STUDY GUIDE

INSTRUCTOR'S EDITION

Principles of Biology

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PRINCIPLES OF BIOLOGY

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nature EDUCATION
25 First Street, Suite 104
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Preface

π ñ ò ó Biology is not a collection of static facts and figures. It is the study of the infinitely complex, continually evolving living world we inhabit and interact with every day. Thousands of biological researchers help us glimpse increasingly broader cross-sections of this living world every year through keen observation, thoughtful experimentation, data collection, and the formulation of new ideas and concepts. To learn biology is to learn, above all, how scientists have built up over hundreds of years our current state of knowledge about humans and other living organisms, and how we — and you — can extend it even further through curiosity, creativity, and rigor.

Principles of Biology is intended to guide you to the threshold of becoming a contributing member of the world of science, whether as a budding researcher, a teacher, a journalist, a parent, or an informed voter. By the end of this book, you will have learned core concepts in cell biology, chemistry, genetics, physiology, and ecology; acquired a familiarity with scientific papers, research methods, and analytical techniques; and gained the ability to recognize everywhere around you the role that science plays in enriching the future of life on earth, whether through the treatment of pandemic diseases, preservation of the environment, or improvement of our global food supply. You may some day forget vocabulary terms you learned in this book. But we believe that, if you work your way carefully through Principles of Biology, you will always remember the fundamental laws through which life operates and continually evolves on Earth, and the extraordinary power that science has to unlock its mysteries.

Contents

Principles of Biology

I

Eukaryotic Cells

Eukaryotic cells contain structures that help them carry out the process of living.

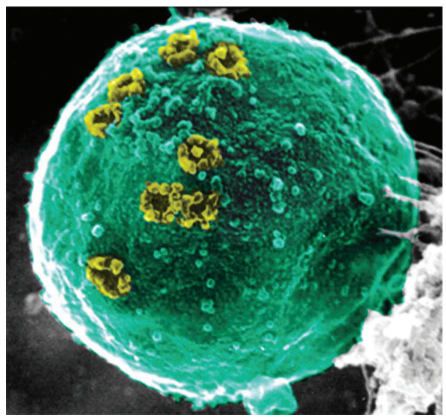
KEY TERMS

endoplasmic reticulum • Extensive series of membrane enclosed compartments throughout the cell; comes in two forms: smooth and rough.

mitochondria • Powerhouse of eukaryotic cell; site of aerobic respiration. Present in both autotrophic and heterotrophic cells.

peroxisomes • Vacuoles that contain enzymes to break down toxic materials.

vacuoles • Vesicles usually derived from the Golgi apparatus or endoplasmic reticulum; allow for materials to be sequestered from the rest of the cell and transported into, out of, or through the cell.



LEARNING OBJECTIVES

- Identify cellular structures on a micrograph or diagram and name their functions.
- Relate the forms of different cell structures to their functions.
- Compare and contrast the structure and function of organelles found in animal and plant cells.

Components of a Eukaryotic Cell

What makes eukaryotic cells different from bacterial and other prokaryotic cells? How did this difference evolve? The first organisms on Earth were likely prokaryotic. These organisms consumed carbohydrates, amino acids, and other biological molecules; such food molecules were likely replenished at a very slow rate in the primordial seas. This would have led to extreme food competition among these early prokaryotes, and it is theorized that this competitive pressure drove the evolution of new and more efficient metabolic pathways.

Utilizing new food sources required the development of more complicated chemical reactions. Digestion of some molecules would have required specific environmental conditions that differed from those inside the cytoplasm. How did early eukaryotes cope with these new physiological demands? One evolutionary solution to this complex problem was to restrict chemical reactions to specific compartments within the cell. Environmental conditions differ within each cellular compartment, similar to how a series of greenhouses can provide unique environments that support specialized tropical, desert, and cold-weather plants. The evolution of compartmentalization allowed eukaryotic cells to exploit a wide-range of new food sources thanks to the greatly expanded range of chemical reactions that could be performed within a cell.

The compartments in eukaryotic cells are mainly organelles: membrane-bound structures bound with a semi-permeable phospholipid membrane that is very similar in composition to the plasma membrane. Organelles are the primary feature that distinguishes eukaryotic cells from prokaryotic cells (Figures 1 and 2). Another major difference between prokaryotes and eukaryotes is the location of the chromosomes. In prokaryotic cells, chromosomes are localized in the nucleoid region, whereas eukaryotic cells have many chromosomes contained within a membrane-bound organelle called the **nucleus**.

FIGURE 1 A typical animal cell. This figure is an interactive. To see it, visit your Principles of Biology online textbook.

Figures 1 and 2 illustrate typical animal and plant cells and their common organelles. It is important to remember that eukaryotic cells come in all shapes and sizes. Eukaryotic cells are typically specialized in size and shape based on their function.

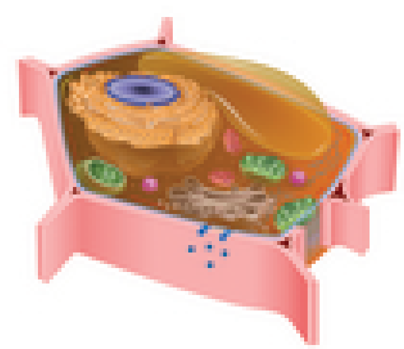


FIGURE 2 A typical plant cell. This figure is an interactive. To see it, visit your Principles of Biology online textbook.

Why is the nucleus important?

A membrane-bound nucleus that functions much like the brain of the cell is a complex adaptation unique to eukaryotes (Figure 3). A eukaryotic cell's nucleus alone is often larger than an entire prokaryote. The **nucleus** is the control center of the cell, processing inputs from the cytoplasm, storing and retrieving information, and carrying out instructions contained within the genetic material in the nucleus. The nucleus contains the cell's chromosomes. Chromosomes are made up of DNA, which contains the genetically transmitted instructions for reproduction and for synthesizing proteins and RNA.

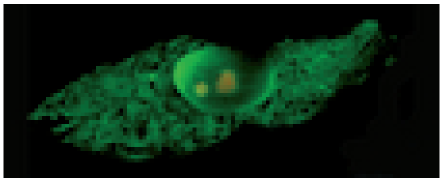


FIGURE 3 The nucleus. Green fluorescent labeling highlights an entire mammalian cell, including its nucleus. The nucleolus (orange) and surrounding nuclear envelope surrounding it lie at the center of the cell.

The nucleus is bound in a membrane called the **nuclear envelope**. The nuclear envelope is made up of two lipid bilayers. The nuclear membrane also contains prominent **nuclear pores**. These channels allow large molecules, such as messenger RNA, to enter or leave the nucleus. The nucleus also contains a dark-staining area called the **nucleolus**. The nucleolus synthesizes ribosomal rRNA. The rRNA combines with proteins to form the small and large subunits of the **ribosomes**, which are the protein-producing factories of the cell. These subunits move into the cytoplasm, where a large and small subunit will assemble together to become a ribosome.

SELF-TEST QUESTION

What is the definition of a chromosome?

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Though ribosomes are made in the nucleolus, they synthesize proteins in the cytoplasm or in another organelle called the endoplasmic reticulum, which is suspended in the cytosol outside of the nucleus. If the DNA is inside the nucleus and the protein-synthesizing organelles are somewhere else in the cell, how do the cells make proteins based on the blueprints contained within the DNA?

In the same way that we keep important documents in a safe place and make copies as needed, the DNA never leaves the protected confines of the nucleus. Instead, a transcript of the blueprint is made in the form of a messenger RNA (mRNA) molecule. True to its name, the mRNA carries the transcribed instructions out of the nucleus to a ribosome. The ribosome constructs the protein as instructed on the RNA transcript.

The mRNA, like any good messenger, must know where to deliver its message. Some ribosomes float freely in the cytoplasm, and these ribosomes are usually in charge of making proteins that will be used inside the cell. Ribosomes responsible for producing proteins that will be exported from the cell are located on an organelle called the endoplasmic reticulum.

SELF-TEST QUESTION

What is the role of mRNA in protein synthesis?

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The endomembrane system is a group of interrelated organelles.

The **endoplasmic reticulum** (ER) is an extensive network of membrane-enclosed compartments that connect directly to the nuclear envelope. **Smooth endoplasmic reticulum** does not contain ribosomes, and it is primarily involved in lipid synthesis and in breaking down toxic substances in the cell, such as alcohol. **Rough endoplasmic reticulum** (RER) appears rough because it is studded with ribosomes. What kind of proteins can the RER ribosomes produce? One example is found within the skin cells of a poison dart frog. The RER ribosomes in these cells produce a mixture of proteins, lipids, and a very powerful neurotoxin that harms predators who touch the frog's colorful skin. When the ribosomes have completed the job of synthesizing a poison molecule, this new protein is deposited into a membrane-bound transport organelle called a **transport vesicle**. When inside the transport vesicle, the poison molecules cannot harm the cell and can be safely transported through the cytoplasm to another organelle: the Golgi apparatus.

The **Golgi apparatus** is the "shipping and receiving" center of the cell's endomembrane system (Figure 4). This organelle modifies, stores, and exports substances from the cell. When a substance, such as our frog's poison molecule, passes through the consecutive chambers of the Golgi apparatus, phosphate or sugar groups may be added or removed. Whether any of these chemical groups are added or removed depends on the intended use of the new molecules. Many substances are also tagged with a small molecule in the Golgi apparatus. Like a postal address, this molecular tag tells cellular machinery where to send the substance in the body. Once all modifications are complete, the substance is packaged into another transport vesicle. This vesicle transports the molecules from the Golgi apparatus to the plasma membrane. Once it reaches the plasma membrane, the substance is released from the vesicle to the outside of the cell, a process called exocytosis (Figure 5).

FIGURE 4 Golgi apparatus. The Golgi apparatus is part of the endomembrane system of the cell, modifying, storing and exporting substances from the cell.

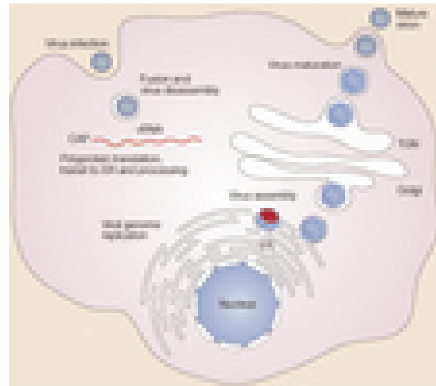

FIGURE 5 Viral exocytosis by the Golgi apparatus. A virus infects a cell, where it takes advantage of the cell’s own functions to replicate itself and then move on to infect other cells. The Golgi apparatus uses exocytosis to remove a foreign virus from the cell, but not before the virus has utilized other cellular functions.

Lysosomes are the cell's digestive system and recycling center.

The RER and Golgi apparatus produce another membrane-bound organelle, the lysosome. **Lysosomes** are vesicles containing powerful enzymes that digest food items engulfed by the cell. The vesicles of lysosomes are specifically designed to maintain a low pHenvironment within the cell. This acidic environment provides the optimal conditions for the digestive enzymes to function.

Most eukaryotic organisms ingest their nutrients. How can cells utilize the food that eukaryotes take in? One way that cells take in nutrients is by engulfing large substances through the process of **phagocytosis** (Figure 6). In phagocytosis for the purpose of accuiring nutrients, the cell first surrounds a nutrient with its plasma membrane. Once the plasma membrane completely surrounds the nutrient, the membrane pinches off to form a vesicle inside the cytoplasm of the cell. This vesicle, containing the engulfed food item, is called a **food vacuole**. Lysosomes bind with these food vaculoes and secrete their digestive enzymes onto the food items. Once the lysozymes have completely digested the food, the products of digestion (including simple sugars, amino acids, and other monomers) are small enough to diffuse out of the vacuole and into the cytoplasm so that the rest of the cell can use them for energy. Another way that a cell uses phagocytosis is to defend against invading organisms like a bacterium. In this case, the physical processes of engulfing and digesting are very similar.

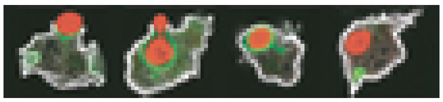

FIGURE 6 Phagocytosis by an amoeba. This amoeba, a single-celled eukaryote, is engulfing a yeast cell (red) using phagocytosis. The amoeba surrounds the yeast with an extension of its cell membrane and encases the yeast within a membrane-bound food vacuole.

In addition to their digestive functions, lysosomes can also use their digestive enzymes to recycle cellular components by autophagy. **Autophagy** is the process of breaking-down and recycling malfunctioning or worn out cell organelles. This process reclaims vital molecules from worn — out organelles-valuable materials that would otherwise be lost.

Future perspectives.

Imagine what it would be like to watch proteins and other molecules move around inside a living cell in real time. We would be able to see not only which molecules the cell produces but also watch where the molecules go after they are produced, either inside or outside the cell. Fortunately, thanks to a jellyfish and some new advances in microscopy, this ability is now possible.

The jellyfish in question is *Aequoria victoria*. It produces a protein called green fluorescent protein (GFP), which glows a striking fluorescent green color when viewed under blue light. Cell and molecular biologists quickly recognized the value of GFP as a biomonitoring device. GFP can be easily fused with proteins normally found in the cell. These "tagged" proteins can then be located and tracked using the glow of the attached GFP.

Although tracking molecular movement within individual cells is useful in diagnosing some diseases, scientists' ultimate goal is to track molecules as they move throughout the entire body. Current whole-body imaging methods, such as magnetic resonance imaging (MRI), show detailed anatomy but cannot visualize or track molecules within the body. Green Fluorescent Proteins (GFP) can be joined to a gene of a protein of interest so that the protein will fluoresce and demonstrate its expression throughout a cell or organism. In addition, tagged molecules can be located and their three-dimensional distribution within tissues and organs can be shown. While the resolution of these images is not yet sharp enough for medical use, further research is underway. Within the next decade, we may be able to watch molecules moving through our bodies just as easily as we watch the television!

The mitochondria and chloroplasts are energy-converting organelles.

We now know that eukaryotic cells evolved complex structures that allow the cell to carry out specialized tasks. But how do cells get the energy to carry out those tasks? Eukaryotic cells have power-generating organelles called **mitochondria** (Figure 7 and 8) and **chloroplasts** (Figure 9), and these organelles are quite different from the others. These energy-producing organelles have a double-membrane layer, similar to the nuclear envelope. They also contain their own set of DNA and ribosomes, and are capable of synthesizing their own proteins and dividing on their own. Why are mitochondria and chloroplasts semi-autonomous in this way?

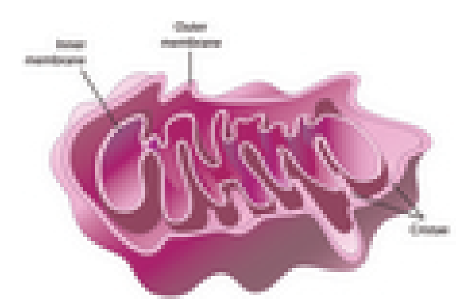

FIGURE 7 Mitochondria. Cross section of intestinal epithelial cell mitochondria. Note the cristae, or folds of the inner mitochondrial membrane.

The **endosymbiotic theory** suggests that early single-celled eukaryotes obtained mitochondria and chloroplasts by engulfing energy-processing prokaryotes. The early eukaryotes allowed the engulfed prokaryotes to live within their cytoplasm. In exchange, these prokaryotes provided their host with energy in the form of adenosine triphosphate

(ATP), the cells' "refined fuel" molecule. The symbiotic, or mutually beneficial, relationship between the prokaryotic cell and the host eukaryotic cell ultimately evolved to a point where the two cells were no longer independent. Much of the prokaryotic DNA was transferred to the nucleus of the host cell, and the cell became an integrated organelle called the mitochondrion. Both animal and plant cells have mitochondria, but plant cells also contain chloroplasts. Plant cells arose well after animal cells, but evolved in a similar way. Over time, prokaryotic bacteria evolved with the ability to process energy from sunlight. Existing mitochondria-containing eukaryotic cells incorporated these photosynthetic prokaryotes into their cytoplasm via endocytosis.

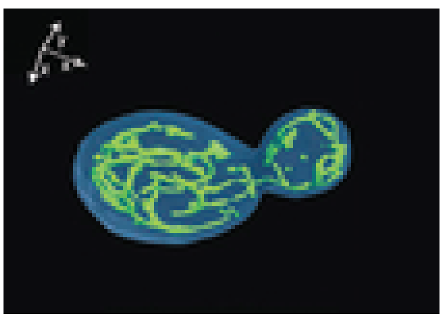

FIGURE 8 The dynamic nature of mitochondria. Like most organelles of the cell, mitochondria are dynamic, constantly morphing into different shapes. They can also merge with and split apart from one another. A network of connected mitochondria, as illustrated in the figure above, can share resources related to cellular respiration, such as oxygen. The ability to share oxygen allows all mitochondria to continuously function, even if they are situated in oxygen-poor areas of the cell.

