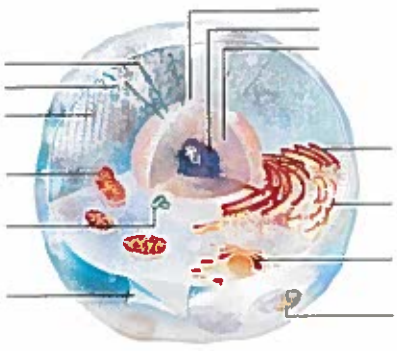
Table 4.2 Summary of Typical Components of Prokaryotic and Eukaryotic Cells

Cell Component	Function	Prokaryotic	Eukaryotic			
		Bacteria, Archaea	Protists	Fungi	Plants	Animals
Cell wall	Protection, structural support	✓*	✓*	✓	✓	*None*
Plasma membrane	Control of substances moving into and out of cell	✓	✓	✓	✓	✓
Nucleus	Physical separation and organization of DNA	*None*	✓	✓	✓	✓
DNA	Encoding of hereditary information	✓	✓	✓	✓	✓
RNA	Transcription, translation of DNA messages into polypeptide chains of specific proteins	✓	✓	✓	✓	✓
Nucleolus	Assembly of subunits of ribosomes	*None*	✓	✓	✓	✓
Ribosome	Protein synthesis	✓	✓	✓	✓	✓
Endoplasmic reticulum (ER)	Initial modification of many of the newly forming polypeptide chains of proteins; lipid synthesis	*None*	✓	✓	✓	✓
Golgi body	Final modification of proteins, lipids; sorting and packaging them for use inside cell or for export	*None*	✓	✓	✓	✓
Lysosome	Intracellular digestion	*None*	✓	✓*	✓*	✓
Mitochondrion	ATP formation	**	✓	✓	✓	✓
Photosynthetic pigments	Light-energy conversion	✓*	✓*	*None*	✓	*None*
Chloroplast	Photosynthesis; some starch storage	*None*	✓*	*None*	✓	*None*
Central vacuole	Increasing cell surface area; storage	*None*	*None*	✓*	✓	*None*
Bacterial flagellum	Locomotion through fluid surroundings	✓*	*None*	*None*	*None*	*None*
Flagellum or cilium with 9+2 microtubular array	Locomotion through or motion within fluid surroundings	*None*	✓*	✓*	✓*	✓
Complex cytoskeleton	Cell shape; internal organization; basis of cell movement and, in many cells, locomotion	*Rudimentary***	✓*	✓*	✓*	✓

*Known to be present in cells of at least some groups.
**Many groups use oxygen-requiring (aerobic) pathways of ATP formation, but mitochondria are not involved.
***Protein filaments form a simple scaffold that helps support the cell wall in at least some species.

airways to their lungs. Bacteria form huge populations in the thick mucus. Their metabolic by-products and the inflammation they trigger combine to damage tissues. Males affected by the syndrome can produce sperm, but they are infertile (Figure 4.30). Some have still become fathers with the help of a procedure that injects sperm cells directly into eggs. Explain how an abnormal dynein molecule could cause the observed effects.

4. As they grow and develop, many kinds of plant cells form a secondary wall on the *inner* surface of the primary wall that formed earlier. Speculate on the reason why the secondary wall does not form on the outside.
5. Reflect on Table 4.2. Notice how most prokaryotes, all plant cells, and many protist and fungal cells have walls, and that animal cells have none. Why do you suppose animal cells alone do not form walls?



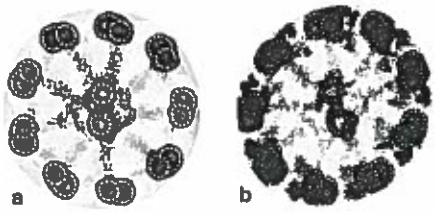


Figure 4.30 Cross-section through the flagellum of a sperm cell from (**a**) a male affected by Kartagener syndrome and (**b**) an unaffected male. Check the dynein arms projecting from the microtubule pairs.

5 A CLOSER LOOK AT CELL MEMBRANES

One Bad Transporter and Cystic Fibrosis

Each living cell is engaged in risky business. Think of how it has to move something as ordinary as water in one direction or the other across its plasma membrane. If all goes well, it takes in or sends out water in just the right amounts—not too little, not too much. But who is to say life always goes well?

CFTR is one of the protein channels across the plasma membrane of epithelial cells. Sheets of these cells line sweat glands, airways and sinuses, and ducts in the digestive and reproductive systems. Chloride ions move through them, and water follows to form a thin film on the free surface of the linings. Mucus, which lubricates tissues and helps prevent infection, slides freely on the watery film.

