbed from the tubules into the blood, while wastes remain in the filtrate. Additional wastes may be secreted by the tubules and added to the filtrate, and the final waste product, urine, is eliminated from the body.

It may seem odd that the vertebrate kidney should filter out almost everything from blood plasma (except proteins, which are too large to be filtered) and then spend energy to take back or reabsorb what the body needs. But selective reabsorption provides great flexibility, because various vertebrate groups have evolved the ability to reabsorb different molecules that are especially valuable in particular habitats. This flexibility is a key factor underlying the successful colonization of many diverse environments by the vertebrates.

Many invertebrates filter fluid into a system of tubules and then reabsorb ions and water, leaving waste products for excretion. Insects create an excretory fluid by secreting K^+ into tubules, which draws water osmotically. The vertebrate kidney produces a filtrate that enters tubules and is modified to become urine.

Evolution of the Vertebrate Kidney

The kidney is a complex organ made up of thousands of repeating units called **nephrons**, each with the structure of a bent tube (figure 58.12). Blood pressure forces the fluid in blood past a filter, called the *glomerulus*, at the top of each nephron. The glomerulus retains blood cells, proteins, and other useful large molecules in the blood but allows the water, and the small molecules and wastes dissolved in it, to pass through and into the bent tube part of the nephron. As the filtered fluid passes through the nephron tube, useful sugars and ions are recovered from it by active transport, leaving the water and metabolic wastes behind in a fluid urine.

Although the same basic design has been retained in all vertebrate kidneys, there have been a few modifications. Because the original glomerular filtrate is isotonic to blood, all vertebrates can produce a urine that is isotonic to blood by reabsorbing ions and water in equal proportions or hypotonic to blood—that is, more dilute than the blood, by reabsorbing relatively less water blood. Only birds and mammals can reabsorb enough water from their glomerular filtrate to produce a urine that is hypertonic to blood—that is, more concentrated than the blood, by reabsorbing relatively more water.

Freshwater Fish

Kidneys are thought to have evolved first among the freshwater teleosts, or bony fish. Because the body fluids of a freshwater fish have a greater osmotic concentration than the surrounding water, these animals face two serious problems: (1) water tends to enter the body from the environment; and (2) solutes tend to leave the body and

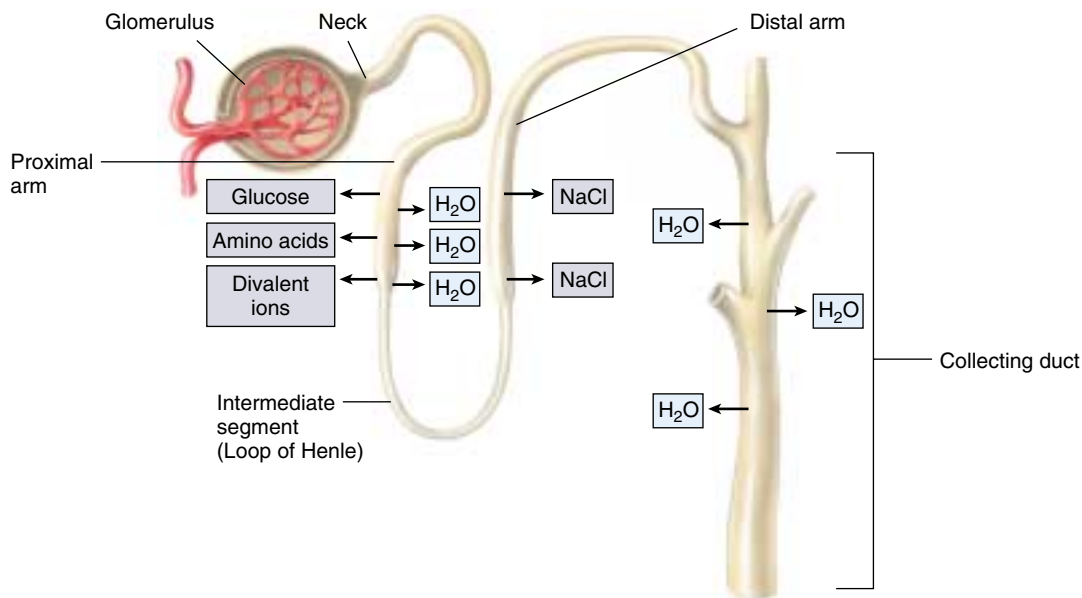
enter the environment. Freshwater fish address the first problem by *not* drinking water and by excreting a large volume of dilute urine, which is hypotonic to their body fluids. They address the second problem by reabsorbing ions across the nephron tubules, from the glomerular filtrate back into the blood. In addition, they actively transport ions across their gill surfaces from the surrounding water into the blood.

Marine Bony Fish

Although most groups of animals seem to have evolved first in the sea, marine bony fish (teleosts) probably evolved from freshwater ancestors, as was mentioned in chapter 48. They faced significant new problems in making the transition to the sea because their body fluids are hypotonic to the surrounding seawater. Consequently, water tends to leave their bodies by osmosis across their gills, and they also lose water in their urine. To compensate for this continuous water loss, marine fish drink large amounts of seawater (figure 58.13).

Many of the divalent cations (principally Ca^{++} and Mg^{++}) in the seawater that a marine fish drinks remain in the digestive tract and are eliminated through the anus. Some, however, are absorbed into the blood, as are the monovalent ions K^+ , Na^+ , and Cl^- . Most of the monovalent ions are actively transported out of the blood across the gill surfaces, while the divalent ions that enter the blood are secreted into the nephron tubules and excreted in the urine. In these two ways, marine bony fish eliminate the ions they get from the seawater they drink. The urine they excrete is isotonic to their body fluids. It is more concentrated than the urine of freshwater fish, but not as concentrated as that of birds and mammals.

FIGURE 58.12
The basic organization of the vertebrate nephron. The nephron tubule of the freshwater fish is a basic design that has been retained in the kidneys of marine fish and terrestrial vertebrates that evolved later. Sugars, amino acids, and divalent ions such as Ca^{++} are recovered in the proximal arm; monovalent ions such as Na^+ and Cl^- are recovered in the distal arm; and water is recovered in the collecting duct.