Many scientists suspect that eukaryotes could have gained other organelles through endosymbiosis. Recent genetic studies have found that eukaryotic DNA contains genes not only from bacteria, but also from Archeans. Could the ancestor of all eukaryotes actually have been an Archean that engulfed its membrane-bound organelles, including the double-membrane nucleus? The debate rages on more than 40 years after Lynn Margulis first published her endosymbiotic theory of the evolution of eukaryotes.

Mitochondria create energy via cellular respiration — the reverse process to photosynthesis. They do this by breaking down carbohydrates, specifically glucose, to create ATP. Mitochondria are therefore an essential component in almost all eukaryotic cells, including those that also contain chloroplasts.

As with chloroplasts, mitochondria possess inner and outer membranes. To maximize the surface area on which chemical reactions occur, the inner membrane is folded, forming pockets called **cristae**. This inner membrane surrounds the matrix compartment, which contains the mitochondrial DNA, ribosomes, and many of the enzymes used in ATP production. Between the inner and outer membranes, we find the intermembrane space. This important compartment maintains the ion diffusion gradients required to generate ATP (Figure 8).

FIGURE 9 Chloroplast. The chloroplast is the energy powerhouse of the plant cell converting the sun’s energy and basic compounds into glucose, a sugar that can be broken down to release energy.

Chloroplasts perform **photosynthesis**: the conversion of light energy, CO_2, and water into carbohydrates like sugars and starch. Appropriate to their function, chloroplasts house **photosynthetic pigments**, such as chlorophyll molecules that absorb light energy. These pigments are contained within the inner membrane of the chloroplast, called the thylakoid membrane. The thylakoid membrane is shaped into towers called grana that look like stacks of dinner plates. Within the thylakoid, light energy is converted into ATP, which in turn powers the construction of sugars in the stroma. The stroma is the fluid-filled area between the thylakoid membrane and the outer membrane. Here in the stroma, CO_2

molecules are used as building blocks to construct carbohydrates (Figure 10).

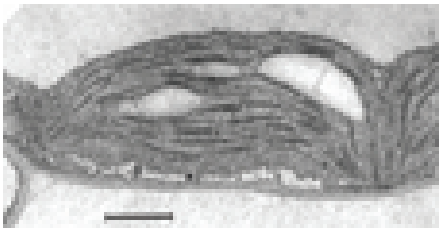

FIGURE 10 Chloroplast micrograph. Cross section of a chloroplast. Note the darkly-stained stacks of thylakoid membrane surrounded by the grayish-colored stroma.

SELF-TEST QUESTION

Why could we say that chloroplasts and mitochondria perform opposite functions?

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Future perspectives.

Parkinson's disease has received a lot of attention over the last few years following the diagnosis of the actor Michael J. Fox. This devastating condition causes gradual reduction in muscle coordination and control within its victims. Parkinson's patients often lose the ability to walk, perform crafts, play sports, or even communicate.

Dr. Bin Zheng and his team at the Center for Neurologic Diseases at Harvard Medical School actively study Parkinson's disease. Their research suggests that there is a link between Parkinson's disease and mitochondria. After analyzing the DNA from more than 400 Parkinson's-afflicted brain samples, Dr. Zheng's group was able to link the onset of Parkinson's disease with genes that control mitochondrial function and energy production. They found that one specific group of these genes is turned off in many Parkinson's patients. If these genes are turned on, the nerve cell damage caused by Parkinson's disease can be greatly slowed or even prevented in some patients. What do these genes do in the cell? Interestingly, they contain the instructions for proteins that regulate the electron transport chain. The electron transport chain is a series of chemical reactions that produce ATP in the mitochondria. Therefore, it appears that mitochondrial functioning is directly related to Parkinson's disease. In response to this new finding, scientists are beginning to test drugs that will stimulate these mitochondria-controlling genes. In the future, Dr. Zheng's research may yield mitochondrial gene therapy that will hopefully prevent Parkinson's disease from progressing beyond its early stages.

Eukaryotic cells contain a number of other structures.

Peroxisomes are the hazardous waste-handlers of the cell (Figures 11 and 12). They contain enzymes that break down toxic molecules by removing hydrogen. The hydrogen atoms are then combined with molecular oxygen (O_2) within the peroxisome, producing hydrogen peroxide — this product is the inspiration for the organelle's name. Hydrogen peroxide is also toxic to cells, so the peroxisome must immediately convert the hydrogen peroxide to water. Peroxisomes are therefore a great example of the compartmentalization of harmful materials and volatile chemical reactions within a membrane-bound organelle.

FIGURE 11 Peroxisomes. The peroxisomes manage the hazardous waste in the cell converting hydrogen sources to hydrogen peroxide which is then converted to water.

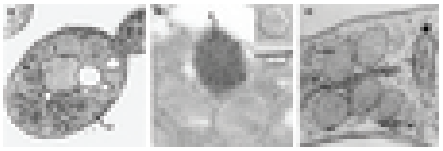

FIGURE 12 Peroxisomes under the microscope. Most cells usually contain several to hundreds of peroxisomes. The number of peroxisomes depends on the function of the cell. The "p" label indicates the location of the peroxisome in yeast (a), fungus (b), and a protist parasite (c).

Vacuoles are large vesicles derived from the ER and Golgi apparatus. They serve as the cell's storage tanks (Figure 13). Food vacuoles, as mentioned previously, form around food that is engulfed by cells. Many freshwater protists possess another kind of vacuole, called a contractile vacuole. The **contractile vacuole** controls the unrelenting osmosis of fresh water into cells by continually pumping out excess water.

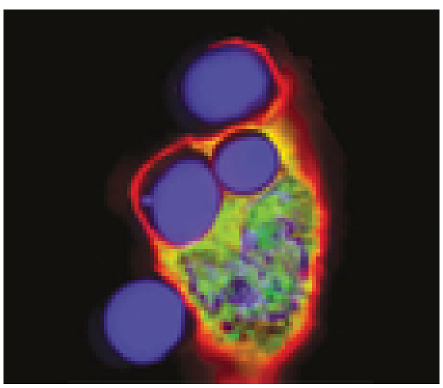

FIGURE 13 Vacuoles. Fluorescence microscopy shows a cell phagocytosing foreign particles (blue discs) and ingesting them into vacuoles with clearly defined membranes (red).

In plant cells, the large central vacuole, or **tono-plast**, also helps control osmotic balance. Plants store ions in the central vacuole, which, like the cytoplasm of the freshwater protists, causes water to diffuse into the cell. When filled with water, tonoplasts force the cytoplasm against the cell wall. This gives the plant cell, and therefore the entire plant, a firm and rigid structure. When water is not available, the tonoplasts shrink, the plant cells become more flaccid, and the plant wilts.

SELF-TEST QUESTION

Which two cellular structures give shape and support to plant cells?

Diverse Form and Function of Eukaryotic Cells

Though plant and animal cells are both eukaryotic, containing membrane-bound organelles, they have adapted functional differences according to their environment and organism function. Eukaryotic cells have evolved these membrane-bound organelles for more complex functionality and greater metabolic control. It is important to remember that cells are dynamic living things that move and change shape to accomplish their function.

In the animation below (Figure 14) notice how some of the organelles in the white blood cell change shape as they phagocytose a bacterium. When scien-tists examine real images of cells, they look nothing like this animation. We must remember that as cells move and act, the cell and its organelles appear differently depending on their state of activity. When we draw diagrams and illustrations to show this activity, it is merely an interpretation of a snapshot in time.

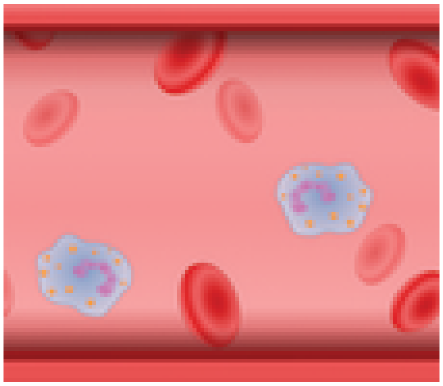

FIGURE 14 Eukaryotic phagocytosis. This figure is an interactive. To see it, visit your Principles of Biology online textbook.

SUMMARY

- **Identify cellular structures on a micrograph or diagram and name their functions.Identify cellular structures on a micrograph or diagram and name their functions.Relate the forms of different cell structures to their functions.Relate the forms of different cell structures to their functions.**

  Eukaryotic cells have a nucleus and membrane-bound organelles. None of these traits are possessed by prokaryotes. In addition, eukaryotes can reproduce sexually while prokaryotes only reproduce asexually. The nucleus contains chromosomes: long strands of DNA organized around histone proteins. DNA contains the instructions for creating all proteins required by the cell. The nucleus also contains the ribosome-subunit-producing area called the nucleolus. All structures of the nucleus are surrounded by the double-layered nuclear envelope. During protein synthesis the instructions for making a protein are transcribed from DNA onto a messenger RNA molecule. The mRNA then leaves the nucleus and fuses with a ribosome. The ribosome constructs the protein based on the instructions on the mRNA transcript. Proteins produced in the rough endoplasmic reticulum are often destined for secretion outside of the cell. These proteins are placed in a membranous transport sac called a transport vesicle, which travels to the Golgi apparatus. In the Golgi apparatus, the proteins are modified and then placed into another vesicle that releases the substance outside of the cell membrane via exocytosis. The smooth endoplasmic reticulum is responsible for synthesizing lipids and detoxifying the cell. Lysosomes are vesicles containing digestive enzymes. Lysosomes fuse with food vacuoles brought into the cell by endocytosis. The enzymes digest the food item, after which the nutritive molecules diffuse into the cytoplasm. Mitochondria break down carbohydrates to produce ATP. Peroxisomes contain enzymes that break down toxic substances within the cell.

- **Compare and contrast the structure and function of organelles found in animal and plant cells.Compare and contrast the structure and function of organelles found in animal and plant cells.**

Chloroplasts and mitochondria likely arose in eukaryotic cells through the endocytosis of early prokaryotes. Chloroplasts perform photosynthesis to build carbohydrates using CO_2, water, and the energy from sunlight. Plasmodesmata are gaps in the cell walls of adjacent plant cells that allow cell-to-cell communication to occur. Vacuoles are membrane-bound organelles used to store substances within the cell. The tonoplast of plant cells retains water to give the plant cell rigidity and support.

TEST YOUR KNOWLEDGE

Question 1

Eukaryotes possess which of the following traits?

a. Compartmentalization
b. Chromosomes that float freely in the cytoplasm
c. Membrane-bound organelles
d. Both the first and second answer choices
e. Both the first and third answer choices

Question 2

While observing plant cells in a biology lab, you see a group of misshapen cells. You insert a fluorescent protein in the cells that binds to proteins on the cell's vacuoles. Upon looking through microscopes, however, you see very small patches of fluorescent color. Which organelle is most likely malfunctioning and causing the collapse in cell shape?

a. chloroplasts
b. lysosome
c. mitochondria
d. rough endoplasmic reticulum
e. central vacuole/tonoplast

Question 3

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What role does the indicated structure play in protein synthesis?

a. Ribosomes enter the nucleus to bind with DNA, initiating protein synthesis.
b. DNA leaves the nucleus through a pore and binds with a ribosome, initiating protein synthesis.
c. mRNA enters the nucleus through a pore to bind with the nucleosome, initiating protein synthesis.
d. mRNA leaves the nucleus through a pore to bind with a ribosome, initiating protein synthesis.
e. Ribosomes enter the nucleus through a pore and bind with RNA, initiating protein synthesis.

Question 4

Which of the following is found in plant cells but not in animal cells?

a. central vacuole/tonoplast
b. lysosome
c. golgi apparatus
d. mitochondria
e. nucleus

Question 5

Which cell structure best exemplifies the compartmentalization of a chemical reaction that requires different environmental conditions from the cytoplasm?

a. vesicle
b. cytoskeleton
c. lysosome
d. ribosome
e. chromosome

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Acids and Bases

KEY TERMS

LEARNING OBJECTIVES

- Explain how the dissociation of water forms hydrogen ions.
- Differentiate between hydrogen ions and hydronium ions.
- Explain the use of logarithms in the pH scale.
- Describe how a buffer contributes to pH stability.
- Give examples of how changes in acidity affect organisms.

Understanding Hydrogen Ions

Most people recognize water as a neutral substance. Yet water dissociates into ions that lead to the formation of acidic and basic solutions. Water, a polar covalent compound, consists of two hydrogen atoms and one oxygen atom. Each water molecule dissociates into two ions — a hydrogen-oxygen pair and a single hydrogen ion, or proton (Figure 1). The hydrogen-oxygen pair has a stronger electronegativity than the single hydrogen atom and therefore steals the electron from the single hydrogen, forming a **hydroxide ion**$[OH^-]$. The free **hydrogen ion** $[H^+]$. rarely occurs by itself in nature. In most cases, it combines with another water molecule to form a **hydronium ion** $[H_3O^+]$.

SELF-TEST QUESTION

Describe what happens when a water molecule dissociates.

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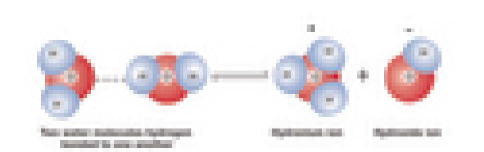

FIGURE 1 Dissociation of water. Water dissociates into a hydronium ion and a hydroxide ion.

All scientists use the same system to measure acids and bases.

What makes a solution acidic or basic? In pure water, the concentration of hydrogen ions (protons) and hydroxide ions is the same, approximately 10^{-7}. The product of the concentrations of these two ions is 10^{-14}. This product remains constant such that if the concentration of hydrogen ions increases, the concentration of hydroxide ions must decrease. The amount of change in ion concentrations is typically determined by the concentration of hydrogen ions and is described as the acidity of an aqueous solution. An acidic solution has a higher concentration of hydrogen ions (<10^{-7}), and vice versa for a basic solution (<10^{-7}).

$[H^+] [OH^-] = 10^{-14}$

To measure the level of acidity in a solution, scientists use the negative logarithm of the hydrogen ion concentration, called the **pH.**

$pH = -\log [H^+]$

For example, an acid adds hydrogen ions to a solution. As the concentration of hydrogen ions increases, the pH of the solution decreases. A base removes hydrogen ions from a solution. As the concentration of hydrogen ions decreases, the pH of the solution increases. A pH of 7 indicates a neutral solution. For example, a 0.1 N solution of hydrochloric acid (HCl) has a pH of 1.

▶ BIOSKILL Interpreting the pH Scale

As solutions trend away from the neutral pH, they become more acidic or basic. Because pH is measured on a log scale, each unit away from a neutral position marks a change in strength by a factor of 10. For example, baking soda has a pH of 8. Since a change of pH from 7 to 8 represents a change in strength of 10, baking soda is 10 times more basic than pure water. Bleach has a pH of 9. This substance is approximately 100 times more basic than pure water. The opposite end of the pH scale depicts acidic substances. A change of pH from 7 to 6 also represents a change in strength of 10 (Figure 2).

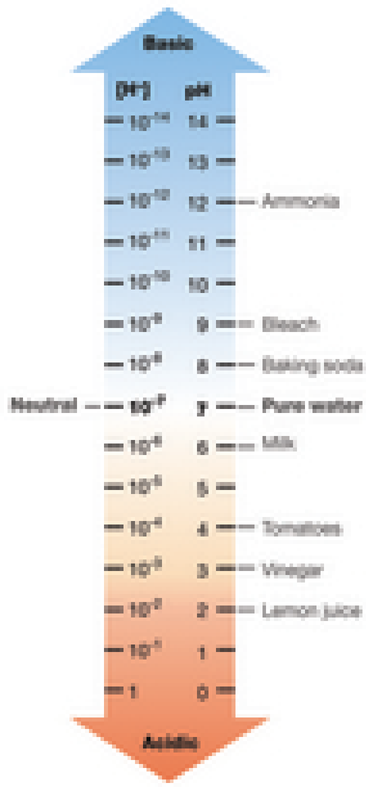

FIGURE 2 **The pH scale** Scientists measure how acidic or basic a substance is by assigning it a pH value. pH is a logarithmic measurement, meaning that a solution that has a pH of 9 is 100 times as basic as solution with a pH of 7.

SELF-TEST QUESTION

List where tomatoes, milk, and lemon juice fall on the pH scale from most acidic to most basic and describe their relative strength to one another.

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The transfer of hydrogen ions creates acids and bases.

Other compounds besides water can produce hydrogen ions. An **acid** is a substance that *increases* the concentration of hydrogen ions in a solution. A strong acid dissociates completely when placed in solution. Hydrogen chloride (HCl), an extremely strong acid, produces hydrogen ions and chloride ions when placed in an aqueous solution (Figure 3).