Sometimes mutation changes how CFTR works. Not enough chloride and water reach the lining's free surface, so the film does not form. Mucus dries out and thickens. Among other things, it clogs ducts from the pancreas, so digestive enzymes cannot get to the small intestine where most food is digested and absorbed. Weight loss follows. Sweat glands secrete too much salt and alter the water–salt balance for the internal environment, which affects the heart and other organs. Males become sterile.

Problems also develop in airways to the lungs, where ciliated cells are supposed to sweep away bacteria and other particles stuck in mucus. Now the mucus makes cilia too sticky, and **biofilms** form. Biofilms are microbial populations anchored to one epithelial lining or another by stiff, sticky polysaccharides of their own making. They resist the body's defenses and antibiotics. *Pseudomonas aeruginosa*, the most efficient of the colonizers, cause low-grade infections that may last for years. Most patients can expect to live no longer than thirty years, at which time their lungs usually fail. At present there is no cure.

These symptoms—outcomes of mutation in the CFTR protein—characterize *cystic fibrosis* (CF), the most common fatal genetic disorder in the United States. More than 10 million people carry a mutant form of the gene. CF develops when they inherited a mutated gene from both parents. This happens in about 1 of every 3,300 live births (Figure 5.1).

CFTR is one of the ABC transporters in all prokaryotic and eukaryotic cells (Figure 5.2). Some of these proteins, including CFTR, are channels that let hydrophobic substances cross a membrane. Others pump substances across. By their action, some types affect what other membrane proteins are doing.

In all but 10 percent of CF patients, loss of a single amino acid during protein synthesis causes the disorder. Before a new CFTR protein is shipped to the plasma membrane, it is supposed to be modified in that endomembrane system you read about in Chapter 4. Copies of the mutant protein do enter the ER, but enzymes destroy 99 percent of them before they reach Golgi bodies. Thus few chloride channels reach their normal destinations.

Mutant CFTR may also contribute to the sinus problems of an estimated 30 million people in the United States

Figure 5.1 Child affected by cystic fibrosis, or CF, who each day endures chest thumps, back thumps, and repositionings to dislodge thick mucus that collects in airways to the lungs. Symptoms vary from one affected individual to the next, partly because the abnormal protein that causes CF has mutated in more than 500 ways. Environmental factors and a person's genetic makeup also affect the outcome.

IMPACTS, ISSUES

Figure 5.2 Model for part of an ABC transporter, a category of membrane proteins that includes CFTR. The parts shown here are ATP-driven motors that can widen an ion channel across the plasma membrane.

alone. In *sinusitis*, the linings of cavities inside the skull (around the nose) are chronically inflamed. In one study at Johns Hopkins University, researchers found a single copy of a mutant CFTR gene in 10 of 147 sinusitis patients. And they were only looking for 16 of more than 500 known mutant forms of the CFTR gene!

Think about it. A startling percentage of the human population can develop problems when the copies of even one kind of membrane protein don't work.

Your life depends on the functions of thousands of kinds of proteins and other molecules. Breathing, eating, moving, sleeping, crying, thinking—whatever you might be doing starts at the level of individual cells. And each cell functions properly only if it can be responsive to conditions in the microenvironments on both sides of its plasma membrane. Each eukaryotic cell also has to be responsive to conditions on both sides of its organelle membranes. *Cell membranes*—these thin boundary layers make the difference between organization and chaos.

How Would You Vote?

The ability to detect mutant genes that cause severe disorders raises bioethical questions. Should we encourage the mass screening of prospective parents for mutant genes that cause cystic fibrosis? Should society encourage women to give birth only if their child will not develop severe medical problems? See BiologyNow for details, then vote online.

Key Concepts

MEMBRANE STRUCTURE AND FUNCTION

Cell membranes have a thin, oily, water-insoluble lipid bilayer that functions as a boundary between the outside environment and the cell interior.