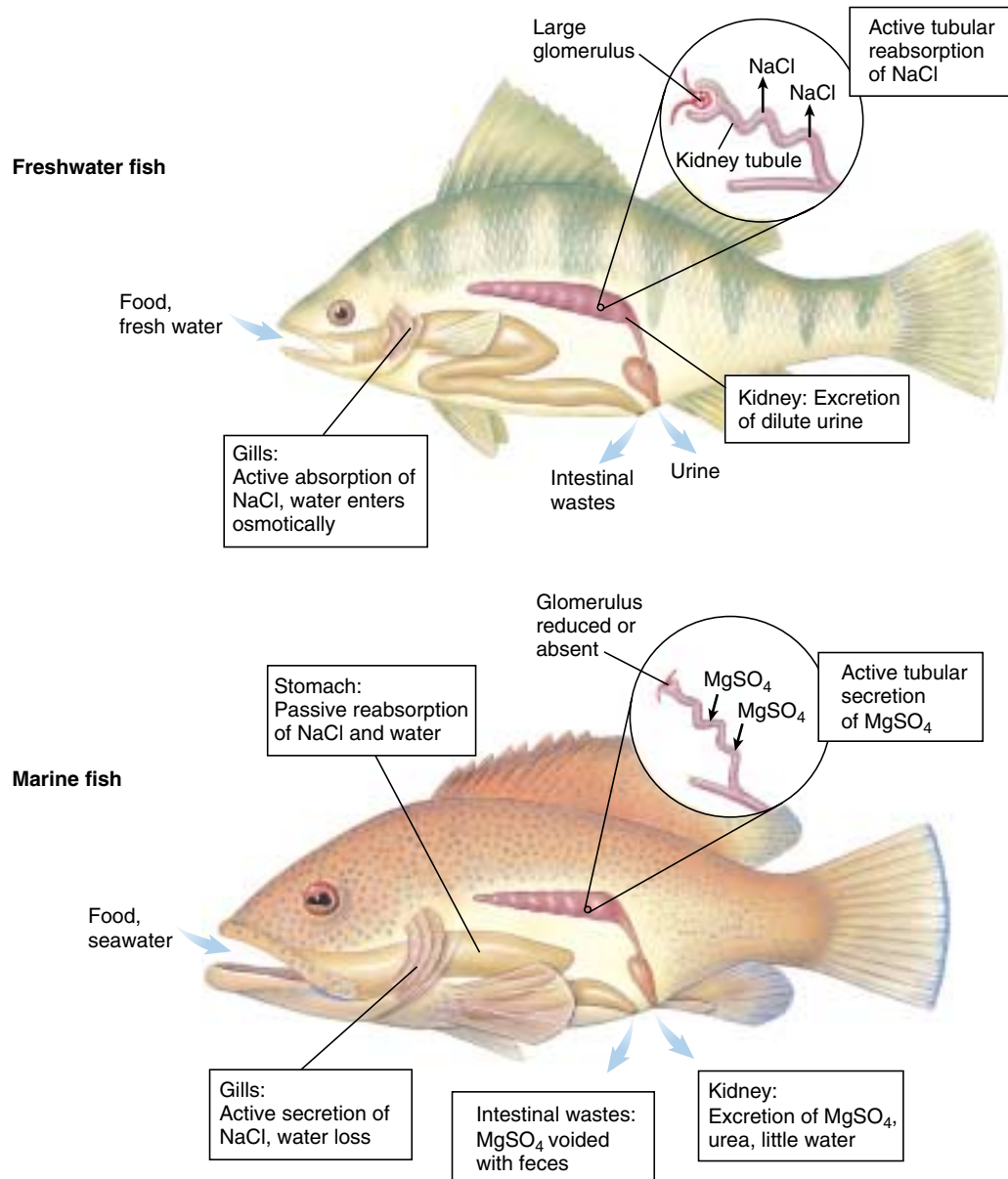


FIGURE 58.13

Freshwater and marine teleosts (bony fish) face different osmotic problems. Whereas the freshwater teleost is hypertonic to its environment, the marine teleost is hypotonic to seawater. To compensate for its tendency to take in water and lose ions, a freshwater fish excretes dilute urine, avoids drinking water, and reabsorbs ions across the nephron tubules. To compensate for its osmotic loss of water, the marine teleost drinks seawater and eliminates the excess ions through active transport across epithelia in the gills and kidneys.

Cartilaginous Fish

The elasmobranchs, including sharks and rays, are by far the most common subclass in the class Chondrichthyes (cartilaginous fish). Elasmobranchs have solved the osmotic problem posed by their seawater environment in a different way than have the bony fish. Instead of having body fluids that are hypotonic to seawater, so that they have to continuously drink seawater and actively pump out ions, the elasmobranchs reabsorb urea from the nephron tubules and main-

tain a blood urea concentration that is 100 times higher than that of mammals. This added urea makes their blood approximately isotonic to the surrounding sea. Because there is no net water movement between isotonic solutions, water loss is prevented. Hence, these fishes do not need to drink seawater for osmotic balance, and their kidneys and gills do not have to remove large amounts of ions from their bodies. The enzymes and tissues of the cartilaginous fish have evolved to tolerate the high urea concentrations.

Amphibians and Reptiles

The first terrestrial vertebrates were the amphibians, and the amphibian kidney is identical to that of freshwater fish. This is not surprising, because amphibians spend a significant portion of their time in fresh water, and when on land, they generally stay in wet places. Amphibians produce a very dilute urine and compensate for their loss of Na^+ by actively transporting Na^+ across their skin from the surrounding water.

Reptiles, on the other hand, live in diverse habitats. Those living mainly in fresh water occupy a habitat simi-

lar to that of the freshwater fish and amphibians and thus have similar kidneys. Marine reptiles, including some crocodylians, sea turtles, sea snakes, and one lizard, possess kidneys similar to those of their freshwater relatives but face opposite problems; they tend to lose water and take in salts. Like marine teleosts (bony fish), they drink the seawater and excrete an isotonic urine. Marine teleosts eliminate the excess salt by transport across their gills, while marine reptiles eliminate excess salt through salt glands located near the nose or the eye (figure 58.14).

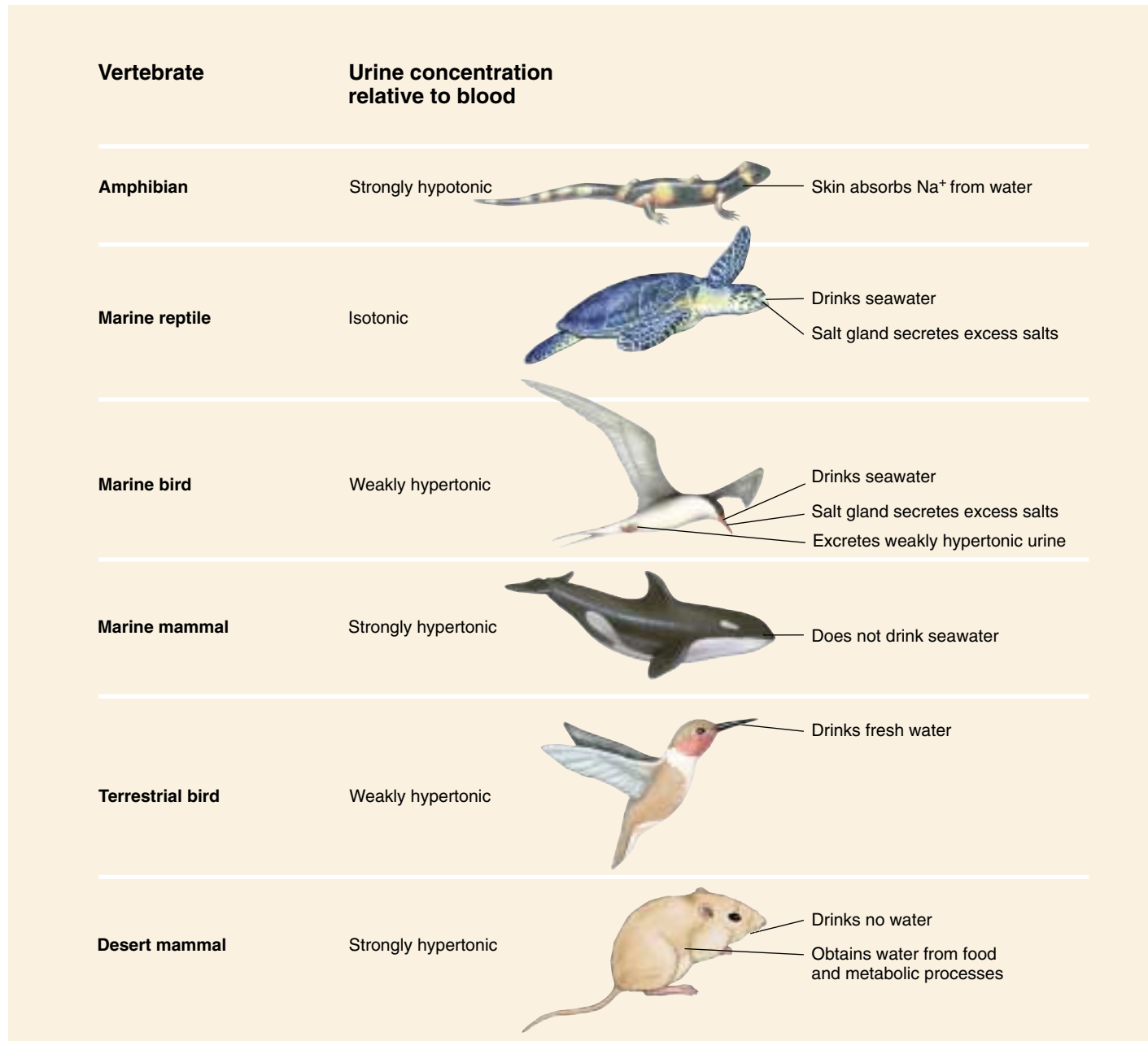


FIGURE 58.14

Osmoregulation by some vertebrates. Only birds and mammals can produce a hypertonic urine and thereby retain water efficiently, but marine reptiles and birds can drink seawater and excrete the excess salt through salt glands.

The kidneys of terrestrial reptiles also reabsorb much of the salt and water in their nephron tubules, helping somewhat to conserve blood volume in dry environments. Like fish and amphibians, they cannot produce urine that is more concentrated than the blood plasma. However, when their urine enters their cloaca (the common exit of the digestive and urinary tracts), additional water can be reabsorbed.