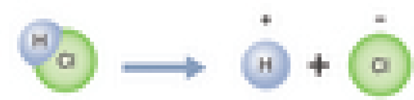

FIGURE 3 **A Strong Acid** Hydrogen chloride completely dissociates into chloride and hydrogen ions when placed in solution. The addition of many hydrogen ions causes an increase in acidity.

A weak acid also contributes hydrogen ions to a solution. An example of a weak acid, carbonic acid (H_2CO_3), dissociates into two ions—a bicarbonate ion (HCO_3^-) and a hydrogen ion (H^+). In a weak acid solution, there are many molecules of the weak acid, some of which dissociate and some of which do not (Figure 4).

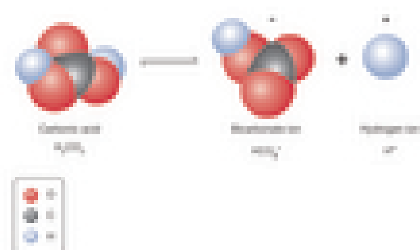

FIGURE 4 **A weak acid.** Carbonic acid dissociates, but not completely in solution. In other words, this weak acid contributes some hydrogen ions, causing a smaller increase in acidity.

SELF-TEST QUESTION

Describe how hydrochloric acid dissociates in water.

A **base** is a substance that *decreases* the concentration of hydrogen ions in a solution. It does so by bonding to the free hydrogen ions in the solution. Like a strong acid, a strong base dissociates completely in solution. An example of a strong base, sodium hydroxide (NaOH), dissociates into sodium ions and hydroxide ions (Figure 5). The hydroxide ions can then combine with any free hydrogen ions, forming water.

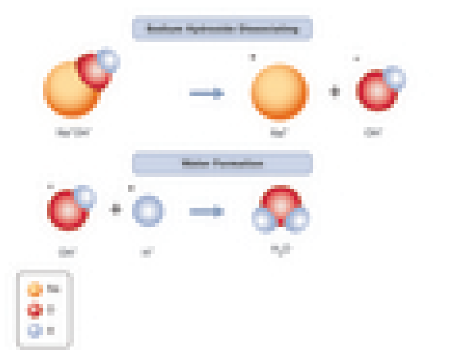

FIGURE 5 **Dissociation of sodium hydroxide.** After sodium hydroxide breaks down into ions, the hydroxide ion can bind with a hydrogen ion to form water.

A weak base also reduces the concentration of hydrogen ions in a solution. One weak base, ammonia (NH_3), combines with a hydrogen ion to form a ammonium ion (NH_4^+). Notice how ammonia can reduce acidity in a different way other than forming water.

The Effect of Changes in Acidity on Living Things

Most biological fluids have a pH between 6 and 8 — roughly neutral. A shift beyond this range can have negative effects on an organism due to cells' sensitivity to the concentration of hydrogen and hydroxide ions. For example, blood maintains a pH close to 7. A blood cell can only survive a few minutes if the pH moves above or below that number.

Cells must protect themselves against changes in acidity.

Many different metabolic processes generate or consume protons, which could lead to dangerous changes in pH. The structures and functions of most biological molecules are sensitive to changes in pH. Organisms and cells have developed systems to stabilize pH to prevent extreme changes. This system is possible because of the large number of weak acids and bases that can absorb excess protons or give up extra protons. These substances therefore act as buffers against pH changes. A **buffer** is a substance that minimizes changes in the hydrogen and hydroxide ions in a solution. A buffer works by accepting a hydrogen ion when a solution becomes too acidic and donating a hydrogen ion when the solution becomes too basic. A buffer typically consists of a weak acid and the corresponding weak base, though many different substances can act as buffers in biological systems. Maximal buffering occurs at a pH where half the compound is dissociated; different compounds reach this point at different characteristic pH values.

Human blood protects against shifts in pH by using carbon dioxide as a buffer. Carbon dioxide (CO_2) reacts with the water in blood plasma, producing the weak acid carbonic acid (H_2CO_3). Carbonic acid dissociates to form bicarbonate (HCO_3^-) and a hydrogen ion. If protons begin to accumulate, the reaction shifts back toward carbonic acid. If protons begin to diminish, more carbonic acid dissociates (Figure 6). Because the reaction is reversible, small shifts in the quantities of carbonic acid and bicarbonate can maintain a constant pH as hydrogen ions are added to or removed from the solution.

FIGURE 6 Carbonic acid as a buffer. Carbonic acid dissociates to form a hydroxide ion and a bicarbonate ion.

When the concentration of hydrogen ions decreases, blood pH increases. In response, the buffer reaction shifts to the right to produce more hydrogen ions. When the concentration of hydrogen ions increases, blood pH decreases. In response, the buffer reaction shifts to the left to consume hydrogen ions. This process maintains a pH within a normal range in order for blood cells to continue to function.

SELF-TEST QUESTION

Explain how blood maintains a stable pH.

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Changes in environmental pH affect ecosystems.

Many human activities can alter the composition of the atmosphere. Carbon dioxide, sulfur dioxide and nitrous oxide are chemical pollutants that can be dangerous to organisms. For example, as the concentration of atmospheric pollutants increases, the pH of rain becomes altered. **Acid precipitation** describes rain, snow, or fog with a pH lower than 5.2. The acid precipitation affects many things detrimentally, including aquatic habitats and organisms, trees, terrestrial animals and soil composition. In general, acids corrode whatever they come into contact with.

SELF-TEST QUESTION

The northeastern United States has been adversely affected by acid precipitation. Explain how acid precipitation forms and how it affects the environment.

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Ocean Buffering System

Ocean acidification describes the decrease in ocean water pH. Click through Figure 7 to view how this phenomenon occurs.

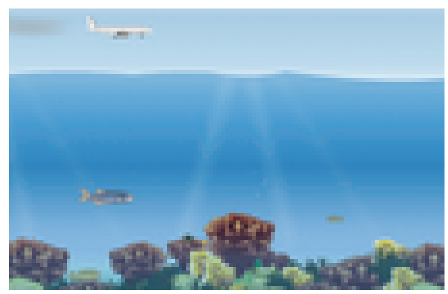

FIGURE 7 Ocean acidification. This figure is an interactive. To see it, visit your Principles of Biology online textbook.

Future perspectives.

As carbon dioxide enters the ocean, ocean water pH decreases. To compensate, the weak acid buffer carbonic acid dissolves calcium carbonate. The free carbonate ion bonds with the excess hydrogen ions, stabilizing pH. Scientists fear that the dissolution of calcium carbonate could have profound impact on organisms living in the ocean.

Many organisms produce shells composed of calcium carbonate. The shells allow the organisms to remain buoyant in the ocean, provide protection, and help organisms maintain their internal chemistry. As the ocean pH falls, the shells of these organisms begin to dissolve to buffer the acidity. Organisms vulnerable to low pH include copepods, snails, sea urchins, and brittlestars. The change in pH can also affect these organisms' ability to grow or reproduce. Although small, these organisms mark the base of the food chain. As their numbers diminish, other organisms in the ocean higher in the food chain become affected.

How can ocean acidification be stopped? Scientists believe one of the most effective ways to stop ocean acidification is to shift away from a fossil fuel-based energy economy. One way to slow the output of carbon dioxide into the atmosphere is to declare carbon dioxide as a pollutant under the Clean Air Act. To help the affected organisms, scientists also suggest establishing additional marine protected areas where vulnerable species can grow and reproduce in a protected environment. Regulating fishing limits may also improve species recovery.

▶ CAREERS Chemical Oceanographers

Chemical oceanographers are scientists who apply their knowledge of chemistry to the ocean. These scientists study the compounds in ocean water, including salt, nutrients, and more recently pollutants. They study the relationships and interaction between these various chemical compounds. They also examine the effect of ocean chemistry on organisms living in the ocean. Their expertise is of particular importance as concerns grow over ocean acidification.

Chemical oceanography involves many disciplines. Chemical oceanographers must have a fundamental understanding of a variety of scientific disciplines to address questions that affect society. They constantly monitor the ocean to collect data to answer important scientific questions. They also work with other scientists and engineers to develop instruments to improve data collection.

SUMMARY

- **Explain how the dissociation of water forms hydrogen ions.Explain how the dissociation of water forms hydrogen ions.**
  Water is a polar covalent compound composed of two hydrogen atoms and one oxygen atom. When a water molecule dissociates, it produces two ions. The hydroxide ion has a stronger electronegativity than the hydrogen ion and takes the electron.

- **Differentiate between hydrogen ions and hydronium ions.Differentiate between hydrogen ions and hydronium ions.**
  A hydrogen ion, or proton, H^+, rarely remains isolated in nature. It often combines with another water molecule to form a hydronium ion, H_3O^+ .

- **Explain the use of logarithms in the pH scale.Explain the use of logarithms in the pH scale.**
  Scientists place the relative strength of acids and bases on the pH scale. pH describes the negative logarithmic concentration of hydrogen ions in a solution. The pH scale ranges from 0 to 14. A pH of 7 describes a neutral solution with an equal number of hydrogen ions and hydroxide ions. A base has a pH greater than 7, and an acid has a pH that is less than 7. A 1-point change in pH is equivalent to a magnitude change in concentration of protons or hydrogen ions. For example, a solution with a pH of 7 has 10 times more hydrogen ions than a solution with a pH of 8.

- **Describe how a buffer contributes to pH stability.Describe how a buffer contributes to pH stability.**
  A buffer is a weak acid, in combination with a corresponding weak base, that stabilizes the pH of a solution. When the concentration of hydrogen ions increases in the solution, the weak acid shifts to the left of the reaction and consumes a portion of the excess acid. When the

concentration of hydrogen ions decreases, the weak acid reaction shifts to the right and contributes hydrogen ions to the solution. A buffer is essential for many biological systems, because it stabilizes pH within a range where a cell can function. Human blood is a buffered system. The ocean is also a buffered system.

▶ **Give examples of how changes in acidity affect organisms.Give examples of how changes in acidity affect organisms.**

Increased burning of fossil fuels injects carbon dioxide into the atmosphere. As the concentration of atmospheric carbon dioxide increases, more carbon dioxide is pumped into freshwater and saltwater systems. When carbon dioxide reacts with water, it forms carbonic acid. This weak acid can gradually lower the pH of water systems, resulting in ocean acidification and acid precipitation. Both scenarios affect plants and animals living in and near the water systems. Scientists are working with policy makers and industry to find ways to curb the use of fossil fuels and protect the environment.

TEST YOUR KNOWLEDGE

Question 1

Which of the following describes how a hydronium ion forms?

a. $H^+ + H_2O$

b. $H^+ + OH^-$

c. $H^+ + Cl^-$

d. $H^+ + NH_3$

e. None of the above

Question 2

Which substance dissociates completely to reduce the concentration of hydrogen ions in a solution?

a. NaOH

b. H_2O

c. HCl

d. NH_3

e. CO_3^{+2}

Question 3

Oven cleaner has a higher pH than baking soda. This is because oven cleaner has

a. a greater concentration of hydroxide ions.

b. a lower concentration of hydroxide ions.

c. a balance of hydronium and hydroxide ions.

d. a complete lack of hydrogen ions.

e. None of the above

Question 4

A buffer is typically a

a. weak acid

b. strong acid

c. strong base

d. hydronium ion

e. none of the above

Question 5

Which factors contribute to ocean acidification?

a. coal-burning power plants

b. automobiles

c. natural gas processing plant

d. air travel

e. all of the above

3 Proteins

Proteins are a diverse group of polymers that play a critical role in nearly all cell functions.

KEY TERMS

amino acid • Monomer composed of central carbon atom surrounded by an amino group, a carboxyl group, a hydrogen atom, and a side chain. The different amino acids are determined by differences in the side chains.

denaturation • Breakdown of the secondary and tertiary structure of a protein by exposure to environmental stresses, making it nonfunctional.

protein • Class of biologically important molecules made up of one or more peptides; most diverse form and function of the biological molecule groups.

LEARNING OBJECTIVES

- Describe the chemical structure of an amino acid.
- Explain the four levels of protein structure.
- Associate protein structure to function.

Nineteenth century scientists applied the name *proteins* to define the "primary" class of molecules in living things, after the Greek word "proteus." Were the scientists justified in applying this authoritative label given that they lacked sophisticated technologies for biochemical analysis? Decades of protein research vindicated their pronouncement, which shed light on the critical role of proteins in nearly every cell function and structure.

Four Levels of Protein Structure

The human body contains tens of thousands of proteins. Why does the body need so many? Proteins are sophisticated and complex structures. Proteins carry out most of the cell's varied life functions and contribute to the diversity of cell structures. Table 1 summarizes the relationship between major protein functions and structure.

Major protein function	**Structural significance**
Metabolism — catalyzing chemical reactions	Enzymes are **catalysts**, or molecules that lower the energy required for a chemical reaction to proceed. Most enzymes are proteins. Proteins catalyze reactions by binding to reactants. A protein binding site must perfectly match the reactant. The cell needs thousands of different enzymes to catalyze all of its metabolic reactions.
Signaling — delivering chemical messages throughout the body	Proteins serve as both message transmitters and receivers, linked by structure. For example, brain cells contain multiple receptors for messenger molecules called neurotransmitters. A receptor's structure allows it to bind to a specific neurotransmitter.
Transport — carrying molecules throughout the body	Proteins transport nutrients, waste products, and other substances between cells, within cells, and across cell membranes. Each transport protein has a unique structure to bind to a specific substance, just as hemoglobin in red blood cells binds to oxygen to transport it throughout the body.
Structure — forming organelles and other cell structures as well as the basis of macroscopic structures	Proteins provide structural support at several levels — organelles, cells, and organs. Organelle proteins provide structure and carry out related functions. Proteins determine a cell's overall shape and form as well as the form of tissues and organs such as skin.
Movement — moving substances, cells, and body parts	Protein structure controls contractile and motor functions. These proteins can move substances within cells. Coordinated movements in tissue cells produce macroscopic movements of larger body parts, like when muscle tissue contracts to move bone.
Defense — defending the body against disease-causing agents	Proteins in the immune system such as antibodies bind to and destroy invasive bacteria and viruses. The structure of an antibody is specific to a certain bacteria or virus. The body builds immunity by producing new antibodies for each new bacteria and virus it encounters.

Table 1: Major protein functions. A protein's structure is intimately linked to its function.

At the most basic level, **proteins** are made up of one or more polypeptides. **Polypeptides** are chains of amino acids linked together by peptide bonds. How can these chains form thousands of different molecular structures? The protein chains, or polypeptides, form up to four layers of structure resulting in structural diversity.

Primary structure: Amino acids link together to form a linear polypeptide.

The **primary structure** of a protein is a linear chain of amino acids. An **amino acid**monomer is composed of a central carbonatom, called the alpha (α) carbon. An *alpha carbon* bonds to

1. an amino group,
2. a side chain or R-group,
3. a carboxyl group, and
4. a hydrogen atom (Figure 1).

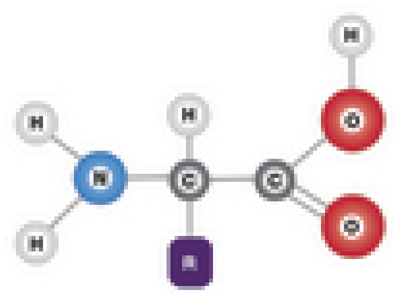

FIGURE 1 Amino acid structure. An amino acid contains an amino group, a side chain, a carboxyl group, and a hydrogen atom all bound to a central carbon atom.

Amino acids differ by the type of attached side chain. Amazingly, cells use only 20 amino acids (Figure 2), to build the many thousands of proteins needed to maintain life functions. How does this work?

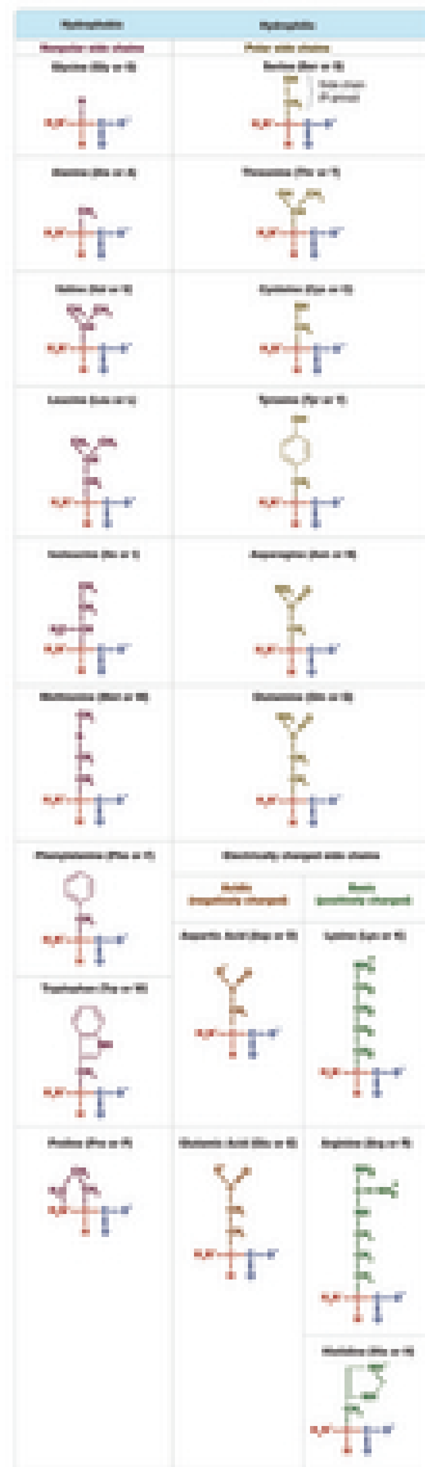

FIGURE 2 The 20 amino acids. The amino group and the carboxyl group are always the same, but the R-group differs in each of the 20 amino acids.