The lipid bilayer consists primarily of phospholipids. Many diverse proteins are embedded in the bilayer or are positioned at one of its surfaces. The proteins carry out most membrane functions, such as transport across the bilayer and cell-to-cell recognition. Sections 5.1, 5.2

DIFFUSION ACROSS MEMBRANES

Metabolism requires concentration gradients that drive the directional movements of substances. Cells have built-in mechanisms for increasing or decreasing water and solute concentrations across the plasma membrane and internal cell membranes. Section 5.3

TRANSPORT ACROSS MEMBRANES

In passive transport, a solute crosses a membrane by diffusing through a channel inside a transport protein. In active transport, a different kind of transport protein pumps the solute across a membrane, against its concentration gradient. An input of energy, typically from ATP, jump-starts active transport. Section 5.4

OSMOSIS

By a molecular behavior called osmosis, water diffuses across any selectively permeable membrane to a region where its concentration is lower. Section 5.5

MEMBRANE TRAFFIC

Larger packets of substances and, in some cases, engulfed cells move across the plasma membrane by processes of endocytosis and exocytosis. Membrane cycling pathways extend from the plasma membrane to organelles of the endomembrane system. Section 5.6

Links to Earlier Concepts

Reflect again on the road map in Section 1.1. Here you will see how complex lipids and proteins become organized in cell membranes (3.4, 4.1). Remember the different levels of protein organization? You will consider some examples of how protein structure translates into specific functions (3.6). You will be applying your knowledge of the properties of water molecules to the movement of water across membranes (2.5). You will see how the endomembrane system (4.6) helps cycle membranes.

5.1 Organization of Cell Membranes

LINKS TO SECTIONS 3.4, 4.1

Cell membranes consist of a lipid bilayer in which many different kinds of proteins are embedded. The membrane is a continuous boundary layer that selectively controls the flow of substances across it.

REVISITING THE LIPID BILAYER

Think back on the phospholipids, the most abundant components of cell membranes (Section 3.4 and Figure 5.3*a*). Each has a phosphate-containing head and two fatty acid tails attached to one glycerol backbone. The head is hydrophilic, meaning it dissolves fast in water. The tails are hydrophobic; water repels them.

Immerse a lot of phospholipids in water, and they interact with water molecules and with one another until they spontaneously cluster into a sheet or film at the water's surface. Some line up as two layers, with all fatty acid tails sandwiched between the outward-facing hydrophilic heads. This is a **lipid bilayer**, the basic framework for cell membranes (Figure 5.3*c*).

THE FLUID MOSAIC MODEL

By the **fluid mosaic model**, every cell membrane has a mixed composition—or a *mosaic*—of phospholipids, glycolipids, sterols, and proteins. The lipids form an oily bilayer that serves as a barrier to water-soluble substances. Diverse proteins are either embedded in the bilayer or attached to one of its surfaces. They carry out most membrane functions.

The membrane is *fluid* because of interactions and motions of its components. The phospholipids differ in their heads and the length of their fatty acid tails. At least one of the tails is usually kinked, or unsaturated. Remember, an unsaturated fatty acid has one or more double covalent bonds in its carbon backbone; a fully saturated type has none. Also, most phospholipids drift sideways, spin around their long axis, and flex their tails, so they do not bunch up as a solid layer.

Figure 5.4 shows the fluid mosaic model. Section 5.2 is an overview of the membrane proteins that you will be reading about in many chapters to come.

DO MEMBRANE PROTEINS STAY PUT?

Some time ago, researchers figured out how to split a frozen plasma membrane down the middle of its bilayer. They found that proteins were not spread like a coat on the bilayer, as some had thought, but rather that many were embedded in it (Figure 5.5*a*). Were those proteins rigidly positioned in the membrane? No one knew until researchers designed an ingenious