Mammals and Birds

Mammals and birds are the only vertebrates able to produce urine with a higher osmotic concentration than their body fluids. This allows these vertebrates to excrete their waste products in a small volume of water, so that more water can be retained in the body. Human kidneys can produce urine that is as much as 4.2 times as concentrated as blood plasma, but the kidneys of some other mammals are even more efficient at conserving water. For example, camels, gerbils, and pocket mice of the genus *Perognathus* can excrete urine 8, 14, and 22 times as concentrated as their blood plasma, respectively. The kidneys of the kangaroo rat (figure 58.15) are so efficient it never has to drink water; it can obtain all the water it needs from its food and from water produced in aerobic cell respiration!

The production of hypertonic urine is accomplished by the *loop of Henle* portion of the nephron (see figure 58.18), found only in mammals and birds. A nephron with a long loop of Henle extends deeper into the renal medulla, where the hypertonic osmotic environment draws out more water, and so can produce more concentrated urine. Most mammals have some nephrons with short loops and other nephrons with loops that are much longer (see figure 58.17). Birds, however, have relatively few or no nephrons with long loops, so they cannot produce urine that is as concentrated as that of mammals. At most, they can only reabsorb enough water to produce a urine that is about twice the concentration of their blood. Marine birds solve the problem of water loss by drinking salt water and then excreting the excess salt from salt glands near the eyes (figure 58.16).

The moderately hypertonic urine of a bird is delivered to its cloaca, along with the fecal material from its digestive tract. If needed, additional water can be absorbed across the wall of the cloaca to produce a semisolid white paste or pellet, which is excreted.

The kidneys of freshwater fish must excrete copious amounts of very dilute urine, while marine teleosts drink seawater and excrete an isotonic urine. The basic design and function of the nephron of freshwater fishes have been retained in the terrestrial vertebrates. Modifications, particularly the presence of a loop of Henle, allow mammals and birds to reabsorb more water and produce a hypertonic urine.



FIGURE 58.15

The kangaroo rat, *Dipodomys panamintensis*. This mammal has very efficient kidneys that can concentrate urine to a high degree by reabsorbing water, thereby minimizing water loss from the body. This feature is extremely important to the kangaroo rat's survival in dry or desert habitats.

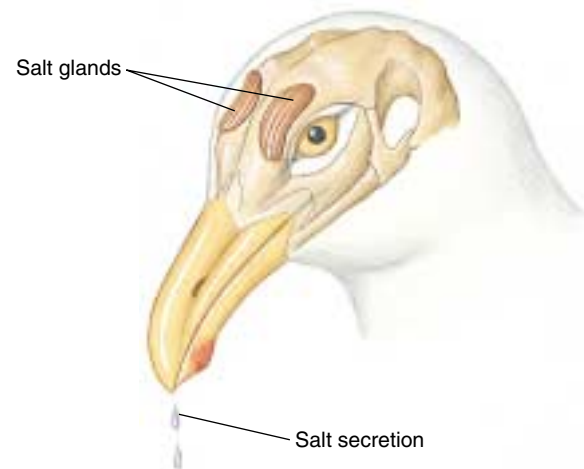


FIGURE 58.16

Marine birds drink seawater and then excrete the salt through salt glands. The extremely salty fluid excreted by these glands can then dribble down the beak.

58.3 The functions of the vertebrate kidney are performed by nephrons.

The Mammalian Kidney

In humans, the kidneys are fist-sized organs located in the region of the lower back. Each kidney receives blood from a renal artery, and it is from this blood that urine is produced. Urine drains from each kidney through a **ureter**, which carries the urine to a **urinary bladder**. Within the kidney, the mouth of the ureter flares open to form a funnel-like structure, the *renal pelvis*. The renal pelvis, in turn, has cup-shaped extensions that receive urine from the renal tissue. This tissue is divided into an outer **renal cortex** and an inner **renal medulla** (figure 58.17). Together, these structures perform filtration, reabsorption, secretion, and excretion.

Nephron Structure and Filtration

On a microscopic level, each kidney contains about one million functioning *nephrons*. Mammalian kidneys contain a mixture of juxtamedullary nephrons, which have long loops which dip deeply into the medulla, and cortical nephrons with shorter loops (see figure 58.17). The significance of the length of the loops will be explained a little later.

Each nephron consists of a long tubule and associated small blood vessels. First, blood is carried by an *afferent arteriole* to a tuft of capillaries in the renal cortex, the **glomerulus** (figure 58.18). Here the blood is filtered as the blood pressure forces fluid through the porous capillary walls. Blood cells and plasma proteins are too large to enter

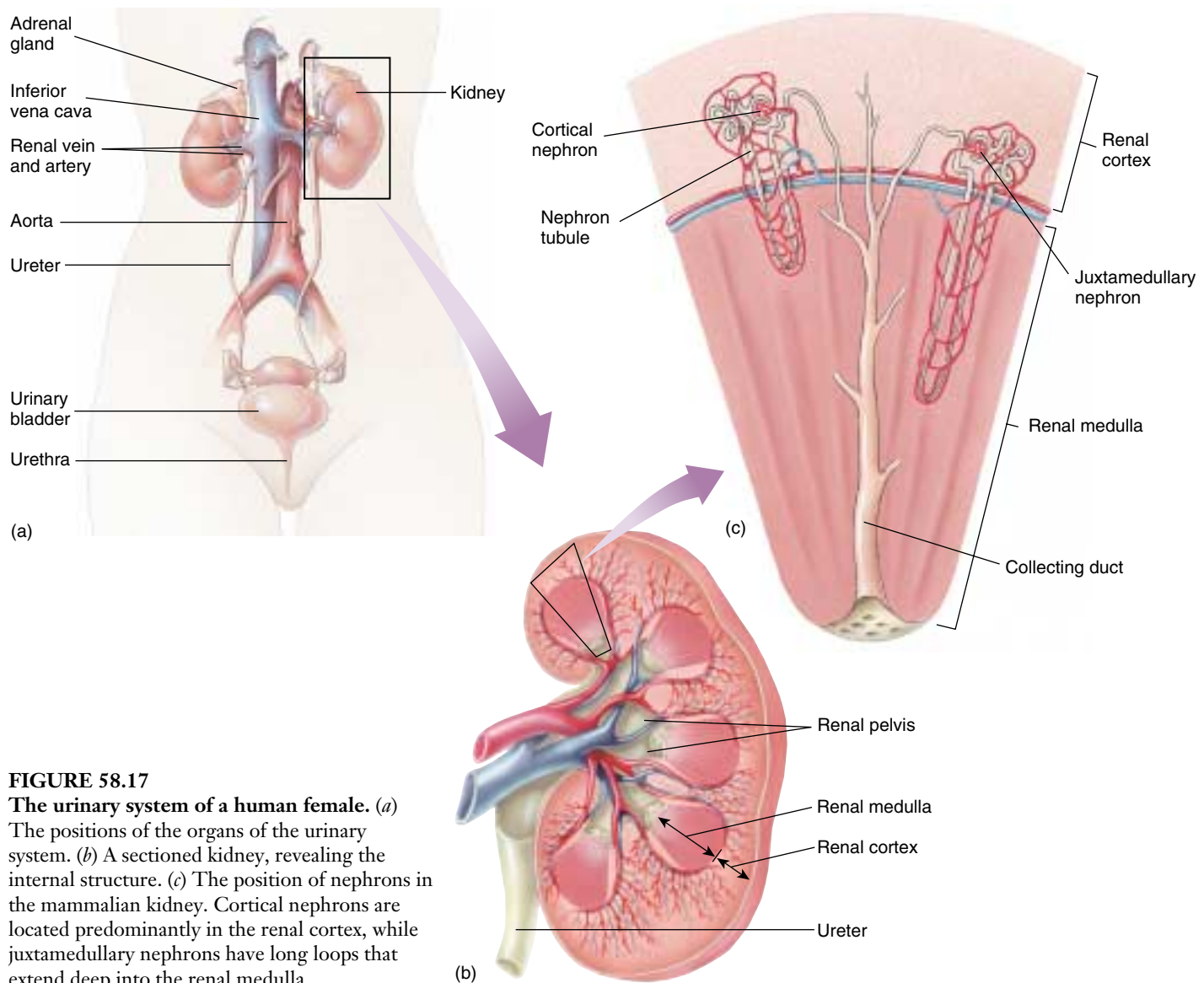


FIGURE 58.17

The urinary system of a human female. (a) The positions of the organs of the urinary system. (b) A sectioned kidney, revealing the internal structure. (c) The position of nephrons in the mammalian kidney. Cortical nephrons are located predominantly in the renal cortex, while juxtamedullary nephrons have long loops that extend deep into the renal medulla.