Notice that the R-groups have different states of electronegativity, which affect their chemical behavior. Recall that nonpolar molecules are hydrophobic and tend to bond with only nonpolar molecules. Polar molecules are hydrophilic and bond easily with water. Charged molecules can attract oppositely charged molecules. The amino acids combine in different orders, which changes the electronegativities of the molecules and how different parts of the chain bind together to form tertiary and quaternary levels of structure. Mathematically, the 20 amino acids can combine to form millions of different proteins in chains of varying length.

How does the cell link the amino acids together? A carboxyl group can bond to an amino group by a dehydration reaction-the removal of a water molecule. This reaction forms a peptide bond. Dehydration reactions link amino acids into polypeptide chains. A polypeptide backbone forms from a chain of alpha carbons which are carboxyl and amino groups linked by peptide bonds, excluding the R-groups. **Peptide bonds** are the chemical bonds of carbon to nitrogen after dehydration (Figure 3). Side groups, as their name suggests, stick out to the sides of the backbone. Polypeptide chains range in length from a few amino acids to more than a thousand.

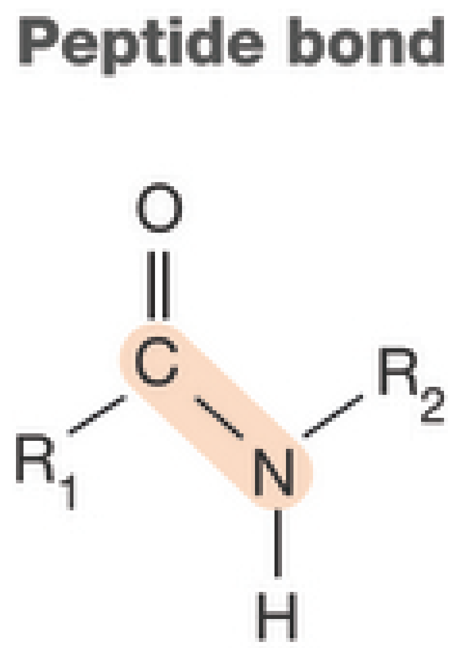

FIGURE 3 **Peptide bond.** A peptide bond is formed between the carboxyl and amino groups of adjacent amino acids.

Secondary structure: Hydrogen bonds between atoms in the polypeptide backbone create a folded or coiled shape.

Segments of the polypeptide chain can form coiled or folded patterns, called the **secondary structure**. The chemical tendencies of R-groups determine tertiary and quaternary structures. What, then, determines the formation of secondary structures?

Hydrogen bonds between repeating units in the polypeptide chain backbone produce a coiled and folded patterns. However, the amino acid sequence does influence the formation of secondary structure attributable in part to geometric variations between amino acids. Different segments of a polypeptide chain can form different secondary structures. Some segments may lack secondary structure.

Consider two types of secondary structure in detail. Looping coils called **α helices** develop from the hydrogen bonds that form between the oxygen of a carboxyl group and the hydrogen of the fourth amino group in the chain. Folded patterns called **β pleated sheets** form when two or more strands of a polypeptide line up parallel to one another. Hydrogen bonds form between adjacent carboxyl and amino groups. Hydrogen bonds that form between elements in slightly different planes produce a pleated pattern. The hydrogen bonds also serve to hold the parallel strands together in a sheet-like structure (Figure 4).

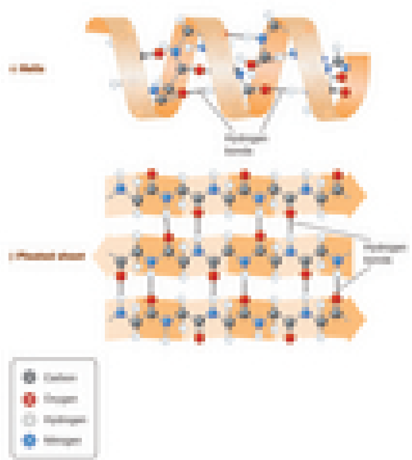

FIGURE 4 **Secondary structures.** Hydrogen bonds between amino and carboxyl groups hold together structures such as α helices and β pleated sheets. In ribbon diagrams, the flat arrow points to the carboxyl end of the polypeptide.

Tertiary structure: Interactions between side chains create a three-dimensional shape.

Tertiary structure is the main, three-dimensional shape of a polypeptide unit. This shape results from, and is held together by, bonds and interactions between R-groups and between R-groups and elements on the backbone. These bonds and interactions include:

- **Hydrophobic effect**— clustering of nonpolar side chains or burial of the core of the protein molecule in a manner that reduces contact with water molecules in the surrounding fluid.
- Hydrogen bonding-hydrogen atoms in R-groups can form hydrogen bonds. Hydrogen bonds can also form between R-group hydrogen atoms and oxygen atoms in the backbone.
- Covalent bonding-two sulfur atoms can bond together covalently. This is most likely to occur at the terminal sulfur atoms in cysteine. Scientists often refer to these sulfur — sulfur bonds as **disulfide bridges** because of their structural linkage role.
- Ionic bonding-ions in oppositely charged side groups can form ionic bonds.
- van der Waal interactions-weak electrostatic forces can add stability to the structure once it is already in place.

A complex web of these interactions results from the ordering of amino acids in a polypeptide unit, giving each different polypeptide unit a unique tertiary structure. Click on the image in Figure 5 to see an animation of how tertiary structure builds on primary and secondary structure.

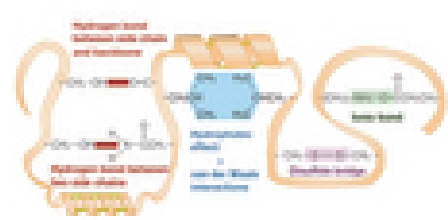

FIGURE 5 Primary, secondary and tertiary structure. This figure is an interactive. To see it, visit your Principles of Biology online textbook.

Denaturation is the breakdown of secondary and tertiary protein structures as a result of external stresses such as temperature or an acid or base.

SELF-TEST QUESTION

How does a protein's tertiary structure depend on its primary structure?

Quaternary structure: Associations of polypeptides form a functional protein.

Many proteins contain multiple polypeptide units assembled into a functional macromolecule, which may include multiple copies of the same polypeptide unit, different polypeptide units, or both. These proteins have a**quaternary structure**resulting from the aggregation of the tertiary structures that may be the same subunits or different subunits. Quaternary structure uses the same palette of bonds and interactions used to form tertiary structure; only the bonds and interactions occur between atoms of separate polypeptide units.

Hemoglobin is an oxygen-transport protein found in red blood cells. The four polypeptide units form a quaternary structure, sometimes called a *tetramer*. Click on the interactive diagram in Figure 6 to investigate the levels of structure in hemoglobin.

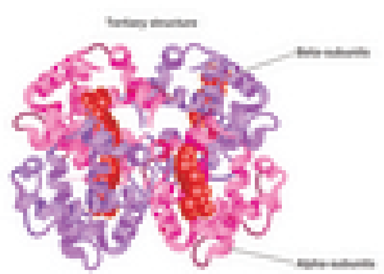

FIGURE 6 **Layers of structure in hemoglobin. This figure is an interactive. To see it, visit your Principles of Biology online textbook.**

Protein Function

Table 1 provides a wide range of critical functions carried out by proteins and the intimate link between a protein's structure and its function. Let's take a closer look at examples of protein function.

Collagen is one of the most ubiquitous proteins in the bodies of vertebrates. It plays an important role in connective tissues, including cartilage, tendons as well as bone and skin tissues. Collagen is made up of three identical α-helices woven into a durable triple helix (Figure 7). This quaternary structure is stabilized by the hydrogen bonds that form between each of the three initial polypeptide chains.

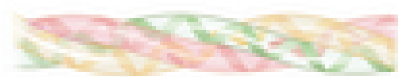

FIGURE 7 **Structure of collagen.** The fibrous structure of collagen supports its function in connective tissue. Three polypeptides twisted into alpha-helices are bound together in a durable triple-helix by hydrogen bonds.

SELF-TEST QUESTION

How does the structure of collagen relate to its function?

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Future perspectives.

Receptors in brain cells receive communications from the body, supporting the brain's role in maintaining homeostasis. Researcher Eric Gouaux and his colleagues recently completed a map of a complex and very important brain receptor called the glutamate receptor. When the neurotransmitter glutamate binds to the receptor, an "ion channel" opens in the neuronal membrane. This allows ions to flow across the membrane, thereby transmitting an electrical pulse down the nerve (Figure 8). At the top are two prongs, which can bend to modify the receptor. Below this is the area where glutamate binds, opening the ion channel located at the bottom. Gouaux likened the channel structure to "a Mayan temple." Gouaux also reports his surprise at finding out that the receptor is made up of four subunits that are chemically identical but are folded differently. "The completely astonishing thing was that two subunits are completely different from the other two. That difference was totally unanticipated." Resolving the structure of the glutamate receptor will allow researchers to, among other things, develop drugs to treat neurological pathologies that occur as a result of problems along pathways involving this ubiquitous receptor.

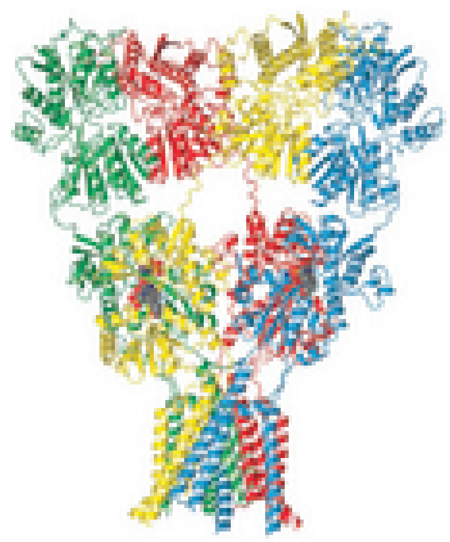

FIGURE 8 Structure of the glutamate receptor. Glutamate has two prong-shaped subunits at the top that can bend and attach to a receptor modifying the receptor’s structure and opening the ion channel at the bottom.

▶BIOSKILL X-ray Crystallography is an Important Technique in Determining Protein Structure

Scientists use **x-ray crystallography** — a technique that measures the angle and intensity with which x-rays are diffracted when passing through a crystalline structure to determine the structures of many biological molecules. Most famously, Rosalind Franklin (1920–1958) used this technique in the discovery of DNA's double helix (Figure 9).

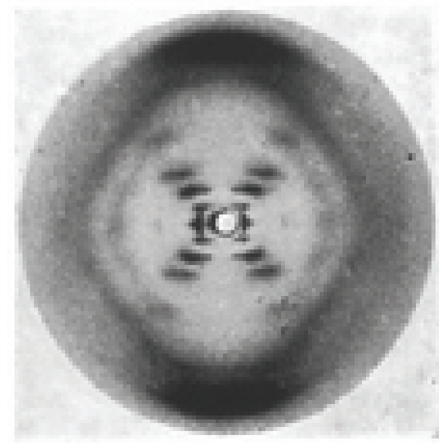

FIGURE 9 X-ray diffraction. Rosalind Franklin showed DNA with x-ray diffraction in 1953. This process and image became the foundation for establishing the shape of many other biological molecules including proteins.

Dorothy Crowfoot Hodgkin (1910–1994), Franklin's contemporary, developed the methodological and technological path for protein structure discovery by advancing techniques for resolving fine details of macromolecules. Hodgkin's important discoveries, including the structures of penicillin, insulin, and vitamin B_{12}, won her a Nobel Prize in 1964 and led to medical advances that directly improved the health of millions. A technological pioneer in biochemistry, she was the first person to use an electronic computer-an early IBM-for biochemical analysis in the 1940s. She used the computer to perform calculations of x-ray output data. Hodgkin pioneered techniques for developing three-dimensional models of biological molecules. Today, tens of thousands of proteins have been analyzed by x-ray crystallography at angstrom-level resolution. Researchers use the x-ray crystallography data to produce three-dimensional models.

First, researchers crystallize the proteins. Although softer and more flexible than mineral crystals, biological molecules are highly ordered and patterned. To crystallize proteins, researchers prepare a concentrated, pure solution of the protein sample and allow it to nucleate and crystallize on a slide. Then researchers bombard the protein crystals with x-rays, which diffract when they interact with atoms in the crystal. By measuring the locations of x-rays exiting the crystal, researchers can, with a considerable amount of mathematical computation, calculate a map of electron densities in the crystal. Peaks in the electron density map correspond to the atomic positions in the molecule and intermolecular distances. From that map, researchers can construct a three-dimensional model of the molecule (Figure 10).

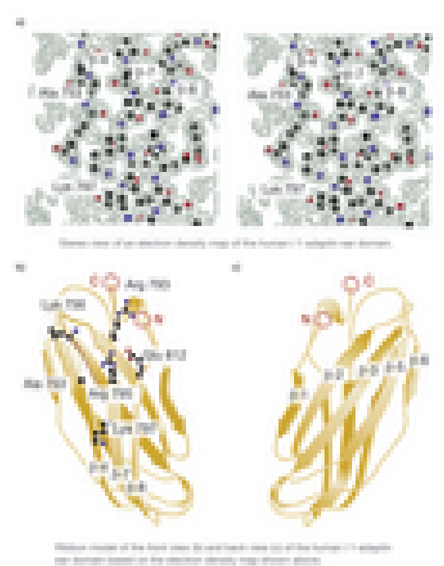

FIGURE 10 Comparing electron density maps with three-dimensional ribbon models. Pay attention to the locations of the structures on the electron map marked by researchers and where these locations correspond to the model. Scientists interpret the electron density map to identify the locations of amino acids such as Ala 753 as seen in panel A to get the structure of and position of the same part of the protein in panel B.

SELF-TEST QUESTION

Describe the secondary and tertiary structure of this protein.

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Future perspectives.

In the 1990s, research confirmed the existence of strange infectious proteins called prions. These highly unusual pathogens lack genetic material. Modified prion proteins cause fatal neurodegenerative diseases such as bovine spongiform encephalopathy (BSE, commonly called mad cow disease) and Creutzfeldt-Jakob disease (CJD). A person can be infected with these diseases by ingesting brain matter that contains the infectious proteins. Researchers have discovered that normal cellular prion protein (PrPC), which is naturally occurring in the brain, is converted structurally into the infectious prion protein PrPSc through a process that increases its beta-sheet content. Many aspects of prions remain mysterious. For example, some evidence suggests that normal PrP plays a protective role in the maintenance of myelin nerve sheaths protecting the brain from developing plaques that are a symptom of Alzheimer's disease. Researchers are still working to shed light on prions and their role in neurological disorders.

SUMMARY

- **Describe the chemical structure of an amino acid.Describe the chemical structure of an amino acid.**
  An amino acid is a monomer composed of a central carbon atom, or alpha (α) carbon, surrounded by an amino group, a side chain or R-group, a carboxyl group, and a hydrogen atom. Twenty different amino acids exist, each with a unique R-group.
- **Explain the four levels of protein structure.Explain the four levels of protein structure.**
  Protein structure occurs at four levels. Primary structure is the order of amino acids linked together in a polypeptide chain. These chains can form secondary structures: coiled or pleated sheets held together by hydrogen bonds in the backbone. Tertiary structures emerge from

chemical bonds and interactions among R-groups and between R-groups and atoms on the backbone. Proteins with combinations of multiple polypeptide units have quaternary structure resulting from the aggregation of the tertiary structures.

- **Associate protein structure to function.Associate protein structure to function.**
  The structure and function of proteins are inextricably linked. Proteins perform multiple critical functions, including transport, signaling, movement, immune defense, and structural support. Each of the many thousands of proteins in a typical vertebrate has a unique structure related to its specific function.