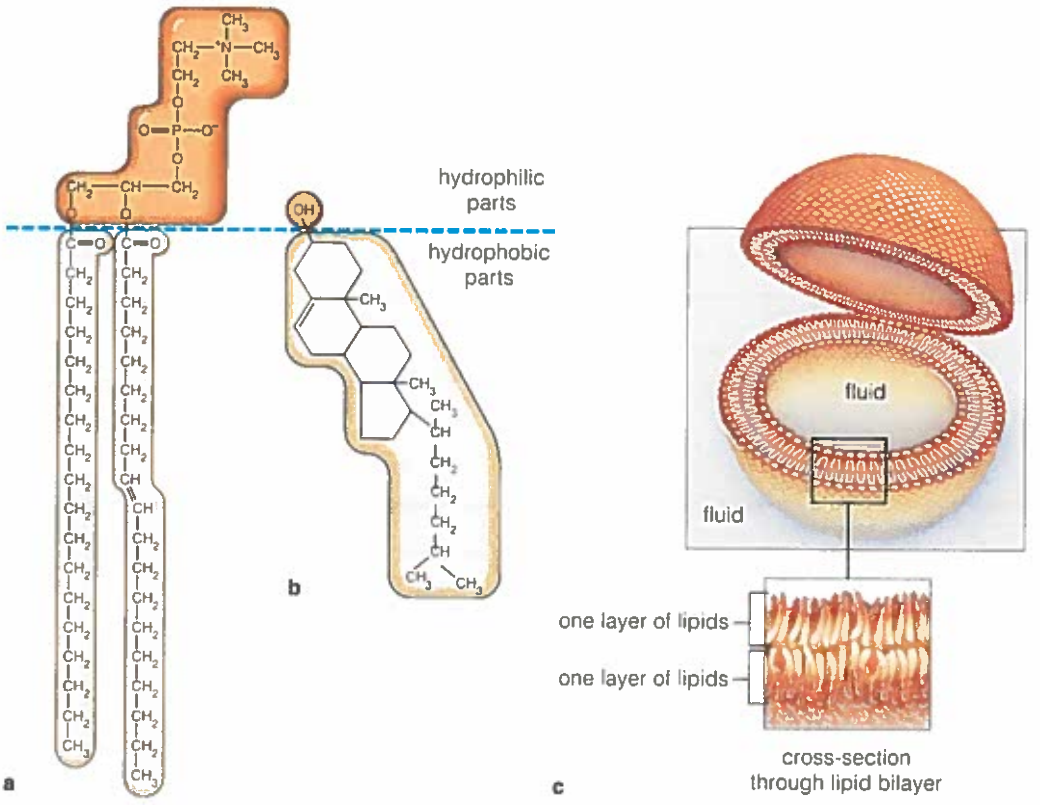


Figure 5.3 (**a**) Structural formula for phosphatidylcholine. This phospholipid is one of the most common molecules of animal cell membranes. *Orange* signifies its hydrophilic head, and *yellow*, its hydrophobic tails.

(**b**) Structural formula for cholesterol, the main sterol in animal tissues. Phytosterols are its equivalent in plant tissues.

(**c**) Spontaneous organization of lipid molecules into two layers (a bilayer structure). When immersed in liquid water, their hydrophobic tails become sandwiched between their hydrophilic heads, which dissolve in the water.