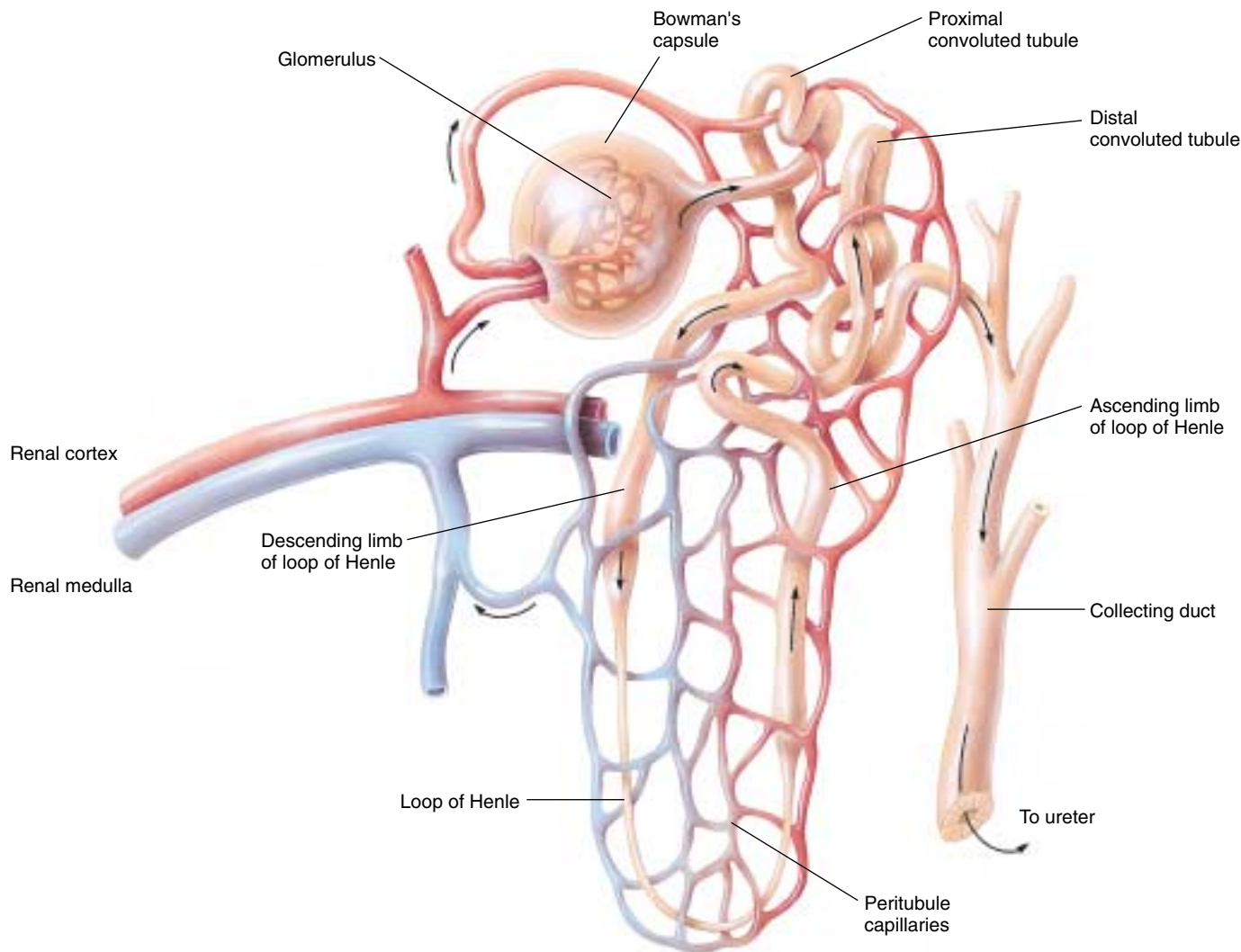


FIGURE 58.18

A nephron in a mammalian kidney. The nephron tubule is surrounded by peritubular capillaries, which carry away molecules and ions that are reabsorbed from the filtrate.

this **glomerular filtrate**, but large amounts of water and dissolved molecules leave the vascular system at this step. The filtrate immediately enters the first region of the nephron tubules. This region, *Bowman's capsule*, envelops the glomerulus much as a large, soft balloon surrounds your fist if you press your fist into it. The capsule has slit openings so that the glomerular filtrate can enter the system of nephron tubules.

After the filtrate enters Bowman's capsule it goes into a portion of the nephron called the **proximal convoluted tubule**, located in the cortex. The fluid then moves down into the medulla and back up again into the cortex in a **loop of Henle**. Only the kidneys of mammals and birds have loops of Henle, and this is why only birds and mammals have the ability to concentrate their urine. After leaving the loop, the fluid is delivered to a **distal convo-**

luted tubule in the cortex that next drains into a **collecting duct**. The collecting duct again descends into the medulla, where it merges with other collecting ducts to empty its contents, now called urine, into the renal pelvis.

Blood components that were not filtered out of the glomerulus drain into an *efferent arteriole*, which then empties into a second bed of capillaries called *peritubular capillaries* that surround the tubules. This is the only location in the body where two capillary beds occur in series. The glomerulus is drained by an arteriole and this second arteriole delivers blood to a second capillary bed, the peritubular capillaries. As described later, the peritubular capillaries are needed for the processes of reabsorption and secretion.

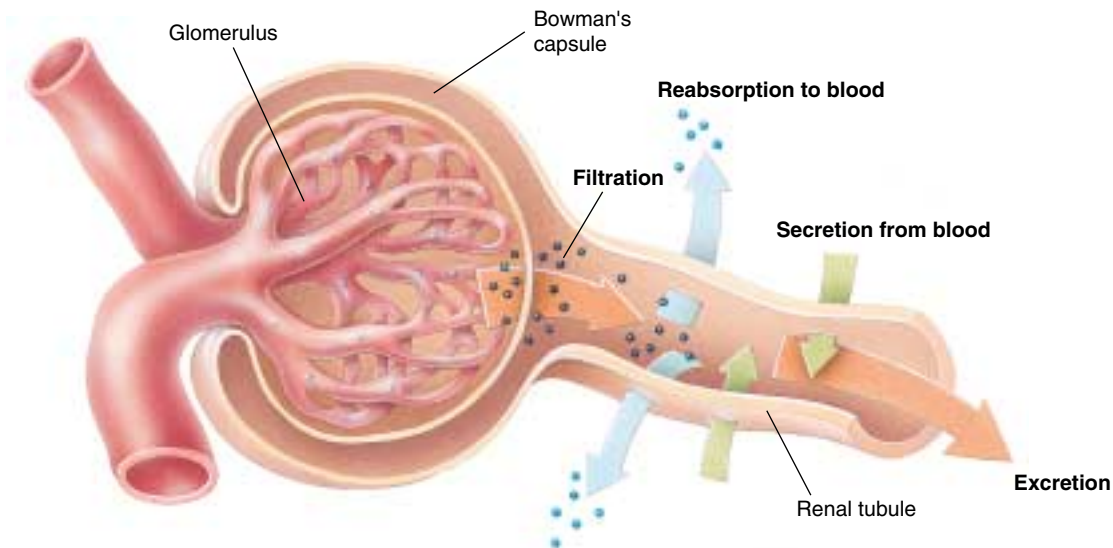


FIGURE 58.19
Four functions of the kidney. Molecules enter the urine by *filtration* out of the glomerulus and by *secretion* into the tubules from surrounding peritubular capillaries. Molecules that entered the filtrate can be returned to the blood by *reabsorption* from the tubules into surrounding peritubular capillaries, or they may be eliminated from the body by *excretion* through the tubule to a ureter, then to the bladder.