TEST YOUR KNOWLEDGE

Question 1

Each of the 20 different amino acids has a unique

a. α – carbon
b. Amino group
c. Carboxyl group
d. Side group
e. All of the above

Question 2

Which of these are secondary structures of proteins?

a. α-helices
b. Amino groups
c. Polypeptide chains
d. Polypeptide units
e. None of the above

Question 3

Which level(s) of protein structure are determined by the order of amino acids in the polypeptide chain?

a. Primary structure
b. Secondary structure
c. Tertiary structure
d. Quaternary structure
e. All of the above

Question 4

What is a possible function of disulfide bridges in the tertiary structure of a protein?

a. Holding together amino acids
b. Forming β-pleated sheets
c. Holding together different α-helices
d. All of the above
e. None of the above

Question 5

Which best describes the relationship between the structure of receptor proteins to the signal molecules?

a. Each receptor protein has a unique structure that allows it to bind to a specific signal molecule.
b. Receptor proteins all have similar structures so that the cell can use them to receive a wide variety of signal molecules.
c. Receptor proteins have changeable structures that allow them to receive many different signal molecules.
d. Receptor proteins have an undefined globular structure until a signal molecule binds to it.
e. None of the above

4

Eukaryotic Cells

Eukaryotic cells contain structures that help them carry out the process of living.

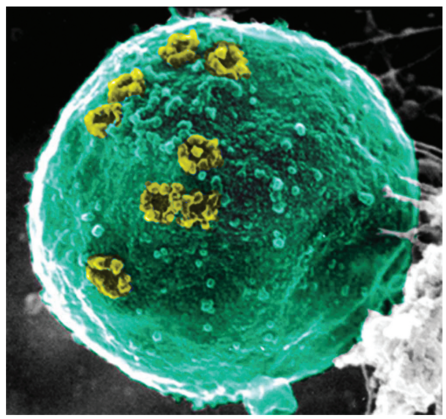
KEY TERMS

endoplasmic reticulum • Extensive series of membrane enclosed compartments throughout the cell; comes in two forms: smooth and rough.

mitochondria • Powerhouse of eukaryotic cell; site of aerobic respiration. Present in both autotrophic and heterotrophic cells.

peroxisomes • Vacuoles that contain enzymes to break down toxic materials.

vacuoles • Vesicles usually derived from the Golgi apparatus or endoplasmic reticulum; allow for materials to be sequestered from the rest of the cell and transported into, out of, or through the cell.



LEARNING OBJECTIVES

- Identify cellular structures on a micrograph or diagram and name their functions.
- Relate the forms of different cell structures to their functions.
- Compare and contrast the structure and function of organelles found in animal and plant cells.

Components of a Eukaryotic Cell

What makes eukaryotic cells different from bacterial and other prokaryotic cells? How did this difference evolve? The first organisms on Earth were likely prokaryotic. These organisms consumed carbohydrates, amino acids, and other biological molecules; such food molecules were likely replenished at a very slow rate in the primordial seas. This would have led to extreme food competition among these early prokaryotes, and it is theorized that this competitive pressure drove the evolution of new and more efficient metabolic pathways.

Utilizing new food sources required the development of more complicated chemical reactions. Digestion of some molecules would have required specific environmental conditions that differed from those inside the cytoplasm. How did early eukaryotes cope with these new physiological demands? One evolutionary solution to this complex problem was to restrict chemical reactions to specific compartments within the cell. Environmental conditions differ within each cellular compartment, similar to how a series of greenhouses can provide unique environments that support specialized tropical, desert, and cold-weather plants. The evolution of compartmentalization allowed eukaryotic cells to exploit a wide-range of new food sources thanks to the greatly expanded range of chemical reactions that could be performed within a cell.

The compartments in eukaryotic cells are mainly organelles: membrane-bound structures bound with a semi-permeable phospholipid membrane that is very similar in composition to the plasma membrane. Organelles are the primary feature that distinguishes eukaryotic cells from prokaryotic cells (Figures 1 and 2). Another major difference between prokaryotes and eukaryotes is the location of the chromosomes. In prokaryotic cells, chromosomes are localized in the nucleoid region, whereas eukaryotic cells have many chromosomes contained within a membrane-bound organelle called the **nucleus**.

FIGURE 1 A typical animal cell. This figure is an interactive. To see it, visit your Principles of Biology online textbook.

Figures 1 and 2 illustrate typical animal and plant cells and their common organelles. It is important to remember that eukaryotic cells come in all shapes and sizes. Eukaryotic cells are typically specialized in size and shape based on their function.

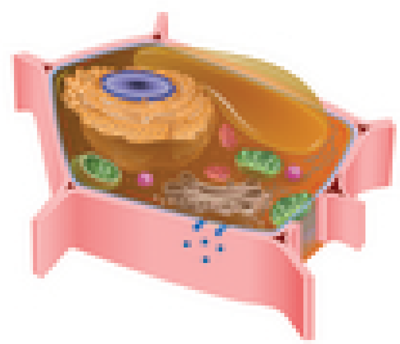


FIGURE 2 A typical plant cell. This figure is an interactive. To see it, visit your Principles of Biology online textbook.

Why is the nucleus important?

A membrane-bound nucleus that functions much like the brain of the cell is a complex adaptation unique to eukaryotes (Figure 3). A eukaryotic cell's nucleus alone is often larger than an entire prokaryote. The **nucleus** is the control center of the cell, processing inputs from the cytoplasm, storing and retrieving information, and carrying out instructions contained within the genetic material in the nucleus. The nucleus contains the cell's chromosomes. Chromosomes are made up of DNA, which contains the genetically transmitted instructions for reproduction and for synthesizing proteins and RNA.

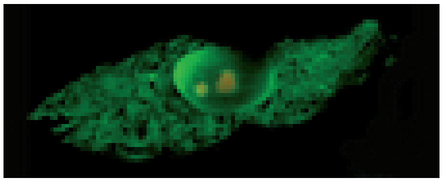


FIGURE 3 The nucleus. Green fluorescent labeling highlights an entire mammalian cell, including its nucleus. The nucleolus (orange) and surrounding nuclear envelope surrounding it lie at the center of the cell.

The nucleus is bound in a membrane called the **nuclear envelope**. The nuclear envelope is made up of two lipid bilayers. The nuclear membrane also contains prominent **nuclear pores**. These channels allow large molecules, such as messenger RNA, to enter or leave the nucleus. The nucleus also contains a dark-staining area called the **nucleolus**. The nucleolus synthesizes ribosomal rRNA. The rRNA combines with proteins to form the small and large subunits of the **ribosomes**, which are the protein-producing factories of the cell. These subunits move into the cytoplasm, where a large and small subunit will assemble together to become a ribosome.

SELF-TEST QUESTION

What is the definition of a chromosome?

Though ribosomes are made in the nucleolus, they synthesize proteins in the cytoplasm or in another organelle called the endoplasmic reticulum, which is suspended in the cytosol outside of the nucleus. If the DNA is inside the nucleus and the protein-synthesizing organelles are somewhere else in the cell, how do the cells make proteins based on the blueprints contained within the DNA?

In the same way that we keep important documents in a safe place and make copies as needed, the DNA never leaves the protected confines of the nucleus. Instead, a transcript of the blueprint is made in the form of a messenger RNA (mRNA) molecule. True to its name, the mRNA carries the transcribed instructions out of the nucleus to a ribosome. The ribosome constructs the protein as instructed on the RNA transcript.

The mRNA, like any good messenger, must know where to deliver its message. Some ribosomes float freely in the cytoplasm, and these ribosomes are usually in charge of making proteins that will be used inside the cell. Ribosomes responsible for producing proteins that will be exported from the cell are located on an organelle called the endoplasmic reticulum.

SELF-TEST QUESTION

What is the role of mRNA in protein synthesis?

The endomembrane system is a group of interrelated organelles.

The **endoplasmic reticulum** (ER) is an extensive network of membrane-enclosed compartments that connect directly to the nuclear envelope. **Smooth endoplasmic reticulum** does not contain ribosomes, and it is primarily involved in lipid synthesis and in breaking down toxic substances in the cell, such as alcohol. **Rough endoplasmic reticulum** (RER) appears rough because it is studded with ribosomes. What kind of proteins can the RER ribosomes produce? One example is found within the skin cells of a poison dart frog. The RER ribosomes in these cells produce a mixture of proteins, lipids, and a very powerful neurotoxin that harms predators who touch the frog's colorful skin. When the ribosomes have completed the job of synthesizing a poison molecule, this new protein is deposited into a membrane-bound transport organelle called a **transport vesicle**. When inside the transport vesicle, the poison molecules cannot harm the cell and can be safely transported through the cytoplasm to another organelle: the Golgi apparatus.

The **Golgi apparatus** is the "shipping and receiving" center of the cell's endomembrane system (Figure 4). This organelle modifies, stores, and exports substances from the cell. When a substance, such as our frog's poison molecule, passes through the consecutive chambers of the Golgi apparatus, phosphate or sugar groups may be added or removed. Whether any of these chemical groups are added or removed depends on the intended use of the new molecules. Many substances are also tagged with a small molecule in the Golgi apparatus. Like a postal address, this molecular tag tells cellular machinery where to send the substance in the body. Once all modifications are complete, the substance is packaged into another transport vesicle. This vesicle transports the molecules from the Golgi apparatus to the plasma membrane. Once it reaches the plasma membrane, the substance is released from the vesicle to the outside of the cell, a process called exocytosis (Figure 5).

FIGURE 4 Golgi apparatus. The Golgi apparatus is part of the endomembrane system of the cell, modifying, storing and exporting substances from the cell.

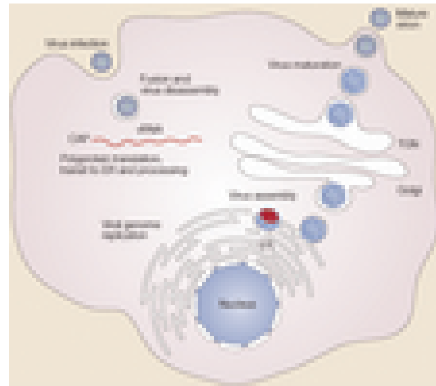


FIGURE 5 Viral exocytosis by the Golgi apparatus. A virus infects a cell, where it takes advantage of the cell’s own functions to replicate itself and then move on to infect other cells. The Golgi apparatus uses exocytosis to remove a foreign virus from the cell, but not before the virus has utilized other cellular functions.

Lysosomes are the cell's digestive system and recycling center.

The RER and Golgi apparatus produce another membrane-bound organelle, the lysosome. **Lysosomes** are vesicles containing powerful enzymes that digest food items engulfed by the cell. The vesicles of lysosomes are specifically designed to maintain a low pHenvironment within the cell. This acidic environment provides the optimal conditions for the digestive enzymes to function.

Most eukaryotic organisms ingest their nutrients. How can cells utilize the food that eukaryotes take in? One way that cells take in nutrients is by engulfing large substances through the process of **phagocytosis** (Figure 6). In phagocytosis for the purpose of accuiring nutrients, the cell first surrounds a nutrient with its plasma membrane. Once the plasma membrane completely surrounds the nutrient, the membrane pinches off to form a vesicle inside the cytoplasm of the cell. This vesicle, containing the engulfed food item, is called a **food vacuole**. Lysosomes bind with these food vaculoes and secrete their digestive enzymes onto the food items. Once the lysozymes have completely digested the food, the products of digestion (including simple sugars, amino acids, and other monomers) are small enough to diffuse out of the vacuole and into the cytoplasm so that the rest of the cell can use them for energy. Another way that a cell uses phagocytosis is to defend against invading organisms like a bacterium. In this case, the physical processes of engulfing and digesting are very similar.

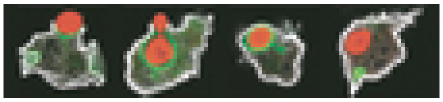


FIGURE 6 Phagocytosis by an amoeba. This amoeba, a single-celled eukaryote, is engulfing a yeast cell (red) using phagocytosis. The amoeba surrounds the yeast with an extension of its cell membrane and encases the yeast within a membrane-bound food vacuole.

In addition to their digestive functions, lysosomes can also use their digestive enzymes to recycle cellular components by autophagy. **Autophagy** is the process of breaking-down and recycling malfunctioning or worn out cell organelles. This process reclaims vital molecules from worn — out organelles-valuable materials that would otherwise be lost.

Future perspectives.

Imagine what it would be like to watch proteins and other molecules move around inside a living cell in real time. We would be able to see not only which molecules the cell produces but also watch where the molecules go after they are produced, either inside or outside the cell. Fortunately, thanks to a jellyfish and some new advances in microscopy, this ability is now possible.

The jellyfish in question is *Aequoria victoria*. It produces a protein called green fluorescent protein (GFP), which glows a striking fluorescent green color when viewed under blue light. Cell and molecular biologists quickly recognized the value of GFP as a biomonitoring device. GFP can be easily fused with proteins normally found in the cell. These "tagged" proteins can then be located and tracked using the glow of the attached GFP.

Although tracking molecular movement within individual cells is useful in diagnosing some diseases, scientists' ultimate goal is to track molecules as they move throughout the entire body. Current whole-body imaging methods, such as magnetic resonance imaging (MRI), show detailed anatomy but cannot visualize or track molecules within the body. Green Fluorescent Proteins (GFP) can be joined to a gene of a protein of interest so that the protein will fluoresce and demonstrate its expression throughout a cell or organism. In addition, tagged molecules can be located and their three-dimensional distribution within tissues and organs can be shown. While the resolution of these images is not yet sharp enough for medical use, further research is underway. Within the next decade, we may be able to watch molecules moving through our bodies just as easily as we watch the television!

The mitochondria and chloroplasts are energy-converting organelles.

We now know that eukaryotic cells evolved complex structures that allow the cell to carry out specialized tasks. But how do cells get the energy to carry out those tasks? Eukaryotic cells have power-generating organelles called **mitochondria** (Figure 7 and 8) and **chloroplasts** (Figure 9), and these organelles are quite different from the others. These energy-producing organelles have a double-membrane layer, similar to the nuclear envelope. They also contain their own set of DNA and ribosomes, and are capable of synthesizing their own proteins and dividing on their own. Why are mitochondria and chloroplasts semi-autonomous in this way?

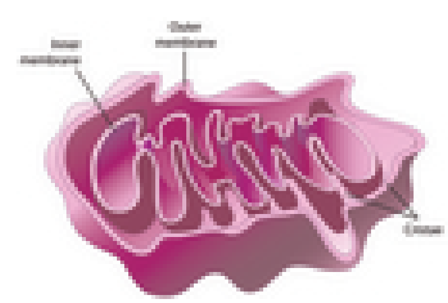


FIGURE 7 Mitochondria. Cross section of intestinal epithelial cell mitochondria. Note the cristae, or folds of the inner mitochondrial membrane.

The **endosymbiotic theory** suggests that early single-celled eukaryotes obtained mitochondria and chloroplasts by engulfing energy-processing prokaryotes. The early eukaryotes allowed the engulfed prokaryotes to live within their cytoplasm. In exchange, these prokaryotes provided their host with energy in the form of adenosine triphosphate

(ATP), the cells' "refined fuel" molecule. The symbiotic, or mutually beneficial, relationship between the prokaryotic cell and the host eukaryotic cell ultimately evolved to a point where the two cells were no longer independent. Much of the prokaryotic DNA was transferred to the nucleus of the host cell, and the cell became an integrated organelle called the mitochondrion. Both animal and plant cells have mitochondria, but plant cells also contain chloroplasts. Plant cells arose well after animal cells, but evolved in a similar way. Over time, prokaryotic bacteria evolved with the ability to process energy from sunlight. Existing mitochondria-containing eukaryotic cells incorporated these photosynthetic prokaryotes into their cytoplasm via endocytosis.

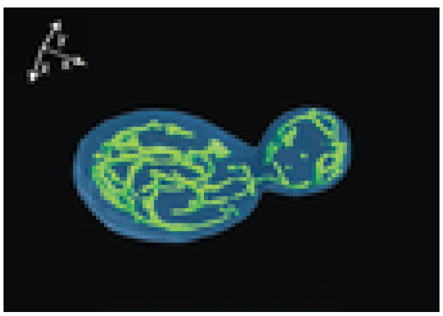


FIGURE 8 The dynamic nature of mitochondria. Like most organelles of the cell, mitochondria are dynamic, constantly morphing into different shapes. They can also merge with and split apart from one another. A network of connected mitochondria, as illustrated in the figure above, can share resources related to cellular respiration, such as oxygen. The ability to share oxygen allows all mitochondria to continuously function, even if they are situated in oxygen-poor areas of the cell.

Many scientists suspect that eukaryotes could have gained other organelles through endosymbiosis. Recent genetic studies have found that eukaryotic DNA contains genes not only from bacteria, but also from Archeans. Could the ancestor of all eukaryotes actually have been an Archean that engulfed its membrane-bound organelles, including the double-membrane nucleus? The debate rages on more than 40 years after Lynn Margulis first published her endosymbiotic theory of the evolution of eukaryotes.

Mitochondria create energy via cellular respiration — the reverse process to photosynthesis. They do this by breaking down carbohydrates, specifically glucose, to create ATP. Mitochondria are therefore an essential component in almost all eukaryotic cells, including those that also contain chloroplasts.

