4 Cell membranes and transport

The fluid mosaic model introduced in 1972 describes the way in which biological molecules are arranged to form cell membranes. The model has stood the test of time as a way to visualise membrane structure and continues to be modified as understanding improves of the ways in which substances cross membranes, how cells interact and how cells respond to signals. The model also provides the basis for our understanding of passive and active movement between cells and their surroundings, cell to cell interactions and long distance cell signalling.

Investigating the effects of different factors on diffusion, osmosis and membrane permeability involves an understanding of the properties of phospholipids and proteins covered in the Topic 2 Biological molecules.

4.1 Fluid mosaic membranes

The structure of cell surface membranes allows movement of substances between cells and their surroundings and allows cells to communicate with each other by cell signalling.

By the end of this section you should be able to:

a) describe and explain the fluid mosaic model of membrane structure, including an outline of the roles of phospholipids, cholesterol, glycolipids, proteins and glycoproteins
b) outline the roles of cell surface membranes including references to carrier proteins, channel proteins, cell surface receptors and cell surface antigens
c) outline the process of cell signalling involving the release of chemicals that combine with cell surface receptors on target cells, leading to specific responses

The cell surface membrane

An organelle with many roles

The **cell surface membrane** is an organelle common to both eukaryotic and prokaryotic cells. It is an extremely thin structure, less than 10 nm thick, yet it has the strength to maintain the integrity of the cell. In addition to holding the cell's contents together, the cell surface membrane forms the barrier across which all substances entering or leaving the cell must pass. This membrane represents the 'identity' of the cell to surrounding cells. It is also the surface across which chemical messages (such as hormones and growth factors) communicate. In fact, movement of molecules across the cell surface membrane is continuous and very heavy. Figure 4.1 is a summary of all this membrane traffic.

The molecular components of membranes

The membranes of cells are made almost entirely of protein and lipid, together with a small and variable amount of carbohydrate. The lipid of membranes is **phospholipids**. The chemical structure of phospholipids is shown in Figure 2.16 on page 43.

Look at its structure again now.

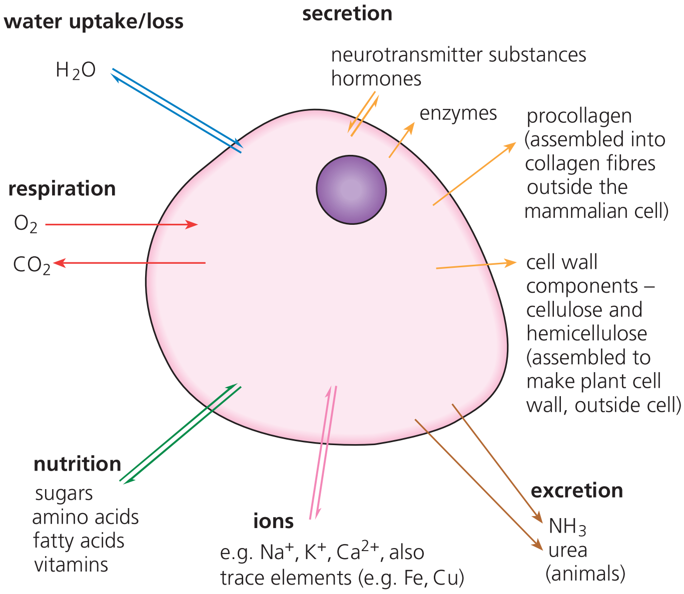


Figure 4.1 The movement of substances across the cell surface membrane

You can see that the phospholipid molecule has a 'head' composed of a glycerol to which is attached an ionised phosphate group. This latter part of the molecule has **hydrophilic properties** (water-loving). For example, **hydrogen bonds** readily form between the phosphate head and water molecules. The remainder of the phospholipid comprises two long, fatty acid residues consisting of hydrocarbon chains. These 'tails' have **hydrophobic properties** (water-hating).

The response of phospholipid to water

A small quantity of phospholipid in contact with a solid surface (a clean glass plate is suitable), remains as a discreet bubble; the phospholipid molecules do not spread. However, when a similar tiny drop of phospholipid is added to water it instantly spreads over the entire surface (as a monolayer of phospholipid molecules, in fact). The molecules float with their hydrophilic 'heads' in contact with the water molecules, and with their hydrocarbon tails exposed above and away from the water, forming a monolayer of phospholipid molecules (Figure 4.2).