Reabsorption and Secretion

Most of the water and dissolved solutes that enter the glomerular filtrate must be returned to the blood (figure 58.19), or the animal would literally urinate to death. In a human, for example, approximately 2000 liters of blood passes through the kidneys each day, and 180 liters of water leaves the blood and enters the glomerular filtrate. Because we only have a total blood volume of about 5 liters and only produce 1 to 2 liters of urine per day, it is obvious that each liter of blood is filtered many times per day and most of the filtered water is reabsorbed. The reabsorption of water occurs as a consequence of salt (NaCl) reabsorption through mechanisms that will be described shortly.

The reabsorption of glucose, amino acids, and many other molecules needed by the body is driven by active transport carriers. As in all carrier-mediated transport, a maximum rate of transport is reached whenever the carriers are saturated (see chapter 6). For the renal glucose carriers, saturation occurs when the concentration of glucose in the blood (and thus in the glomerular filtrate) is about 180 milligrams per 100 milliliters of blood. If a person has a blood glucose concentration in excess of this amount, as happens in untreated diabetes mellitus, the glucose left untransported in the filtrate is expelled in the urine. Indeed, the presence of glucose in the urine is diagnostic of diabetes mellitus.

The secretion of foreign molecules and particular waste products of the body involves the transport of these molecules across the membranes of the blood capillaries and kidney tubules into the filtrate. This process is similar to reabsorption, but it proceeds in the opposite direction. Some secreted molecules are eliminated in the urine so rapidly that they may be cleared from the blood in a single pass through the kidneys. This rapid elimination ex-

plains why penicillin, which is secreted by the nephrons, must be administered in very high doses and several times per day.

Excretion

A major function of the kidney is the elimination of a variety of potentially harmful substances that animals eat and drink. In addition, urine contains nitrogenous wastes, such as urea and uric acid, that are products of the catabolism of amino acids and nucleic acids. Urine may also contain excess K^+ , H^+ , and other ions that are removed from the blood. Urine's generally high H^+ concentration (pH 5 to 7) helps maintain the acid-base balance of the blood within a narrow range (pH 7.35 to 7.45). Moreover, the excretion of water in urine contributes to the maintenance of blood volume and pressure; the larger the volume of urine excreted, the lower the blood volume.

The purpose of kidney function is therefore homeostasis—the kidneys are critically involved in maintaining the constancy of the internal environment. When disease interferes with kidney function, it causes a rise in the blood concentration of nitrogenous waste products, disturbances in electrolyte and acid-base balance, and a failure in blood pressure regulation. Such potentially fatal changes highlight the central importance of the kidneys in normal body physiology.

The mammalian kidney is divided into a cortex and medulla and contains microscopic functioning units called nephrons. The nephron tubules receive a blood filtrate from the glomeruli and modify this filtrate to produce urine, which empties into the renal pelvis and is expelled from the kidney through the ureter.

Transport Processes in the Mammalian Nephron

As previously described, approximately 180 liters (in a human) of isotonic glomerular filtrate enters the Bowman's capsules each day. After passing through the remainder of the nephron tubules, this volume of fluid would be lost as urine if it were not reabsorbed back into the blood. It is clearly impossible to produce this much urine, yet water is only able to pass through a cell membrane by osmosis, and osmosis is not possible between two isotonic solutions. Therefore, some mechanism is needed to create an osmotic gradient between the glomerular filtrate and the blood, allowing reabsorption.

Proximal Tubule

Approximately two-thirds of the NaCl and water filtered into Bowman's capsule is immediately reabsorbed across the walls of the proximal convoluted tubule. This reabsorption is driven by the active transport of Na^+ out of the filtrate and into surrounding peritubular capillaries. Cl^- follows Na^+ passively because of electrical attraction, and water follows them both because of osmosis. Because NaCl and water are removed from the filtrate in proportionate amounts, the filtrate that remains in the tubule is still isotonic to the blood plasma.

Although only one-third of the initial volume of filtrate remains in the nephron tubule after the initial reabsorption of NaCl and water, it still represents a large volume (60 L out of the original 180 L of filtrate produced per day by both human kidneys). Obviously, no animal can excrete that much urine, so most of this water must also be reabsorbed. It is reabsorbed primarily across the wall of the collecting duct because the interstitial fluid of the renal medulla surrounding the collecting ducts is hypertonic. The hypertonic renal medulla draws water out of the collecting duct by osmosis, leaving behind a hypertonic urine for excretion.

Loop of Henle

The reabsorption of much of the water in the tubular filtrate thus depends on the creation of a hypertonic renal medulla; the more hypertonic the medulla is, the steeper the osmotic gradient will be and the more water will leave the collecting ducts. It is the loops of Henle that create the hypertonic renal medulla in the following manner (figure 58.20):

1. The ascending limb of the loop actively extrudes Na^+ , and Cl^- follows. The mechanism that extrudes NaCl from the ascending limb of the loop differs from that which extrudes NaCl from the proximal tubule, but the most important difference is that the ascending limb is *not permeable to water*. As Na^+ exits, the fluid within the ascending limb becomes increasingly dilute (hypotonic) as it enters the cortex, while the surrounding tissue becomes increasingly concentrated (hypertonic).

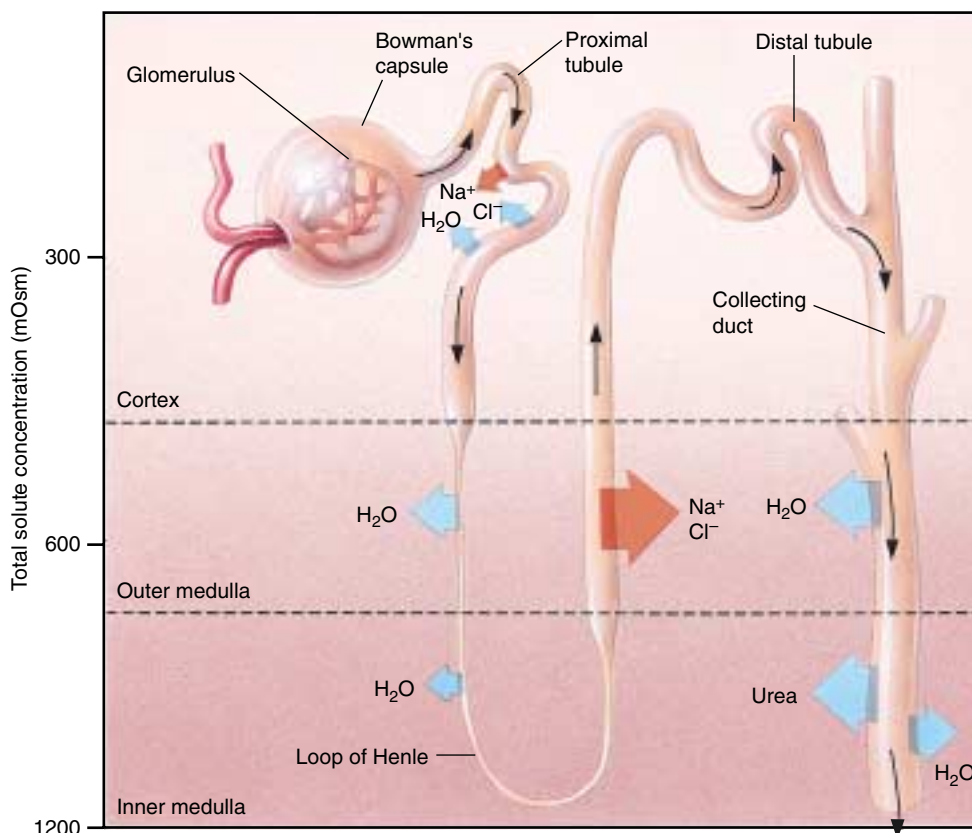


FIGURE 58.20

The reabsorption of salt and water in the mammalian kidney. Active transport of Na^+ out of the proximal tubules is followed by the passive movement of Cl^- and water. Active extrusion of NaCl from the ascending limb of the loop of Henle creates the osmotic gradient required for the reabsorption of water from the collecting duct. The changes in osmolality from the cortex to the medulla is indicated to the left of the figure.