As with chloroplasts, mitochondria possess inner and outer membranes. To maximize the surface area on which chemical reactions occur, the inner membrane is folded, forming pockets called **cristae**. This inner membrane surrounds the matrix compartment, which contains the mitochondrial DNA, ribosomes, and many of the enzymes used in ATP production. Between the inner and outer membranes, we find the intermembrane space. This important compartment maintains the ion diffusion gradients required to generate ATP (Figure 8).

FIGURE 9 Chloroplast. The chloroplast is the energy powerhouse of the plant cell converting the sun’s energy and basic compounds into glucose, a sugar that can be broken down to release energy.

Chloroplasts perform **photosynthesis**: the conversion of light energy, CO_2, and water into carbohydrates like sugars and starch. Appropriate to their function, chloroplasts house **photosynthetic pigments**, such as chlorophyll molecules that absorb light energy. These pigments are contained within the inner membrane of the chloroplast, called the thylakoid membrane. The thylakoid membrane is shaped into towers called grana that look like stacks of dinner plates. Within the thylakoid, light energy is converted into ATP, which in turn powers the construction of sugars in the stroma. The stroma is the fluid-filled area between the thylakoid membrane and the outer membrane. Here in the stroma, CO_2

molecules are used as building blocks to construct carbohydrates (Figure 10).

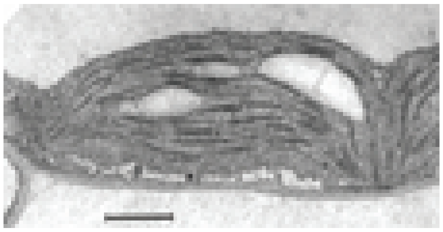


FIGURE 10 **Chloroplast micrograph.** Cross section of a chloroplast. Note the darkly-stained stacks of thylakoid membrane surrounded by the grayish-colored stroma.

SELF-TEST QUESTION

Why could we say that chloroplasts and mitochondria perform opposite functions?

Future perspectives.

Parkinson's disease has received a lot of attention over the last few years following the diagnosis of the actor Michael J. Fox. This devastating condition causes gradual reduction in muscle coordination and control within its victims. Parkinson's patients often lose the ability to walk, perform crafts, play sports, or even communicate.

Dr. Bin Zheng and his team at the Center for Neurologic Diseases at Harvard Medical School actively study Parkinson's disease. Their research suggests that there is a link between Parkinson's disease and mitochondria. After analyzing the DNA from more than 400 Parkinson's-afflicted brain samples, Dr. Zheng's group was able to link the onset of Parkinson's disease with genes that control mitochondrial function and energy production. They found that one specific group of these genes is turned off in many Parkinson's patients. If these genes are turned on, the nerve cell damage caused by Parkinson's disease can be greatly slowed or even prevented in some patients. What do these genes do in the cell? Interestingly, they contain the instructions for proteins that regulate the electron transport chain. The electron transport chain is a series of chemical reactions that produce ATP in the mitochondria. Therefore, it appears that mitochondrial functioning is directly related to Parkinson's disease. In response to this new finding, scientists are beginning to test drugs that will stimulate these mitochondria-controlling genes. In the future, Dr. Zheng's research may yield mitochondrial gene therapy that will hopefully prevent Parkinson's disease from progressing beyond its early stages.

Eukaryotic cells contain a number of other structures.

Peroxisomes are the hazardous waste-handlers of the cell (Figures 11 and 12). They contain enzymes that break down toxic molecules by removing hydrogen. The hydrogen atoms are then combined with molecular oxygen (O_2) within the peroxisome, producing hydrogen peroxide — this product is the inspiration for the organelle's name. Hydrogen peroxide is also toxic to cells, so the peroxisome must immediately convert the hydrogen peroxide to water. Peroxisomes are therefore a great example of the compartmentalization of harmful materials and volatile chemical reactions within a membrane-bound organelle.

FIGURE 11 **Peroxisomes.** The peroxisomes manage the hazardous waste in the cell converting hydrogen sources to hydrogen peroxide which is then converted to water.

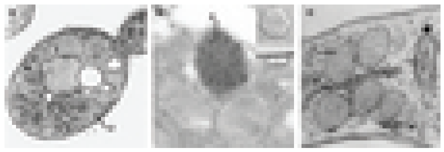


FIGURE 12 Peroxisomes under the microscope. Most cells usually contain several to hundreds of peroxisomes. The number of peroxisomes depends on the function of the cell. The "p" label indicates the location of the peroxisome in yeast (a), fungus (b), and a protist parasite (c).

Vacuoles are large vesicles derived from the ER and Golgi apparatus. They serve as the cell's storage tanks (Figure 13). Food vacuoles, as mentioned previously, form around food that is engulfed by cells. Many freshwater protists possess another kind of vacuole, called a contractile vacuole. The **contractile vacuole** controls the unrelenting osmosis of fresh water into cells by continually pumping out excess water.

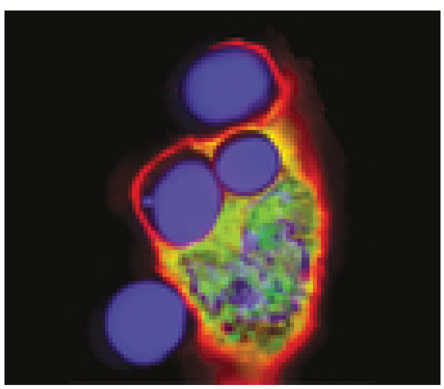


FIGURE 13 Vacuoles. Fluorescence microscopy shows a cell phagocytosing foreign particles (blue discs) and ingesting them into vacuoles with clearly defined membranes (red).

In plant cells, the large central vacuole, or **tonoplast**, also helps control osmotic balance. Plants store ions in the central vacuole, which, like the cytoplasm of the freshwater protists, causes water to diffuse into the cell. When filled with water, tonoplasts force the cytoplasm against the cell wall. This gives the plant cell, and therefore the entire plant, a firm and rigid structure. When water is not available, the tonoplasts shrink, the plant cells become more flaccid, and the plant wilts.

SELF-TEST QUESTION

Which two cellular structures give shape and support to plant cells?

Diverse Form and Function of Eukaryotic Cells

Though plant and animal cells are both eukaryotic, containing membrane-bound organelles, they have adapted functional differences according to their environment and organism function. Eukaryotic cells have evolved these membrane-bound organelles for more complex functionality and greater metabolic control. It is important to remember that cells are dynamic living things that move and change shape to accomplish their function.

In the animation below (Figure 14) notice how some of the organelles in the white blood cell change shape as they phagocytose a bacterium. When scientists examine real images of cells, they look nothing like this animation. We must remember that as cells move and act, the cell and its organelles appear differently depending on their state of activity. When we draw diagrams and illustrations to show this activity, it is merely an interpretation of a snapshot in time.

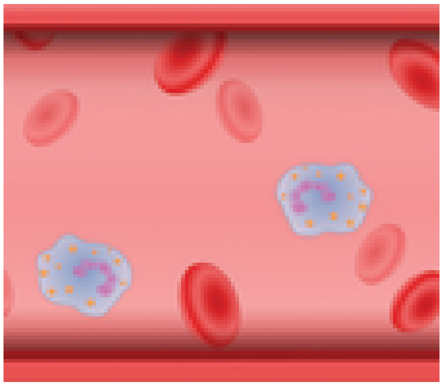


FIGURE 14 Eukaryotic phagocytosis. This figure is an interactive. To see it, visit your Principles of Biology online textbook.

SUMMARY

- **Identify cellular structures on a micrograph or diagram and name their functions.Identify cellular structures on a micrograph or diagram and name their functions.Relate the forms of different cell structures to their functions.Relate the forms of different cell structures to their functions.**

  Eukaryotic cells have a nucleus and membrane-bound organelles. None of these traits are possessed by prokaryotes. In addition, eukaryotes can reproduce sexually while prokaryotes only reproduce asexually. The nucleus contains chromosomes: long strands of DNA organized around histone proteins. DNA contains the instructions for creating all proteins required by the cell. The nucleus also contains the ribosome-subunit-producing area called the nucleolus. All structures of the nucleus are surrounded by the double-layered nuclear envelope. During protein synthesis the instructions for making a protein are transcribed from DNA onto a messenger RNA molecule. The mRNA then leaves the nucleus and fuses with a ribosome. The ribosome constructs the protein based on the instructions on the mRNA transcript. Proteins produced in the rough endoplasmic reticulum are often destined for secretion outside of the cell. These proteins are placed in a membranous transport sac called a transport vesicle, which travels to the Golgi apparatus. In the Golgi apparatus, the proteins are modified and then placed into another vesicle that releases the substance outside of the cell membrane via exocytosis. The smooth endoplasmic reticulum is responsible for synthesizing lipids and detoxifying the cell. Lysosomes are vesicles containing digestive enzymes. Lysosomes fuse with food vacuoles brought into the cell by endocytosis. The enzymes digest the food item, after which the nutritive molecules diffuse into the cytoplasm. Mitochondria break down carbohydrates to produce ATP. Peroxisomes contain enzymes that break down toxic substances within the cell.

- **Compare and contrast the structure and function of organelles found in animal and plant cells.Compare and contrast the structure and function of organelles found in animal and plant cells.**

Chloroplasts and mitochondria likely arose in eukaryotic cells through the endocytosis of early prokaryotes. Chloroplasts perform photosynthesis to build carbohydrates using CO_2, water, and the energy from sunlight. Plasmodesmata are gaps in the cell walls of adjacent plant cells that allow cell-to-cell communication to occur. Vacuoles are membrane-bound organelles used to store substances within the cell. The tonoplast of plant cells retains water to give the plant cell rigidity and support.

TEST YOUR KNOWLEDGE

Question 1

Eukaryotes possess which of the following traits?

a. Compartmentalization
b. Chromosomes that float freely in the cytoplasm
c. Membrane-bound organelles
d. Both the first and second answer choices
e. Both the first and third answer choices

Question 2

While observing plant cells in a biology lab, you see a group of misshapen cells. You insert a fluorescent protein in the cells that binds to proteins on the cell's vacuoles. Upon looking through microscopes, however, you see very small patches of fluorescent color. Which organelle is most likely malfunctioning and causing the collapse in cell shape?

a. chloroplasts
b. lysosome
c. mitochondria
d. rough endoplasmic reticulum
e. central vacuole/tonoplast

Question 3

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What role does the indicated structure play in protein synthesis?

a. Ribosomes enter the nucleus to bind with DNA, initiating protein synthesis.
b. DNA leaves the nucleus through a pore and binds with a ribosome, initiating protein synthesis.
c. mRNA enters the nucleus through a pore to bind with the nucleosome, initiating protein synthesis.
d. mRNA leaves the nucleus through a pore to bind with a ribosome, initiating protein synthesis.
e. Ribosomes enter the nucleus through a pore and bind with RNA, initiating protein synthesis.

Question 4

Which of the following is found in plant cells but not in animal cells?

a. central vacuole/tonoplast
b. lysosome
c. golgi apparatus
d. mitochondria
e. nucleus

Question 5

Which cell structure best exemplifies the compartmentalization of a chemical reaction that requires different environmental conditions from the cytoplasm?

a. vesicle
b. cytoskeleton
c. lysosome
d. ribosome
e. chromosome

5
Acids and Bases

KEY TERMS

LEARNING OBJECTIVES

- Explain how the dissociation of water forms hydrogen ions.
- Differentiate between hydrogen ions and hydronium ions.
- Explain the use of logarithms in the pH scale.
- Describe how a buffer contributes to pH stability.
- Give examples of how changes in acidity affect organisms.

Understanding Hydrogen Ions

Most people recognize water as a neutral substance. Yet water dissociates into ions that lead to the formation of acidic and basic solutions. Water, a polar covalent compound, consists of two hydrogen atoms and one oxygen atom. Each water molecule dissociates into two ions — a hydrogen-oxygen pair and a single hydrogen ion, or proton (Figure 1). The hydrogen-oxygen pair has a stronger electronegativity than the single hydrogen atom and therefore steals the electron from the single hydrogen, forming a **hydroxide ion**[OH^-]. The free **hydrogen ion** [H^+]. rarely occurs by itself in nature. In most cases, it combines with another water molecule to form a **hydronium ion** [H_3O^+].

SELF-TEST QUESTION

Describe what happens when a water molecule dissociates.

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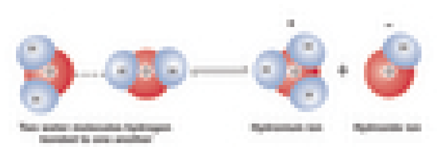

FIGURE 1 Dissociation of water. Water dissociates into a hydronium ion and a hydroxide ion.

All scientists use the same system to measure acids and bases.

What makes a solution acidic or basic? In pure water, the concentration of hydrogen ions (protons) and hydroxide ions is the same, approximately 10^{-7}. The product of the concentrations of these two ions is 10^{-14}. This product remains constant such that if the concentration of hydrogen ions increases, the concentration of hydroxide ions must decrease. The amount of change in ion concentrations is typically determined by the concentration of hydrogen ions and is described as the acidity of an aqueous solution. An acidic solution has a higher concentration of hydrogen ions (<10^{-7}), and vice versa for a basic solution (<10^{-7}).

$[H^+]\,[OH^-] = 10^{-14}$

To measure the level of acidity in a solution, scientists use the negative logarithm of the hydrogen ion concentration, called the **pH.**

$pH = -\log\,[H^+]$

For example, an acid adds hydrogen ions to a solution. As the concentration of hydrogen ions increases, the pH of the solution decreases. A base removes hydrogen ions from a solution. As the concentration of hydrogen ions decreases, the pH of the solution increases. A pH of 7 indicates a neutral solution. For example, a 0.1 N solution of hydrochloric acid (HCl) has a pH of 1.

▶ BIOSKILL Interpreting the pH Scale

As solutions trend away from the neutral pH, they become more acidic or basic. Because pH is measured on a log scale, each unit away from a neutral position marks a change in strength by a factor of 10. For example, baking soda has a pH of 8. Since a change of pH from 7 to 8 represents a change in strength of 10, baking soda is 10 times more basic than pure water. Bleach has a pH of 9. This substance is approximately 100 times more basic than pure water. The opposite end of the pH scale depicts acidic substances. A change of pH from 7 to 6 also represents a change in strength of 10 (Figure 2).

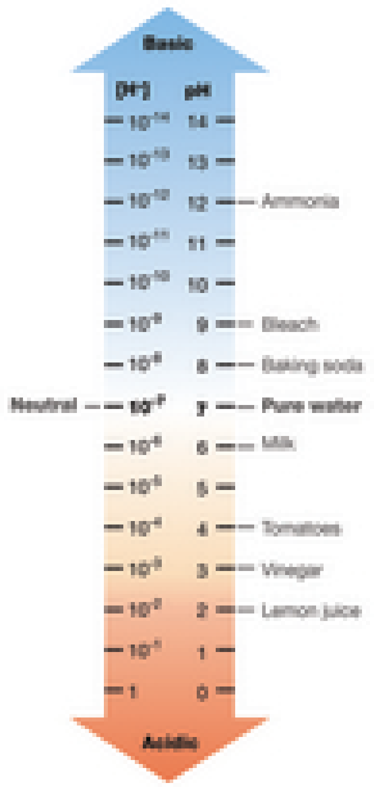

FIGURE 2 The pH scale Scientists measure how acidic or basic a substance is by assigning it a pH value. pH is a logarithmic measurement, meaning that a solution that has a pH of 9 is 100 times as basic as solution with a pH of 7.

SELF-TEST QUESTION

List where tomatoes, milk, and lemon juice fall on the pH scale from most acidic to most basic and describe their relative strength to one another.

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The transfer of hydrogen ions creates acids and bases.

Other compounds besides water can produce hydrogen ions. An **acid** is a substance that *increases* the concentration of hydrogen ions in a solution. A strong acid dissociates completely when placed in solution. Hydrogen chloride (HCl), an extremely strong acid, produces hydrogen ions and chloride ions when placed in an aqueous solution (Figure 3).

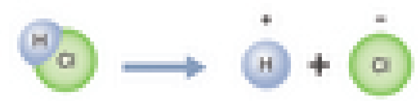

FIGURE 3 A Strong Acid Hydrogen chloride completely dissociates into chloride and hydrogen ions when placed in solution. The addition of many hydrogen ions causes an increase in acidity.

A weak acid also contributes hydrogen ions to a solution. An example of a weak acid, carbonic acid (H_2CO_3), dissociates into two ions— a bicarbonate ion (HCO_3^-) and a hydrogen ion (H^+). In a weak acid solution, there are many molecules of the weak acid, some of which dissociate and some of which do not (Figure 4).

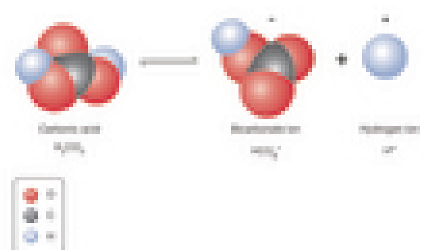

FIGURE 4 A weak acid. Carbonic acid dissociates, but not completely in solution. In other words, this weak acid contributes some hydrogen ions, causing a smaller increase in acidity.