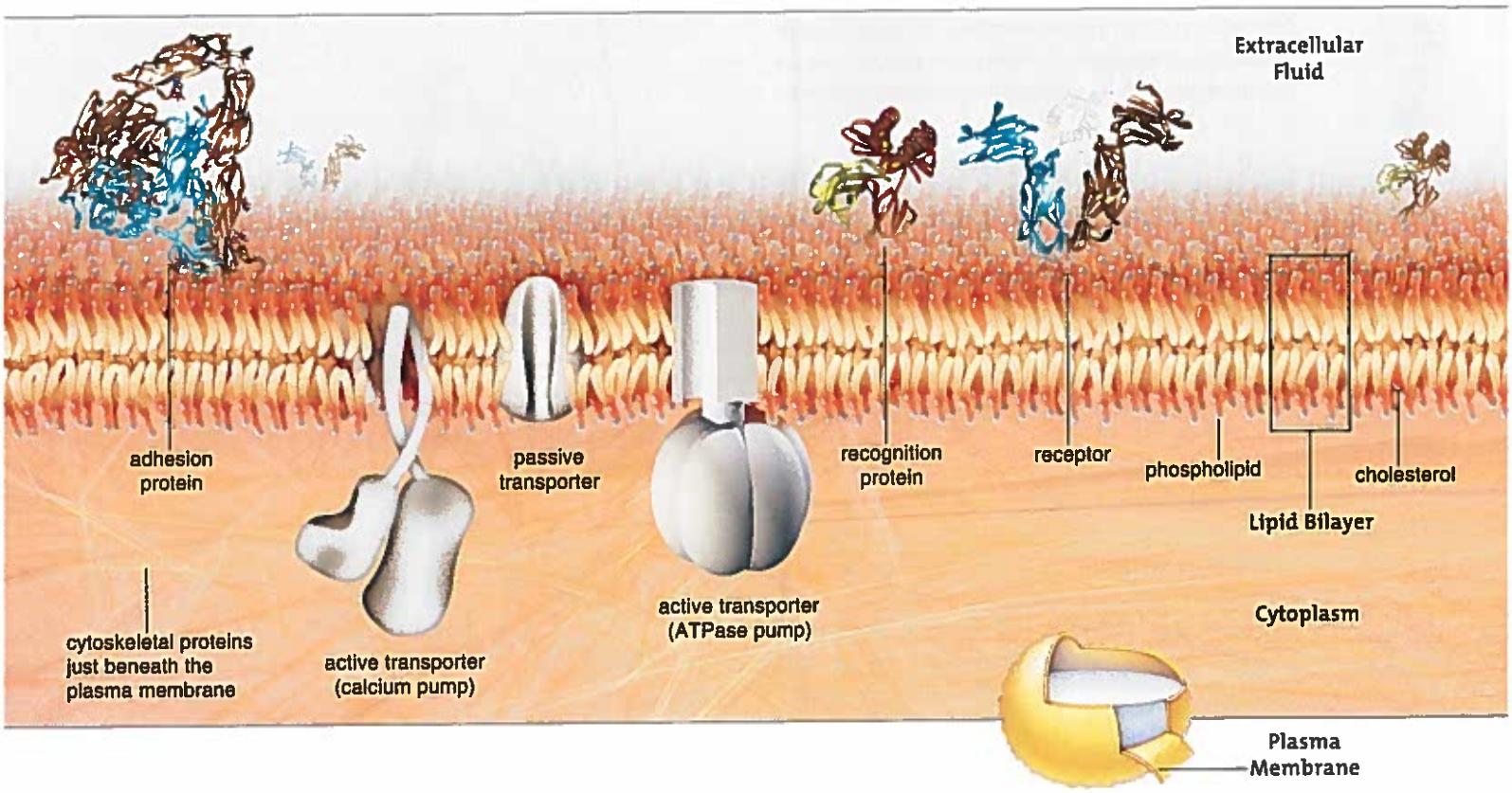


Figure 5.4 ***Animated!*** Fluid mosaic model for the plasma membrane of an animal cell.

experiment. They induced an isolated human cell and an isolated mouse cell to fuse. The plasma membranes from the two species merged to form one continuous membrane in a new, hybrid cell. Most of the proteins mixed together in less than an hour (Figure 5.5*b*).

As we now know, many proteins are free to move laterally through the lipid bilayer, but others stay put. Some unite in complexes and do not move relative to one another. Receptors for acetylcholine, a signaling molecule, are like this. Cytoskeletal elements tether other proteins and restrict their lateral movements. For instance, a mesh of cross-lined spectrin proteins anchor glycophorin, a type of recognition protein, to the surface of all red blood cells. A transport protein that moves chloride one way and bicarbonate the other across the plasma membrane is similarly anchored.

All cell membranes consist of two layers of lipids—mainly phospholipids—and diverse proteins. Hydrophobic parts of the lipids are sandwiched between hydrophilic parts, which are dissolved in cytoplasmic fluid or in extracellular fluid.

All cell membranes have protein receptors, transporters, and enzymes. The plasma membrane also incorporates adhesion, communication, and recognition proteins.

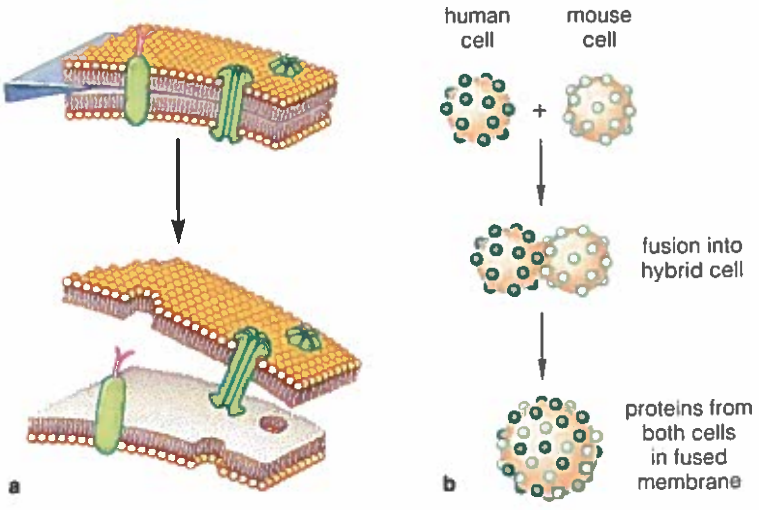


Figure 5.5 ***Animated!*** Studying membranes. (**a**) Researchers split the two layers of a cell membrane's lipid bilayer apart, which revealed that proteins are embedded in the bilayer. (**b**) Result of an experiment in which plasma membranes from cells of two species were induced to fuse. Membrane proteins from both drifted laterally and became mixed.

5.2 Overview of the Membrane Proteins

LINK TO SECTION 3.6

Cells interact with their surroundings through plasma membrane components. In membrane proteins, we see how structural diversity translates into functional diversity.

HOW ARE THE PROTEINS ORIENTED?