- The NaCl pumped out of the ascending limb of the loop is trapped within the surrounding interstitial fluid. This is because the peritubular capillaries in the medulla also have loops, called *vasa recta*, so that NaCl can diffuse from the blood leaving the medulla to the blood entering the medulla. Thus, the *vasa recta* functions in a countercurrent exchange, similar to that described for oxygen in the countercurrent flow of water and blood in the gills of fish (see chapter 53). In the case of the renal medulla, the diffusion of NaCl between the blood vessels keeps much of the NaCl within the interstitial fluid, making it hypertonic.
- The descending limb is permeable to water, so water leaves by osmosis as the fluid descends into the hypertonic renal medulla. This water enters the blood vessels of the *vasa recta* and is carried away in the general circulation.
- The loss of water from the descending limb multiplies the concentration that can be achieved at each level of the loop through the active extrusion of NaCl by the ascending limb. The longer the loop of Henle, the longer the region of interaction between the descending and ascending limbs, and the greater the total concentration that can be achieved. In a human kidney, the concentration of filtrate entering the loop is 300 milliosmolal, and this concentration is multiplied to more than 1200 milliosmolal at the bottom of the longest loops of Henle in the renal medulla.

Because fluid flows in opposite directions in the two limbs of the loop, the action of the loop of Henle in creating a hypertonic renal medulla is known as the *countercurrent multiplier system*. The high solute concentration of the renal medulla is primarily the result of NaCl accumulation by the countercurrent multiplier system, but urea also contributes to the total osmolality of the medulla. This is because the descending limb of the loop of Henle and the collecting duct are permeable to urea, which leaves these regions of the nephron by diffusion.

Distal Tubule and Collecting Duct

Because NaCl was pumped out of the ascending limb, the filtrate that arrives at the distal convoluted tubule and enters the collecting duct in the renal cortex is hypotonic (with a concentration of only 100 mOsm). The collecting duct carrying this dilute fluid now plunges into the medulla. As a result of the hypertonic interstitial fluid of the renal medulla, there is a strong osmotic gradient that pulls water out of the collecting duct and into surrounding blood vessels.

The osmotic gradient is normally constant, but the permeability of the collecting duct to water is adjusted by a hormone, **antidiuretic hormone (ADH)**, also called **vasopressin**, discussed in chapters 52 and 56. When an animal

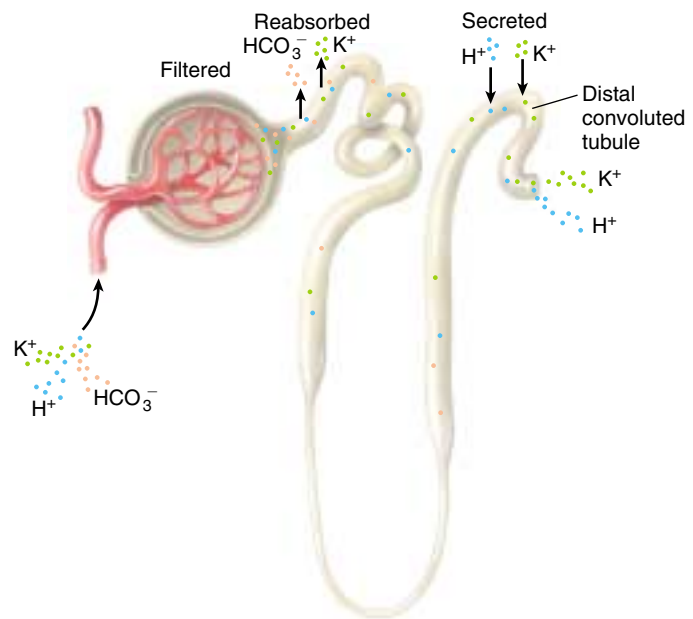


FIGURE 58.21
The nephron controls the amounts of K^+ , H^+ , and HCO_3^- excreted in the urine. K^+ is completely reabsorbed in the proximal tubule and then secreted in varying amounts into the distal tubule. HCO_3^- is filtered but normally completely reabsorbed. H^+ is filtered and also secreted into the distal tubule, so that the final urine has an acidic pH.

needs to conserve water, the posterior pituitary gland secretes more ADH, and this hormone increases the number of water channels in the plasma membranes of the collecting duct cells. This increases the permeability of the collecting ducts to water so that more water is reabsorbed and less is excreted in the urine. The animal thus excretes a hypertonic urine.

In addition to the regulation of water balance, the kidneys regulate the balance of electrolytes in the blood by reabsorption and secretion. For example, the kidneys reabsorb K^+ in the proximal tubule and then secrete an amount of K^+ needed to maintain homeostasis into the distal convoluted tubule (figure 58.21). The kidneys also maintain acid-base balance by excreting H^+ into the urine and reabsorbing bicarbonate (HCO_3^-), as previously described.

The loop of Henle creates a hypertonic renal medulla as a result of the active extrusion of NaCl from the ascending limb and the interaction with the descending limb. The hypertonic medulla then draws water osmotically from the collecting duct, which is permeable to water under the influence of antidiuretic hormone.

Ammonia, Urea, and Uric Acid

Amino acids and nucleic acids are nitrogen-containing molecules. When animals catabolize these molecules for energy or convert them into carbohydrates or lipids, they produce nitrogen-containing by-products called **nitrogenous wastes** (figure 58.22) that must be eliminated from the body.

The first step in the metabolism of amino acids and nucleic acids is the removal of the amino ($-\text{NH}_2$) group and its combination with H^+ to form **ammonia** (NH_3) in the liver. Ammonia is quite toxic to cells and therefore is safe only in very dilute concentrations. The excretion of ammonia is not a problem for the bony fish and tadpoles, which eliminate most of it by diffusion through the gills and less by excretion in very dilute urine. In elasmobranchs, adult amphibians, and mammals, the nitrogenous wastes are eliminated in the far less toxic form of **urea**. Urea is water-soluble and so can be excreted in large amounts in the urine. It is carried in the bloodstream from its place of synthesis in the liver to the kidneys where it is excreted in the urine.

Reptiles, birds, and insects excrete nitrogenous wastes in the form of **uric acid**, which is only slightly soluble in water. As a result of its low solubility, uric acid precipitates

and thus can be excreted using very little water. Uric acid forms the pasty white material in bird droppings called *guano*. The ability to synthesize uric acid in these groups of animals is also important because their eggs are encased within shells, and nitrogenous wastes build up as the embryo grows within the egg. The formation of uric acid, while a lengthy process that requires considerable energy, produces a compound that crystallizes and precipitates. As a precipitate, it is unable to affect the embryo's development even though it is still inside the egg.

Mammals also produce some uric acid, but it is a waste product of the degradation of purine nucleotides (see chapter 3), not of amino acids. Most mammals have an enzyme called *uricase*, which converts uric acid into a more soluble derivative, **allantoin**. Only humans, apes, and the dalmatian dog lack this enzyme and so must excrete the uric acid. In humans, excessive accumulation of uric acid in the joints produces a condition known as *gout*.

The metabolic breakdown of amino acids and nucleic acids produces ammonia as a by-product. Ammonia is excreted by bony fish, but other vertebrates convert nitrogenous wastes into urea and uric acid, which are less toxic nitrogenous wastes.