SELF-TEST QUESTION

Describe how hydrochloric acid dissociates in water.

A **base** is a substance that *decreases* the concentration of hydrogen ions in a solution. It does so by bonding to the free hydrogen ions in the solution. Like a strong acid, a strong base dissociates completely in solution. An example of a strong base, sodium hydroxide (NaOH), dissociates into sodium ions and hydroxide ions (Figure 5). The hydroxide ions can then combine with any free hydrogen ions, forming water.

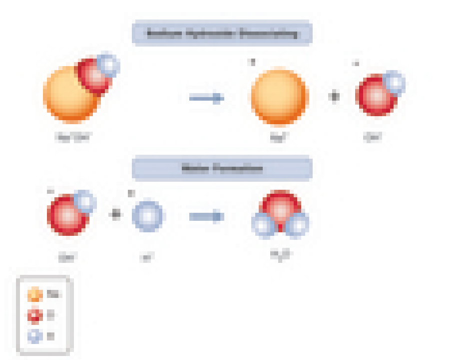

FIGURE 5 **Dissociation of sodium hydroxide.** After sodium hydroxide breaks down into ions, the hydroxide ion can bind with a hydrogen ion to form water.

A weak base also reduces the concentration of hydrogen ions in a solution. One weak base, ammonia (NH_3), combines with a hydrogen ion to form a ammonium ion (NH_4^+). Notice how ammonia can reduce acidity in a different way other than forming water.

The Effect of Changes in Acidity on Living Things

Most biological fluids have a pH between 6 and 8 — roughly neutral. A shift beyond this range can have negative effects on an organism due to cells' sensitivity to the concentration of hydrogen and hydroxide ions. For example, blood maintains a pH close to 7. A blood cell can only survive a few minutes if the pH moves above or below that number.

Cells must protect themselves against changes in acidity.

Many different metabolic processes generate or consume protons, which could lead to dangerous changes in pH. The structures and functions of most biological molecules are sensitive to changes in pH. Organisms and cells have developed systems to stabilize pH to prevent extreme changes. This system is possible because of the large number of weak acids and bases that can absorb excess protons or give up extra protons. These substances therefore act as buffers against pH changes. A **buffer** is a substance that minimizes changes in the hydrogen and hydroxide ions in a solution. A buffer works by accepting a hydrogen ion when a solution becomes too acidic and donating a hydrogen ion when the solution becomes too basic. A buffer typically consists of a weak acid and the corresponding weak base, though many different substances can act as buffers in biological systems. Maximal buffering occurs at a pH where half the compound is dissociated; different compounds reach this point at different characteristic pH values.

Human blood protects against shifts in pH by using carbon dioxide as a buffer. Carbon dioxide (CO_2) reacts with the water in blood plasma, producing the weak acid carbonic acid (H_2CO_3). Carbonic acid dissociates to form bicarbonate (HCO_3^-) and a hydrogen ion. If protons begin to accumulate, the reaction shifts back toward carbonic acid. If protons begin to diminish, more carbonic acid dissociates (Figure 6). Because the reaction is reversible, small shifts in the quantities of carbonic acid and bicarbonate can maintain a constant pH as hydrogen ions are added to or removed from the solution.

FIGURE 6 Carbonic acid as a buffer. Carbonic acid dissociates to form a hydroxide ion and a bicarbonate ion.

When the concentration of hydrogen ions decreases, blood pH increases. In response, the buffer reaction shifts to the right to produce more hydrogen ions. When the concentration of hydrogen ions increases, blood pH decreases. In response, the buffer reaction shifts to the left to consume hydrogen ions. This process maintains a pH within a normal range in order for blood cells to continue to function.

SELF-TEST QUESTION

Explain how blood maintains a stable pH.

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Changes in environmental pH affect ecosystems. Many human activities can alter the composition of the atmosphere. Carbon dioxide, sulfur dioxide and nitrous oxide are chemical pollutants that can be dangerous to organisms. For example, as the concentration of atmospheric pollutants increases, the pH of rain becomes altered. **Acid precipitation** describes rain, snow, or fog with a pH lower than 5.2. The acid precipitation affects many things detrimentally, including aquatic habitats and organisms, trees, terrestrial animals and soil composition. In general, acids corrode whatever they come into contact with.

SELF-TEST QUESTION

The northeastern United States has been adversely affected by acid precipitation. Explain how acid precipitation forms and how it affects the environment.

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Ocean Buffering System

Ocean acidification describes the decrease in ocean water pH. Click through Figure 7 to view how this phenomenon occurs.

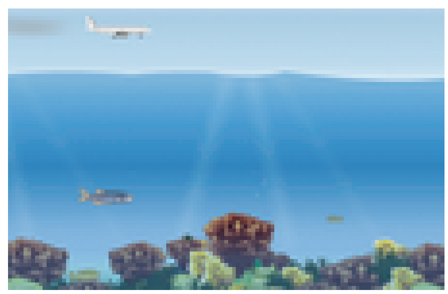

FIGURE 7 Ocean acidification. This figure is an interactive. To see it, visit your Principles of Biology online textbook.

Future perspectives. As carbon dioxide enters the ocean, ocean water pH decreases. To compensate, the weak acid buffer carbonic acid dissolves calcium carbonate. The free carbonate ion bonds with the excess hydrogen ions, stabilizing pH. Scientists fear that the dissolution of calcium carbonate could have profound impact on organisms living in the ocean.

Many organisms produce shells composed of calcium carbonate. The shells allow the organisms to remain buoyant in the ocean, provide protection, and help organisms maintain their internal chemistry. As the ocean pH falls, the shells of these organisms begin to dissolve to buffer the acidity. Organisms vulnerable to low pH include copepods, snails, sea urchins, and brittlestars. The change in pH can also affect these organisms' ability to grow or reproduce. Although small, these organisms mark the base of the food chain. As their numbers diminish, other organisms in the ocean higher in the food chain become affected.

How can ocean acidification be stopped? Scientists believe one of the most effective ways to stop ocean acidification is to shift away from a fossil fuel-based energy economy. One way to slow the output of carbon dioxide into the atmosphere is to declare carbon dioxide as a pollutant under the Clean Air Act. To help the affected organisms, scientists also suggest establishing additional marine protected areas where vulnerable species can grow and reproduce in a protected environment. Regulating fishing limits may also improve species recovery.

▶ CAREERS Chemical Oceanographers

Chemical oceanographers are scientists who apply their knowledge of chemistry to the ocean. These scientists study the compounds in ocean water, including salt, nutrients, and more recently pollutants. They study the relationships and interaction between these various chemical compounds. They also examine the effect of ocean chemistry on organisms living in the ocean. Their expertise is of particular importance as concerns grow over ocean acidification.

Chemical oceanography involves many disciplines. Chemical oceanographers must have a fundamental understanding of a variety of scientific disciplines to address questions that affect society. They constantly monitor the ocean to collect data to answer important scientific questions. They also work with other scientists and engineers to develop instruments to improve data collection.

SUMMARY

- **Explain how the dissociation of water forms hydrogen ions.Explain how the dissociation of water forms hydrogen ions.**
  Water is a polar covalent compound composed of two hydrogen atoms and one oxygen atom. When a water molecule dissociates, it produces two ions. The hydroxide ion has a stronger electronegativity than the hydrogen ion and takes the electron.

- **Differentiate between hydrogen ions and hydronium ions.Differentiate between hydrogen ions and hydronium ions.**
  A hydrogen ion, or proton, H^+, rarely remains isolated in nature. It often combines with another water molecule to form a hydronium ion, H_3O^+ .

- **Explain the use of logarithms in the pH scale.Explain the use of logarithms in the pH scale.**
  Scientists place the relative strength of acids and bases on the pH scale. pH describes the negative logarithmic concentration of hydrogen ions in a solution. The pH scale ranges from 0 to 14. A pH of 7 describes a neutral solution with an equal number of hydrogen ions and hydroxide ions. A base has a pH greater than 7, and an acid has a pH that is less than 7. A 1-point change in pH is equivalent to a magnitude change in concentration of protons or hydrogen ions. For example, a solution with a pH of 7 has 10 times more hydrogen ions than a solution with a pH of 8.

- **Describe how a buffer contributes to pH stability.Describe how a buffer contributes to pH stability.**
  A buffer is a weak acid, in combination with a corresponding weak base, that stabilizes the pH of a solution. When the concentration of hydrogen ions increases in the solution, the weak acid shifts to the left of the reaction and consumes a portion of the excess acid. When the

concentration of hydrogen ions decreases, the weak acid reaction shifts to the right and contributes hydrogen ions to the solution. A buffer is essential for many biological systems, because it stabilizes pH within a range where a cell can function. Human blood is a buffered system. The ocean is also a buffered system.

▸ **Give examples of how changes in acidity affect organisms.Give examples of how changes in acidity affect organisms.**

Increased burning of fossil fuels injects carbon dioxide into the atmosphere. As the concentration of atmospheric carbon dioxide increases, more carbon dioxide is pumped into freshwater and saltwater systems. When carbon dioxide reacts with water, it forms carbonic acid. This weak acid can gradually lower the pH of water systems, resulting in ocean acidification and acid precipitation. Both scenarios affect plants and animals living in and near the water systems. Scientists are working with policy makers and industry to find ways to curb the use of fossil fuels and protect the environment.

TEST YOUR KNOWLEDGE

Question 1

Which of the following describes how a hydronium ion forms?

a. $H^+ + H_2O$

b. $H^+ + OH^-$

c. $H^+ + Cl^-$

d. $H^+ + NH_3$

e. None of the above

Question 2

Which substance dissociates completely to reduce the concentration of hydrogen ions in a solution?

a. NaOH

b. H_2O

c. HCl

d. NH_3

e. CO_3^{+2}

Question 3

Oven cleaner has a higher pH than baking soda. This is because oven cleaner has

a. a greater concentration of hydroxide ions.

b. a lower concentration of hydroxide ions.

c. a balance of hydronium and hydroxide ions.

d. a complete lack of hydrogen ions.

e. None of the above

Question 4

A buffer is typically a

a. weak acid

b. strong acid

c. strong base

d. hydronium ion

e. none of the above

Question 5

Which factors contribute to ocean acidification?

a. coal-burning power plants

b. automobiles

c. natural gas processing plant

d. air travel

e. all of the above

6

Proteins

Proteins are a diverse group of polymers that play a critical role in nearly all cell functions.

KEY TERMS

amino acid • Monomer composed of central carbon atom surrounded by an amino group, a carboxyl group, a hydrogen atom, and a side chain. The different amino acids are determined by differences in the side chains.

denaturation • Breakdown of the secondary and tertiary structure of a protein by exposure to environmental stresses, making it nonfunctional.

protein • Class of biologically important molecules made up of one or more peptides; most diverse form and function of the biological molecule groups.

LEARNING OBJECTIVES

- Describe the chemical structure of an amino acid.
- Explain the four levels of protein structure.
- Associate protein structure to function.

Nineteenth century scientists applied the name *proteins* to define the "primary" class of molecules in living things, after the Greek word "proteus." Were the scientists justified in applying this authoritative label given that they lacked sophisticated technologies for biochemical analysis? Decades of protein research vindicated their pronouncement, which shed light on the critical role of proteins in nearly every cell function and structure.

Four Levels of Protein Structure

The human body contains tens of thousands of proteins. Why does the body need so many? Proteins are sophisticated and complex structures. Proteins carry out most of the cell's varied life functions and contribute to the diversity of cell structures. Table 1 summarizes the relationship between major protein functions and structure.

Major protein function	**Structural significance**
Metabolism — catalyzing chemical reactions	Enzymes are **catalysts**, or molecules that lower the energy required for a chemical reaction to proceed. Most enzymes are proteins. Proteins catalyze reactions by binding to reactants. A protein binding site must perfectly match the reactant. The cell needs thousands of different enzymes to catalyze all of its metabolic reactions.
Signaling — delivering chemical messages throughout the body	Proteins serve as both message transmitters and receivers, linked by structure. For example, brain cells contain multiple receptors for messenger molecules called neurotransmitters. A receptor's structure allows it to bind to a specific neurotransmitter.
Transport — carrying molecules throughout the body	Proteins transport nutrients, waste products, and other substances between cells, within cells, and across cell membranes. Each transport protein has a unique structure to bind to a specific substance, just as hemoglobin in red blood cells binds to oxygen to transport it throughout the body.
Structure — forming organelles and other cell structures as well as the basis of macroscopic structures	Proteins provide structural support at several levels — organelles, cells, and organs. Organelle proteins provide structure and carry out related functions. Proteins determine a cell's overall shape and form as well as the form of tissues and organs such as skin.
Movement — moving substances, cells, and body parts	Protein structure controls contractile and motor functions. These proteins can move substances within cells. Coordinated movements in tissue cells produce macroscopic movements of larger body parts, like when muscle tissue contracts to move bone.
Defense — defending the body against disease-causing agents	Proteins in the immune system such as antibodies bind to and destroy invasive bacteria and viruses. The structure of an antibody is specific to a certain bacteria or virus. The body builds immunity by producing new antibodies for each new bacteria and virus it encounters.

Table 1: Major protein functions. A protein's structure is intimately linked to its function.

At the most basic level, **proteins** are made up of one or more polypeptides. **Polypeptides** are chains of amino acids linked together by peptide bonds. How can these chains form thousands of different molecular structures? The protein chains, or polypeptides, form up to four layers of structure resulting in structural diversity.

Primary structure: Amino acids link together to form a linear polypeptide.

The **primary structure** of a protein is a linear chain of amino acids. An **amino acid**monomer is composed of a central carbonatom, called the alpha (α) carbon. An *alpha carbon* bonds to

1. an amino group,
2. a side chain or R-group,
3. a carboxyl group, and
4. a hydrogen atom (Figure 1).

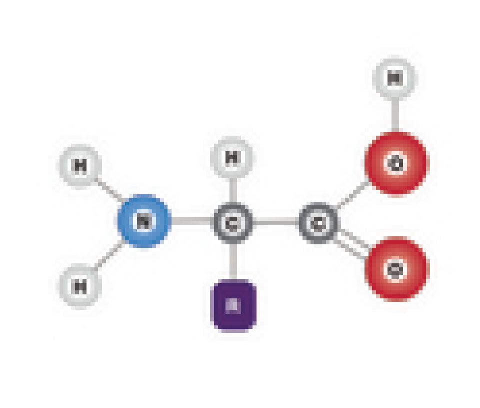

FIGURE 1 Amino acid structure. An amino acid contains an amino group, a side chain, a carboxyl group, and a hydrogen atom all bound to a central carbon atom.

Amino acids differ by the type of attached side chain. Amazingly, cells use only 20 amino acids (Figure 2), to build the many thousands of proteins needed to maintain life functions. How does this work?

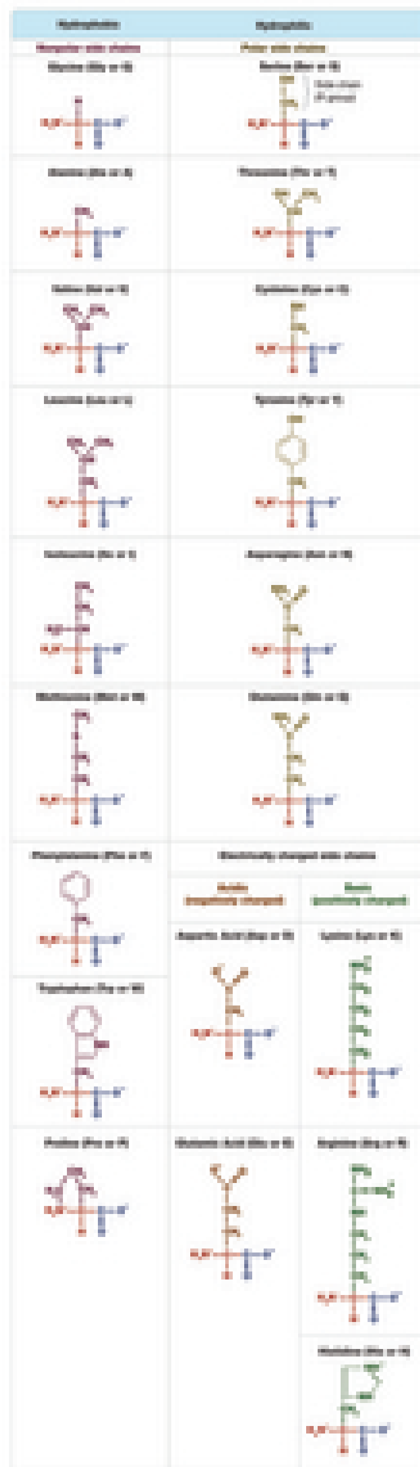

FIGURE 2 The 20 amino acids. The amino group and the carboxyl group are always the same, but the R-group differs in each of the 20 amino acids.