The fluid mosaic model is a good starting point for exploring membranes. But membranes differ in their composition and organization. Even the two surfaces of the same bilayer differ. For instance, many proteins (and lipids) of a plasma membrane have side chains of oligosaccharides and other carbohydrates, but only on the outward-facing surface (Figure 5.6). The kinds and number of side chains differ from one species to the next, even among cells of the same individual.

Integral proteins interact with hydrophobic parts of a bilayer's phospholipids. Most span the bilayer, with hydrophilic domains projecting beyond both surfaces. *Peripheral* proteins are located at one of the bilayer's surfaces. They interact weakly with integral proteins and with polar regions of membrane lipids.

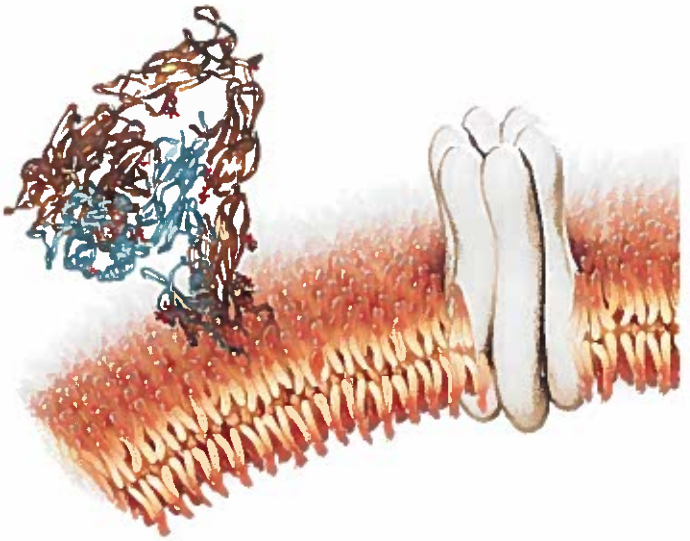
WHAT ARE THEIR FUNCTIONS?

Figure 5.6 shows the main membrane proteins, lists their defining features, and gives some examples. The **transport proteins** either passively let specific solutes diffuse through a membrane-spanning channel in their interior or actively pump them through. Transporters are incorporated into all cell membranes.

The other proteins shown are typical of the plasma membrane. The **receptor proteins** bind extracellular substances, such as hormones, that can trigger change in cell activities. For example, certain enzymes control cell growth and division. They are switched on when somatotropin binds with receptors for it. Cells differ in their combinations of receptors.

Multicelled organisms have **recognition proteins** that are unique identity tags for each species; they are like molecular fingerprints. **Adhesion proteins** help cells of the same type locate each other and remain in the proper tissues. The **communication proteins** form channels that match up across the plasma membranes of two cells. They let signals and substances rapidly flow from the cytoplasm of one into the other.

All cell membranes have transporters that passively and actively assist water-soluble substances across the lipid bilayer. The plasma membrane, especially of multicelled species, has diverse receptors and proteins that function in self-recognition, adhesion, and communication.



Adhesion Proteins

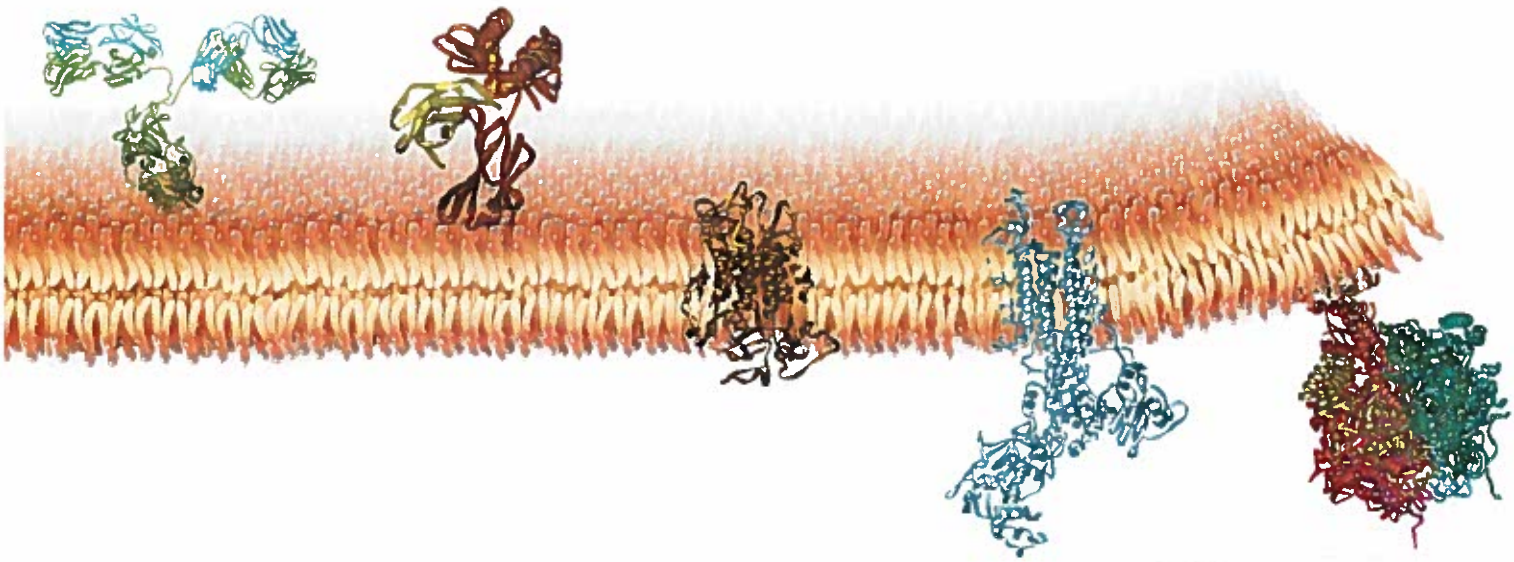
These proteins are embedded in the plasma membrane. They help one cell adhere to another or to a protein, such as collagen, that is part of an extracellular matrix.