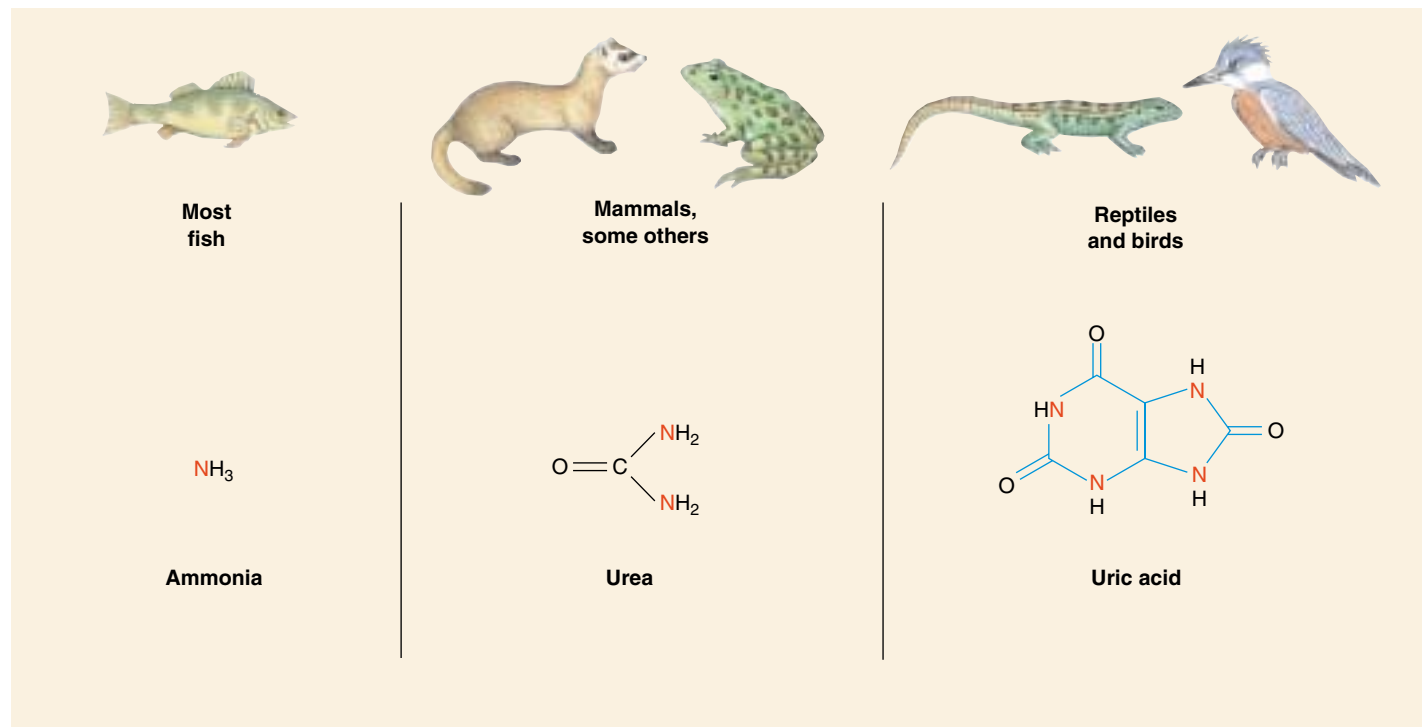


FIGURE 58.22

Nitrogenous wastes. When amino acids and nucleic acids are metabolized, the immediate by-product is ammonia, which is quite toxic but which can be eliminated through the gills of teleost fish. Mammals convert ammonia into urea, which is less toxic. Birds and terrestrial reptiles convert it instead into uric acid, which is insoluble in water.

58.4 The kidney is regulated by hormones.

Hormones Control Homeostatic Functions

In mammals and birds, the amount of water excreted in the urine, and thus the concentration of the urine, varies according to the changing needs of the body. Acting through the mechanisms described next, the kidneys will excrete a hypertonic urine when the body needs to conserve water. If an animal drinks too much water, the kidneys will excrete a hypotonic urine. As a result, the volume of blood, the blood pressure, and the osmolality of blood plasma are maintained relatively constant by the kidneys, no matter how much water you drink. The kidneys also regulate the plasma K^+ and Na^+ concentrations and blood pH within very narrow limits. These homeostatic functions of the kidneys are coordinated primarily by hormones (see chapter 56).

Antidiuretic Hormone

Antidiuretic hormone (ADH) is produced by the hypothalamus and secreted by the posterior pituitary gland. The primary stimulus for ADH secretion is an increase in the osmolality of the blood plasma. The osmolality of plasma increases when a person is dehydrated or when a person eats salty food. Osmoreceptors in the hypothalamus respond to the elevated blood osmolality by sending more nerve signals to the integration center (also in the hypothalamus). This, in turn, triggers a sensation of thirst and an increase in the secretion of ADH (figure 58.23).

ADH causes the walls of the collecting ducts in the kidney to become more permeable to water. This occurs because water channels are contained within the membranes of intracellular vesicles in the epithelium of the collecting ducts, and ADH stimulates the fusion of the vesicle membrane with the plasma membrane, similar to the process of exocytosis. When the secretion of ADH is reduced, the plasma membrane pinches in to form new vesicles that contain the water channels, so that the plasma membrane becomes less permeable to water.

Because the extracellular fluid in the renal medulla is hypertonic to the filtrate in the collecting ducts, water leaves the filtrate by osmosis and is reabsorbed into the blood. Under conditions of maximal ADH secretion, a person excretes only 600 milliliters of highly concentrated urine per day. A person who lacks ADH due to pituitary damage has the disorder known as *diabetes insipidus* and constantly ex-

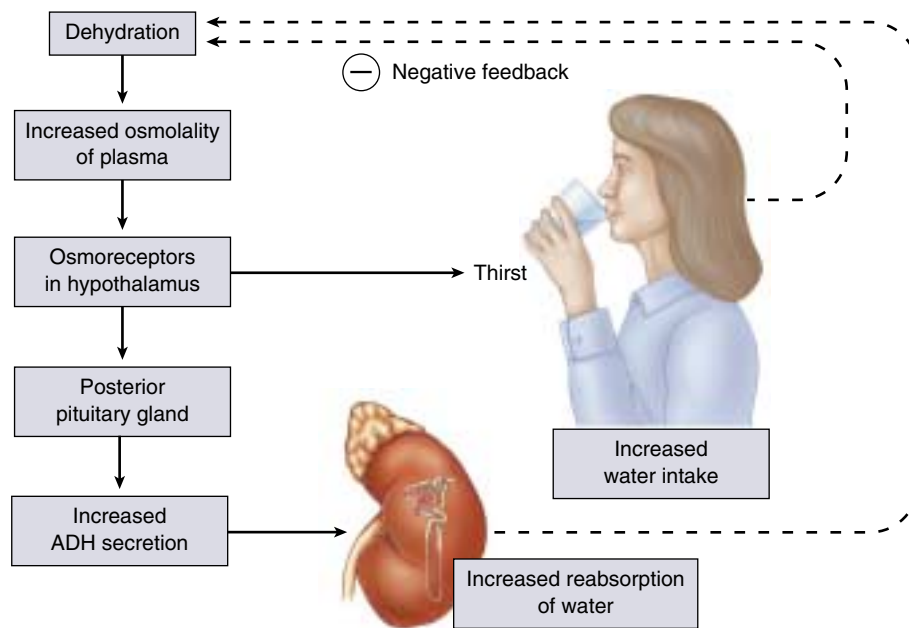


FIGURE 58.23

Antidiuretic hormone stimulates the reabsorption of water by the kidneys. This action completes a negative feedback loop and helps to maintain homeostasis of blood volume and osmolality.

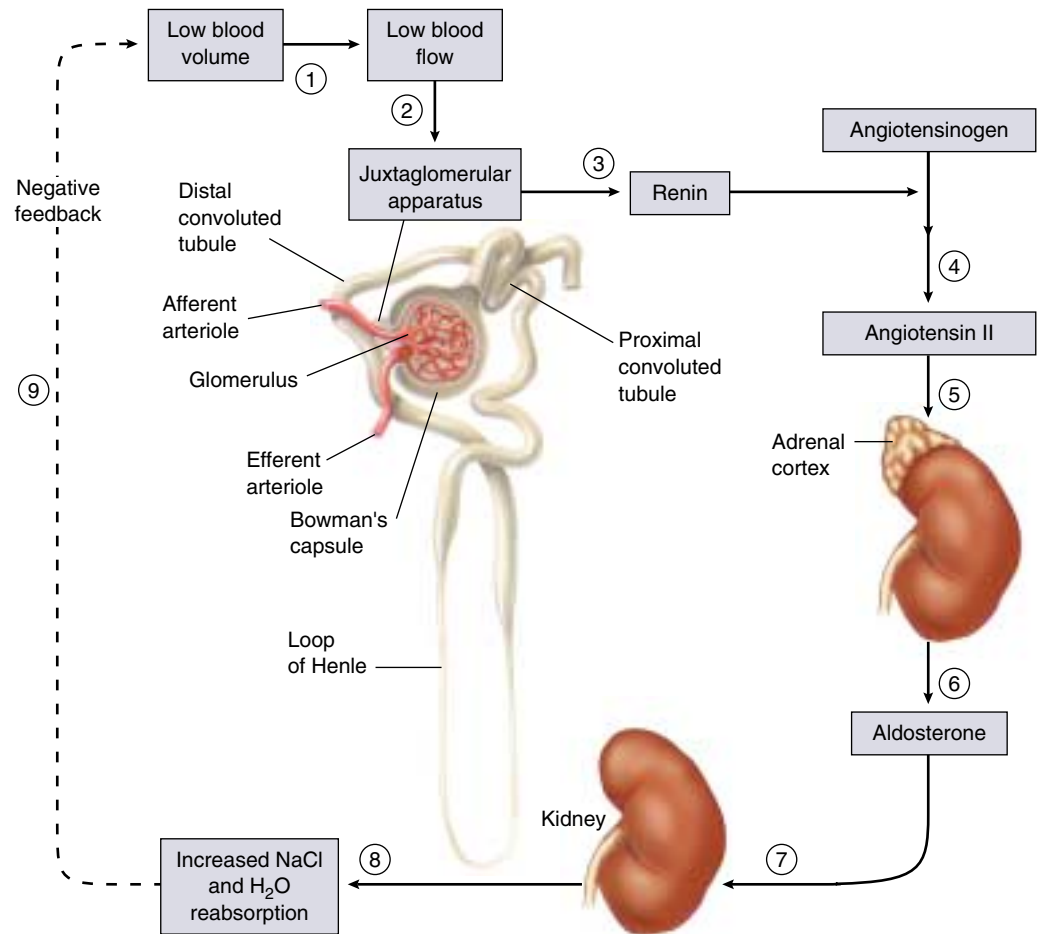
cretes a large volume of dilute urine. Such a person is in danger of becoming severely dehydrated and succumbing to dangerously low blood pressure.