Notice that the R-groups have different states of electronegativity, which affect their chemical behavior. Recall that nonpolar molecules are hydrophobic and tend to bond with only nonpolar molecules. Polar molecules are hydrophilic and bond easily with water. Charged molecules can attract oppositely charged molecules. The amino acids combine in different orders, which changes the electronegativities of the molecules and how different parts of the chain bind together to form tertiary and quaternary levels of structure. Mathematically, the 20 amino acids can combine to form millions of different proteins in chains of varying length.

How does the cell link the amino acids together? A carboxyl group can bond to an amino group by a dehydration reaction-the removal of a water molecule. This reaction forms a peptide bond. Dehydration reactions link amino acids into polypeptide chains. A polypeptide backbone forms from a chain of alpha carbons which are carboxyl and amino groups linked by peptide bonds, excluding the R-groups. **Peptide bonds** are the chemical bonds of carbon to nitrogen after dehydration (Figure 3). Side groups, as their name suggests, stick out to the sides of the backbone. Polypeptide chains range in length from a few amino acids to more than a thousand.

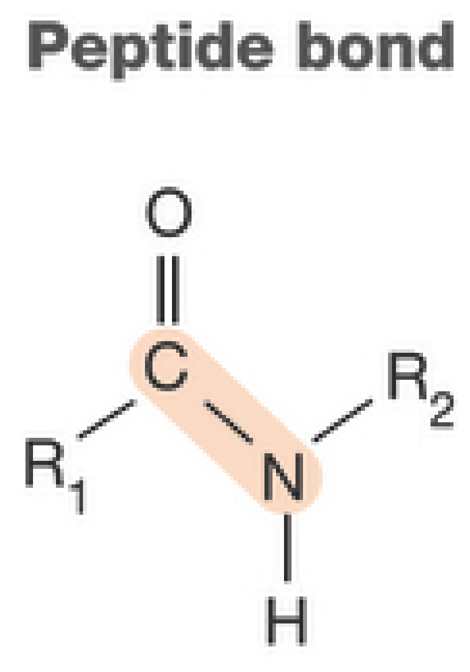

FIGURE 3 **Peptide bond.** A peptide bond is formed between the carboxyl and amino groups of adjacent amino acids.

Secondary structure: Hydrogen bonds between atoms in the polypeptide backbone create a folded or coiled shape.

Segments of the polypeptide chain can form coiled or folded patterns, called the **secondary structure**. The chemical tendencies of R-groups determine tertiary and quaternary structures. What, then, determines the formation of secondary structures?

Hydrogen bonds between repeating units in the polypeptide chain backbone produce a coiled and folded patterns. However, the amino acid sequence does influence the formation of secondary structure attributable in part to geometric variations between amino acids. Different segments of a polypeptide chain can form different secondary structures. Some segments may lack secondary structure.

Consider two types of secondary structure in detail. Looping coils called **α helices** develop from the hydrogen bonds that form between the oxygen of a carboxyl group and the hydrogen of the fourth amino group in the chain. Folded patterns called **β pleated sheets** form when two or more strands of a polypeptide line up parallel to one another. Hydrogen bonds form between adjacent carboxyl and amino groups. Hydrogen bonds that form between elements in slightly different planes produce a pleated pattern. The hydrogen bonds also serve to hold the parallel strands together in a sheet-like structure (Figure 4).

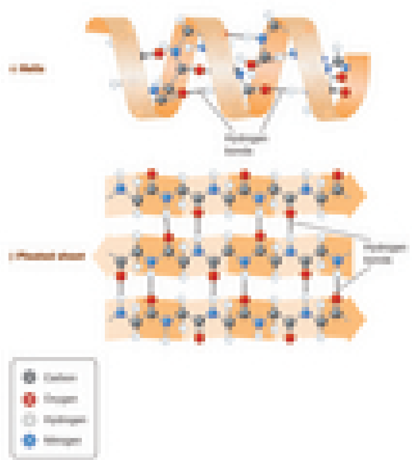

FIGURE 4 **Secondary structures.** Hydrogen bonds between amino and carboxyl groups hold together structures such as α helices and β pleated sheets. In ribbon diagrams, the flat arrow points to the carboxyl end of the polypeptide.

Tertiary structure: Interactions between side chains create a three-dimensional shape.

Tertiary structure is the main, three-dimensional shape of a polypeptide unit. This shape results from, and is held together by, bonds and interactions between R-groups and between R-groups and elements on the backbone. These bonds and interactions include:

- **Hydrophobic effect**— clustering of nonpolar side chains or burial of the core of the protein molecule in a manner that reduces contact with water molecules in the surrounding fluid.
- Hydrogen bonding-hydrogen atoms in R-groups can form hydrogen bonds. Hydrogen bonds can also form between R-group hydrogen atoms and oxygen atoms in the backbone.
- Covalent bonding-two sulfur atoms can bond together covalently. This is most likely to occur at the terminal sulfur atoms in cysteine. Scientists often refer to these sulfur — sulfur bonds as **disulfide bridges** because of their structural linkage role.
- Ionic bonding-ions in oppositely charged side groups can form ionic bonds.
- van der Waal interactions-weak electrostatic forces can add stability to the structure once it is already in place.

A complex web of these interactions results from the ordering of amino acids in a polypeptide unit, giving each different polypeptide unit a unique tertiary structure. Click on the image in Figure 5 to see an animation of how tertiary structure builds on primary and secondary structure.

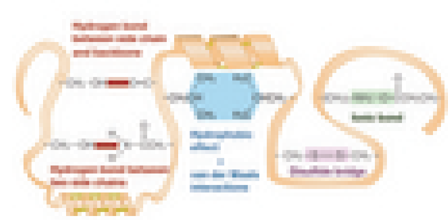

FIGURE 5 **Primary, secondary and tertiary structure. This figure is an interactive. To see it, visit your Principles of Biology online textbook.**

Denaturation is the breakdown of secondary and tertiary protein structures as a result of external stresses such as temperature or an acid or base.

SELF-TEST QUESTION

How does a protein's tertiary structure depend on its primary structure?

Quaternary structure: Associations of polypeptides form a functional protein.

Many proteins contain multiple polypeptide units assembled into a functional macromolecule, which may include multiple copies of the same polypeptide unit, different polypeptide units, or both. These proteins have a**quaternary structure**resulting from the aggregation of the tertiary structures that may be the same subunits or different subunits. Quaternary structure uses the same palette of bonds and interactions used to form tertiary structure; only the bonds and interactions occur between atoms of separate polypeptide units.

Hemoglobin is an oxygen-transport protein found in red blood cells. The four polypeptide units form a quaternary structure, sometimes called a *tetramer*. Click on the interactive diagram in Figure 6 to investigate the levels of structure in hemoglobin.

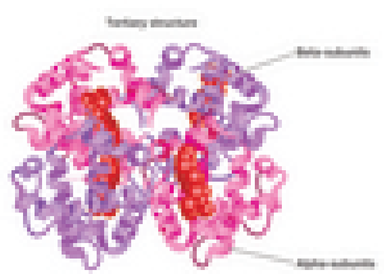

FIGURE 6 Layers of structure in hemoglobin. This figure is an interactive. To see it, visit your Principles of Biology online textbook.

Protein Function

Table 1 provides a wide range of critical functions carried out by proteins and the intimate link between a protein's structure and its function. Let's take a closer look at examples of protein function.

Collagen is one of the most ubiquitous proteins in the bodies of vertebrates. It plays an important role in connective tissues, including cartilage, tendons as well as bone and skin tissues. Collagen is made up of three identical α-helices woven into a durable triple helix (Figure 7). This quaternary structure is stabilized by the hydrogen bonds that form between each of the three initial polypeptide chains.

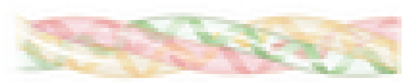

FIGURE 7 Structure of collagen. The fibrous structure of collagen supports its function in connective tissue. Three polypeptides twisted into alpha-helices are bound together in a durable triple-helix by hydrogen bonds.

SELF-TEST QUESTION

How does the structure of collagen relate to its function?

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Future perspectives.

Receptors in brain cells receive communications from the body, supporting the brain's role in maintaining homeostasis. Researcher Eric Gouaux and his colleagues recently completed a map of a complex and very important brain receptor called the glutamate receptor. When the neurotransmitter glutamate binds to the receptor, an "ion channel" opens in the neuronal membrane. This allows ions to flow across the membrane, thereby transmitting an electrical pulse down the nerve (Figure 8). At the top are two prongs, which can bend to modify the receptor. Below this is the area where glutamate binds, opening the ion channel located at the bottom. Gouaux likened the channel structure to "a Mayan temple." Gouaux also reports his surprise at finding out that the receptor is made up of four subunits that are chemically identical but are folded differently. "The completely astonishing thing was that two subunits are completely different from the other two. That difference was totally unanticipated." Resolving the structure of the glutamate receptor will allow researchers to, among other things, develop drugs to treat neurological pathologies that occur as a result of problems along pathways involving this ubiquitous receptor.

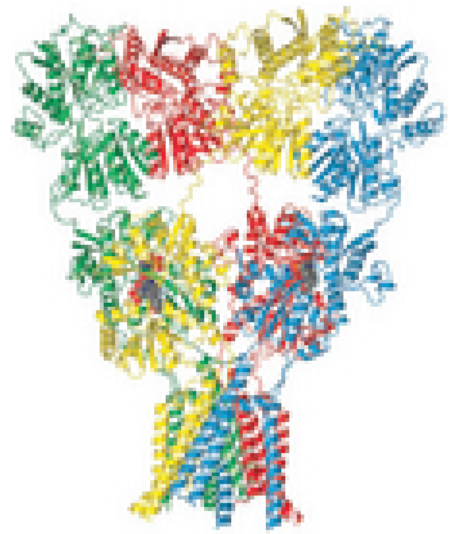

FIGURE 8 Structure of the glutamate receptor. Glutamate has two prong-shaped subunits at the top that can bend and attach to a receptor modifying the receptor’s structure and opening the ion channel at the bottom.

▶ BIOSKILL X-ray Crystallography is an Important Technique in Determining Protein Structure

Scientists use **x-ray crystallography** — a technique that measures the angle and intensity with which x-rays are diffracted when passing through a crystalline structure to determine the structures of many biological molecules. Most famously, Rosalind Franklin (1920–1958) used this technique in the discovery of DNA's double helix (Figure 9).

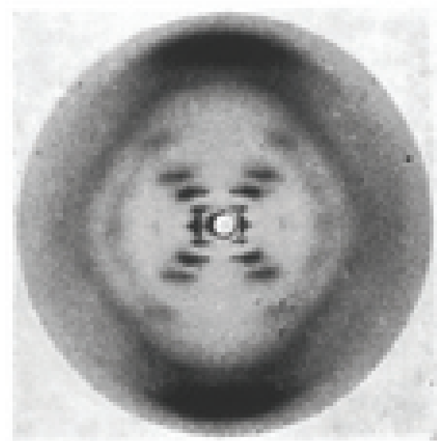

FIGURE 9 X-ray diffraction. Rosalind Franklin showed DNA with x-ray diffraction in 1953. This process and image became the foundation for establishing the shape of many other biological molecules including proteins.

Dorothy Crowfoot Hodgkin (1910–1994), Franklin's contemporary, developed the methodological and technological path for protein structure discovery by advancing techniques for resolving fine details of macromolecules. Hodgkin's important discoveries, including the structures of penicillin, insulin, and vitamin B_{12}, won her a Nobel Prize in 1964 and led to medical advances that directly improved the health of millions. A technological pioneer in biochemistry, she was the first person to use an electronic computer-an early IBM-for biochemical analysis in the 1940s. She used the computer to perform calculations of x-ray output data. Hodgkin pioneered techniques for developing three-dimensional models of biological molecules. Today, tens of thousands of proteins have been analyzed by x-ray crystallography at angstrom-level resolution. Researchers use the x-ray crystallography data to produce three-dimensional models.

First, researchers crystallize the proteins. Although softer and more flexible than mineral crystals, biological molecules are highly ordered and patterned. To crystallize proteins, researchers prepare a concentrated, pure solution of the protein sample and allow it to nucleate and crystallize on a slide. Then researchers bombard the protein crystals with x-rays, which diffract when they interact with atoms in the crystal. By measuring the locations of x-rays exiting the crystal, researchers can, with a considerable amount of mathematical computation, calculate a map of electron densities in the crystal. Peaks in the electron density map correspond to the atomic positions in the molecule and intermolecular distances. From that map, researchers can construct a three-dimensional model of the molecule (Figure 10).

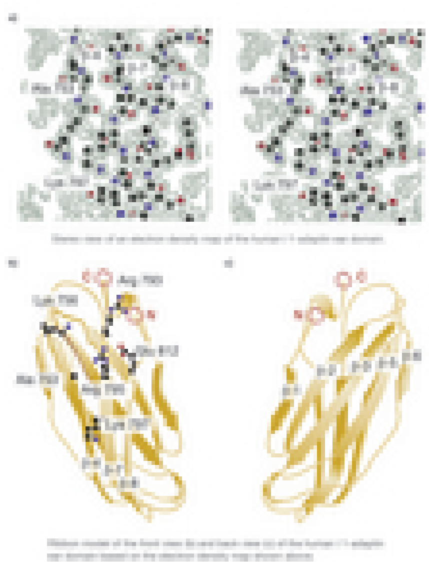

FIGURE 10 Comparing electron density maps with three-dimensional ribbon models. Pay attention to the locations of the structures on the electron map marked by researchers and where these locations correspond to the model. Scientists interpret the electron density map to identify the locations of amino acids such as Ala 753 as seen in panel A to get the structure of and position of the same part of the protein in panel B.

SELF-TEST QUESTION

Describe the secondary and tertiary structure of this protein.

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Future perspectives.

In the 1990s, research confirmed the existence of strange infectious proteins called prions. These highly unusual pathogens lack genetic material. Modified prion proteins cause fatal neurodegenerative diseases such as bovine spongiform encephalopathy (BSE, commonly called mad cow disease) and Creutzfeldt-Jakob disease (CJD). A person can be infected with these diseases by ingesting brain matter that contains the infectious proteins. Researchers have discovered that normal cellular prion protein (PrPC), which is naturally occurring in the brain, is converted structurally into the infectious prion protein PrPSc through a process that increases its beta-sheet content. Many aspects of prions remain mysterious. For example, some evidence suggests that normal PrP plays a protective role in the maintenance of myelin nerve sheaths protecting the brain from developing plaques that are a symptom of Alzheimer's disease. Researchers are still working to shed light on prions and their role in neurological disorders.

SUMMARY

- **Describe the chemical structure of an amino acid.Describe the chemical structure of an amino acid.**
  An amino acid is a monomer composed of a central carbon atom, or alpha (α) carbon, surrounded by an amino group, a side chain or R-group, a carboxyl group, and a hydrogen atom. Twenty different amino acids exist, each with a unique R-group.
- **Explain the four levels of protein structure.Explain the four levels of protein structure.**
  Protein structure occurs at four levels. Primary structure is the order of amino acids linked together in a polypeptide chain. These chains can form secondary structures: coiled or pleated sheets held together by hydrogen bonds in the backbone. Tertiary structures emerge from

chemical bonds and interactions among R-groups and between R-groups and atoms on the backbone. Proteins with combinations of multiple polypeptide units have quaternary structure resulting from the aggregation of the tertiary structures.

- **Associate protein structure to function.Associate protein structure to function.**
  The structure and function of proteins are inextricably linked. Proteins perform multiple critical functions, including transport, signaling, movement, immune defense, and structural support. Each of the many thousands of proteins in a typical vertebrate has a unique structure related to its specific function.

TEST YOUR KNOWLEDGE

Question 1

Each of the 20 different amino acids has a unique

a. α – carbon
b. Amino group
c. Carboxyl group
d. Side group
e. All of the above

Question 2

Which of these are secondary structures of proteins?

a. α-helices
b. Amino groups
c. Polypeptide chains
d. Polypeptide units
e. None of the above

Question 3

Which level(s) of protein structure are determined by the order of amino acids in the polypeptide chain?

a. Primary structure
b. Secondary structure
c. Tertiary structure
d. Quaternary structure
e. All of the above

Question 4

What is a possible function of disulfide bridges in the tertiary structure of a protein?

a. Holding together amino acids
b. Forming β-pleated sheets
c. Holding together different α-helices
d. All of the above
e. None of the above

Question 5

Which best describes the relationship between the structure of receptor proteins to the signal molecules?

a. Each receptor protein has a unique structure that allows it to bind to a specific signal molecule.
b. Receptor proteins all have similar structures so that the cell can use them to receive a wide variety of signal molecules.
c. Receptor proteins have changeable structures that allow them to receive many different signal molecules.
d. Receptor proteins have an undefined globular structure until a signal molecule binds to it.
e. None of the above

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