Integrins, including this one, relay signals across the cell membrane. Cadherins of one cell bind with identical cadherins in adjoining cells. Selectins, which hold cells together, are abundant in endothelium, the special lining of blood vessels and the heart.

Communication Proteins

Communication proteins of one cell match up with identical proteins in the plasma membrane of an adjoining cell. Fingerlike projections of both intertwine in the space between the two cells. The result is a channel that directly connects the cytoplasm of both. Chemical and electrical signals flow fast through the channel.

This protein is one-half of a cardiac gap junction in heart muscle. The other half is in the lipid bilayer of another heart muscle cell (not shown) positioned above it. Signals flow so fast across such channels that heart muscle cells contract as a single functional unit.



Receptor Proteins

Receptors embedded in a membrane are docks for hormones and other signaling molecules that may cause target cells to change their activities.

A signal might make a cell synthesize a certain protein, block or speed a reaction, secrete a substance, or get ready to divide.

Shown above, an antibody, a type of receptor made only by the type of white blood cell known as the B lymphocytes. These receptors are vital for all immune responses (Chapter 39).

Recognition Proteins

Certain glycoproteins (and glycolipids) project above the plasma membrane and identify a cell as *nonself* (foreign) or *self* (belonging to one's own body or a tissue).

Some, such as the HLAs (page 49), function in tissue defense. Foreign fragments bound to HLA sound the alarm for cells that defend the body. Other recognition proteins help cells stick to one another in tissues.

Passive Transporters

Passive transporters have a channel through their interior. Different kinds assist solutes or water simply by letting them diffuse through the channel, down concentration or electric gradients (Section 5.4). They do not require activation by energy inputs.

Shown here, GluT1; when its channel changes shape, glucose can cross a membrane. Aquaporins are open channels for water (page 89).

One cotransporter helps chloride and bicarbonate ions across a membrane at the same time, in opposite directions.

Ion-selective channels have molecular gates. Some gates open or close fast if a small molecule binds to them or if the charge distribution across the membrane shifts. Nerve and muscle cells have gated channels for sodium, calcium, potassium, and chloride ions.

Active Transporters

Active transport proteins pump a solute across the membrane to the side where it is more concentrated and less likely to move on its own. They require energy inputs to do this. Some are cotransporters that let one kind of solute flow passively "downhill" even as they pump a different kind "uphill."

Left, a calcium pump. Like the sodium–potassium pump, it is one of the ATPases.

Right, a type of ATPase that pumps H^+ through its interior channel, against gradients. It also can let H^+ diffuse back through the channel in a way that drives ATP synthesis. Hence its more precise name, ATP synthase (Chapters 7 and 8).

Figure 5.6 ***Animated!*** Major categories of membrane proteins. Included are simple icons and descriptions for membrane proteins that you will encounter in later chapters. The transporters span the lipid bilayer of all cell membranes. The other proteins shown are components of plasma membranes. Bear in mind, cell membranes also incorporate additional kinds of proteins, including some enzymes.