Aldosterone and Atrial Natriuretic Hormone

Sodium ion is the major solute in the blood plasma. When the blood concentration of Na^+ falls, therefore, the blood osmolality also falls. This drop in osmolality inhibits ADH secretion, causing more water to remain in the collecting duct for excretion in the urine. As a result, the blood volume and blood pressure decrease. A decrease in extracellular Na^+ also causes more water to be drawn into cells by osmosis, partially offsetting the drop in plasma osmolality but further decreasing blood volume and blood pressure. If Na^+ deprivation is severe, the blood volume may fall so low that there is insufficient blood pressure to sustain life. For this reason, salt is necessary for life. Many animals have a “salt hunger” and actively seek salt, such as the deer at “salt licks.”

A drop in blood Na^+ concentration is normally compensated by the kidneys under the influence of the hormone aldosterone, which is secreted by the adrenal cortex. Aldosterone stimulates the distal convoluted tubules to reabsorb Na^+ , decreasing the excretion of Na^+ in the urine. Indeed, under conditions of maximal aldosterone secretion, Na^+ may be completely absent from the urine. The reabsorp-

FIGURE 58.24
A lowering of blood volume activates the renin-angiotensin-aldosterone system. (1) Low blood volume accompanies a decrease in blood Na^+ levels. (2) Reduced blood flow past the juxtaglomerular apparatus triggers (3) the release of renin into the blood, which catalyzes the production of angiotensin I from angiotensinogen. (4) Angiotensin I converts into an active form, angiotensin II. (5) Angiotensin II stimulates blood vessel constriction and (6) the release of aldosterone from the adrenal cortex. (7) Aldosterone stimulates the reabsorption of Na^+ in the distal convoluted tubules. (8) Increased Na^+ reabsorption is followed by the reabsorption of Cl^- and water. (9) This increases blood volume. An increase in blood volume may also trigger the release of atrial natriuretic hormone that inhibits the release of aldosterone. These two systems work together to maintain homeostasis.



tion of Na^+ is followed by Cl^- and by water, so aldosterone has the net effect of promoting the retention of both salt and water. It thereby helps to maintain blood volume and pressure.

The secretion of aldosterone in response to a decreased blood level of Na^+ is indirect. Because a fall in blood Na^+ is accompanied by a decreased blood volume, there is a reduced flow of blood past a group of cells called the juxtaglomerular apparatus, located in the region of the kidney between the distal convoluted tubule and the afferent arteriole (figure 58.24). The juxtaglomerular apparatus responds by secreting the enzyme *renin* into the blood, which catalyzes the production of the polypeptide angiotensin I from the protein angiotensinogen (see chapter 52). Angiotensin I is then converted by another enzyme into angiotensin II, which stimulates blood vessels to constrict and the adrenal cortex to secrete aldosterone. Thus, homeostasis of blood volume and pressure can be maintained by the activation of this renin-angiotensin-aldosterone system.

In addition to stimulating Na^+ reabsorption, aldosterone also promotes the secretion of K^+ into the distal convoluted tubules. Consequently, aldosterone lowers the blood K^+

concentration, helping to maintain constant blood K^+ levels in the face of changing amounts of K^+ in the diet. People who lack the ability to produce aldosterone will die if untreated because of the excessive loss of salt and water in the urine and the buildup of K^+ in the blood.

The action of aldosterone in promoting salt and water retention is opposed by another hormone, atrial natriuretic hormone (ANH, see chapter 52). This hormone is secreted by the right atrium of the heart in response to an increased blood volume, which stretches the atrium. Under these conditions, aldosterone secretion from the adrenal cortex will decrease and atrial natriuretic hormone secretion will increase, thus promoting the excretion of salt and water in the urine and lowering the blood volume.

ADH stimulates the insertion of water channels into the cells of the collecting duct, making the collecting duct more permeable to water. Thus, ADH stimulates the reabsorption of water and the excretion of a hypertonic urine. Aldosterone promotes the reabsorption of NaCl and water across the distal convoluted tubule, as well as the secretion of K^+ into the tubule. ANH decreases NaCl reabsorption.

**Summary****Questions****Media Resources****58.1 The regulatory systems of the body maintain homeostasis.**

- Negative feedback loops maintain nearly constant extracellular conditions in the internal environment of the body, a condition called homeostasis.
- Antagonistic effectors afford an even finer degree of control.

1. What is homeostasis? What is a negative feedback loop? Give an example of how homeostasis is maintained by a negative feedback loop.



- Osmoregulation

58.2 The extracellular fluid concentration is constant in most vertebrates.

- Osmoconformers maintain a tissue fluid osmolality equal to that of their environment, whereas osmoregulators maintain a constant blood osmolality that is different from that of their environment.
- Insects eliminate water by secreting K^+ into Malpighian tubules and the water follows the K^+ by osmosis.
- The kidneys of most vertebrates eliminate water by filtering blood into nephron tubules.
- Freshwater bony fish are hypertonic to their environment, and saltwater bony fish are hypotonic to their environment; these conditions place different demands upon their kidneys and other regulatory systems.
- Birds and mammals are the only vertebrates that have loops of Henle and thus are capable of producing a hypertonic urine.

2. What is the difference between an osmoconformer and an osmoregulator? What are examples of each?

3. How does the body fluid osmolality of a freshwater vertebrate compare with that of its environment? Does water tend to enter or exit its body? What must it do to maintain proper body water levels?

4. In what type of animal are Malpighian tubules found? By what mechanism is fluid caused to flow into these tubules? How is this fluid further modified before it is excreted?



- Body fluid distribution
- Water balance

58.3 The functions of the vertebrate kidney are performed by nephrons.

- The primary function of the kidneys is homeostasis of blood volume, pressure, and composition, including the concentration of particular solutes in the blood and the blood pH.
- Bony fish remove the amine portions of amino acids and excrete them as ammonia across the gills.
- Elasmobranchs, adult amphibians, and mammals produce and excrete urea, which is quite soluble but much less toxic than ammonia.
- Insects, reptiles, and birds produce uric acid from the amino groups in amino acids; this precipitates, so that little water is required for its excretion.

5. What drives the movement of fluid from the blood to the inside of the nephron tubule at Bowman's capsule?

6. In what portion of the nephron is most of the $NaCl$ and water reabsorbed from the filtrate?

7. What causes water reabsorption from the collecting duct? How is this influenced by antidiuretic hormone?



- Bioethics case study: Kidney transplant



- Art activities
Urinary system
Anatomy of kidney and lobe
Nephron anatomy



- Kidney function

58.4 The kidney is regulated by hormones.

- Antidiuretic hormone is secreted by the posterior pituitary gland in response to an increase in blood osmolality, and acts to increase the number of water channels in the walls of the collecting ducts.

8. What effects does aldosterone have on kidney function? How is the secretion of aldosterone stimulated?



- Kidney function