5.3 Diffusion, Membranes, and Metabolism

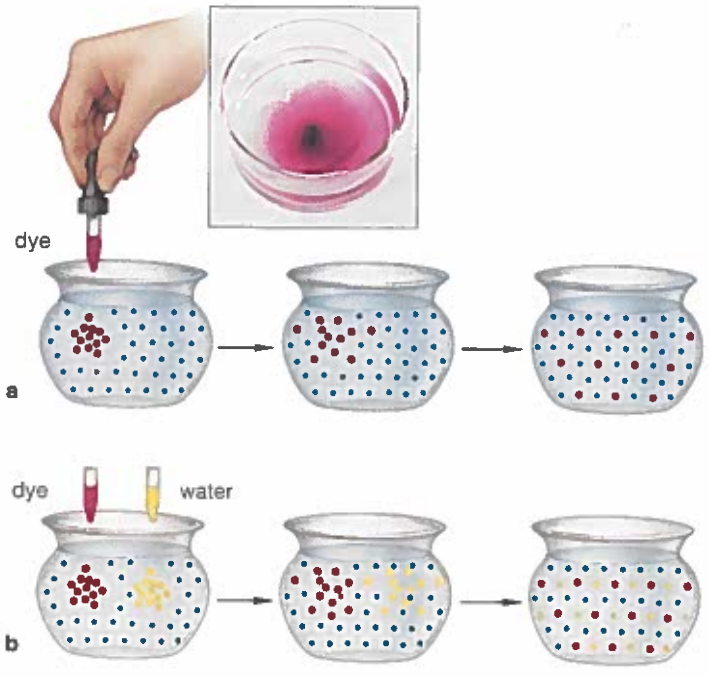
LINKS TO SECTIONS 2.3, 2.5, 3.4

What determines whether a substance will move one way or another to and from a cell, across that cell's membranes, or through the cell itself? Diffusion down concentration gradients is part of the answer.

WHAT IS A CONCENTRATION GRADIENT?

A **concentration gradient** is a difference in the number per unit volume of molecules (or ions) of a substance between two adjoining regions. In the absence of other forces, the molecules move from a region where they are more concentrated to a region where they are not as concentrated. Why? Their inherent thermal energy keeps them in constant motion, so that they collide at random and bounce off one another millions of times each second. This happens more in regions where the molecules are most concentrated, and when you add it all up, the *net* movement is toward the region where they are not colliding and bouncing around as much. The molecules flow down their concentration gradient.

Diffusion is the name for the net movement of like molecules or ions down a concentration gradient. It is a factor in how substances move into, through, and out of cells. In multicelled species, it moves substances between body regions and between the body and its environment. For instance, when photosynthesis is going on in leaf cells, oxygen builds up and diffuses out of the cells and into air spaces in the leaf, where its concentration is lower. It then diffuses into the air outside the leaf, where its concentration is lower still.



Like other substances, oxygen tends to diffuse in a direction set by its *own* concentration gradient, not by gradients of other solutes. You can see the outcome by squeezing a drop of dye into water. The dye molecules diffuse slowly into the region where they are not as concentrated, and the water molecules move into the region where *they* are not as concentrated. Figure 5.7 shows simple examples of diffusion.

WHAT DETERMINES DIFFUSION RATES?

How fast a particular solute diffuses depends on the steepness of its concentration gradient, its size, the temperature, and electric or pressure gradients that may be present.

First, rates are high with steep gradients, because more molecules are moving out of a region of greater concentration compared with the number moving into it. Second, more heat energy makes molecules move faster and collide more often in warmer regions. Third, smaller molecules diffuse faster than large ones do.

Fourth, an electric gradient may alter the rate and direction of diffusion. An **electric gradient** is simply a difference in electric charge between adjoining regions. For example, each ion dissolved in fluids bathing a cell membrane contributes to a local electric charge. Opposite charges attract. Therefore, the fluid having more negative charge overall exerts the greatest pull on positively charged substances, such as sodium ions. Later chapters explain how many cell activities, such as ATP formation and the sending and receiving of signals in nervous systems, require the driving force of electric and concentration gradients.

Fifth, diffusion also may be affected by a **pressure gradient**. This is a difference in pressure exerted per unit volume (or area) between two adjoining regions.

MEMBRANE CROSSING MECHANISMS

Now think about the water bathing the surfaces of a cell membrane. Plenty of substances are dissolved in it, but the kinds and amounts close to its two surfaces

Figure 5.7 ***Animated!*** Two examples of diffusion. (**a**) A drop of dye enters a bowl of water. Gradually, the dye molecules become evenly dispersed through the molecules of water. (**b**) The same thing happens with the water molecules. Here, dye (*red*) and water (*yellow*) are added to the same bowl. Each substance will show a net movement down its own concentration gradient.