When more phospholipid is added and shaken up with water, **micelles** may form. These are tiny spheres of lipids with hydrophilic heads outwards, in contact with the water, and with all the hydrophobic tails pointing inwards.

Alternatively, the phospholipid molecules arrange themselves as a **bilayer**, again with the hydrocarbon tails facing together (Figure 4.2). This is how the molecules of phospholipid are arranged in the cell surface membrane.

In the phospholipid bilayer, attractions between the hydrophobic hydrocarbon tails on the inside and between the hydrophilic glycerol–phosphate heads and the surrounding water on the outside make a stable, strong barrier.

Finally, the phospholipid bilayer has been found to contain molecules of **cholesterol**. Cholesterol has an effect on the flexibility of the cell surface membrane. We return to this feature shortly.

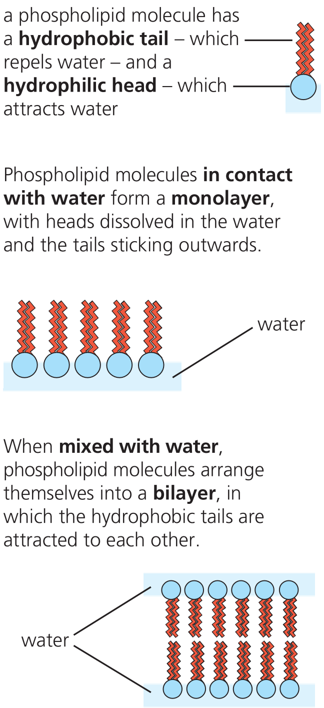


Figure 4.2 Phospholipid molecules arranged in a monolayer and a bilayer

The permeability of a phospholipid membrane

We must note, however, that whilst lipids provide a cohesive structure, they also tend to act as a barrier to the passage of polar molecules and ions. This is particularly the case where close-packing of the hydrocarbon tails occurs. Potentially, water-soluble substances pass through the lipid bilayer with great difficulty. We will return to this issue shortly, too.

The proteins and carbohydrates of membrane

The proteins of membranes are **globular proteins** which are buried in and across the lipid bilayer, with most projecting above the surfaces. Others are superficially attached on either surface of the lipid bilayer.

Proteins that occur partially or fully buried in the lipid bilayer are described as **integral proteins**. Those that are superficially attached on either surface of the lipid bilayers are known as **peripheral proteins**.

Membrane proteins have a range of roles. Some are enzymes, others are receptors, or antigens, and many are channels for transport of metabolites. Those that are involved in transport of molecules across membranes are in the spotlight in the next section. A summary of the various roles of membrane proteins is given in Figure 4.24 (page 94), after the movements of molecules across the membrane have been discussed.

The carbohydrate molecules of the cell surface membrane are relatively short chain **polysaccharides**, some attached to the proteins (**glycoproteins**) and some to the lipids (**glycolipids**) Glycoproteins and glycolipids are only found on the outer surface of the membrane. Together these form the **glycocalyx**. The roles of this glycocalyx are:

- cell–cell recognition
- as receptor sites for chemical signals, such as hormone messengers
- to assist in the binding together of cells to form tissues.

Questions

1. In plants adapted to survive in very low winter temperatures, what seasonal change would you anticipate in the composition of the lipid bilayer of their membranes?
2. What is the difference between a lipid bilayer and the 'double membrane' of many organelles?

The fluid mosaic model of membrane structure

The molecular structure of the cell surface membrane, known as the **fluid mosaic model** by those who first suggested it, is shown in Figure 4.3. The membrane they described as *fluid* because the components (lipids and proteins) move around within their layer. In fact the movements of the lipid molecules are rapid, whereas mobile proteins move about more slowly. The word *mosaic* described the scattered pattern of the proteins, when viewed from above. This is the current view of the structure of the cell surface membrane. It is based on a range of evidence, in part from studies with the electron microscope (Figure 4.4).

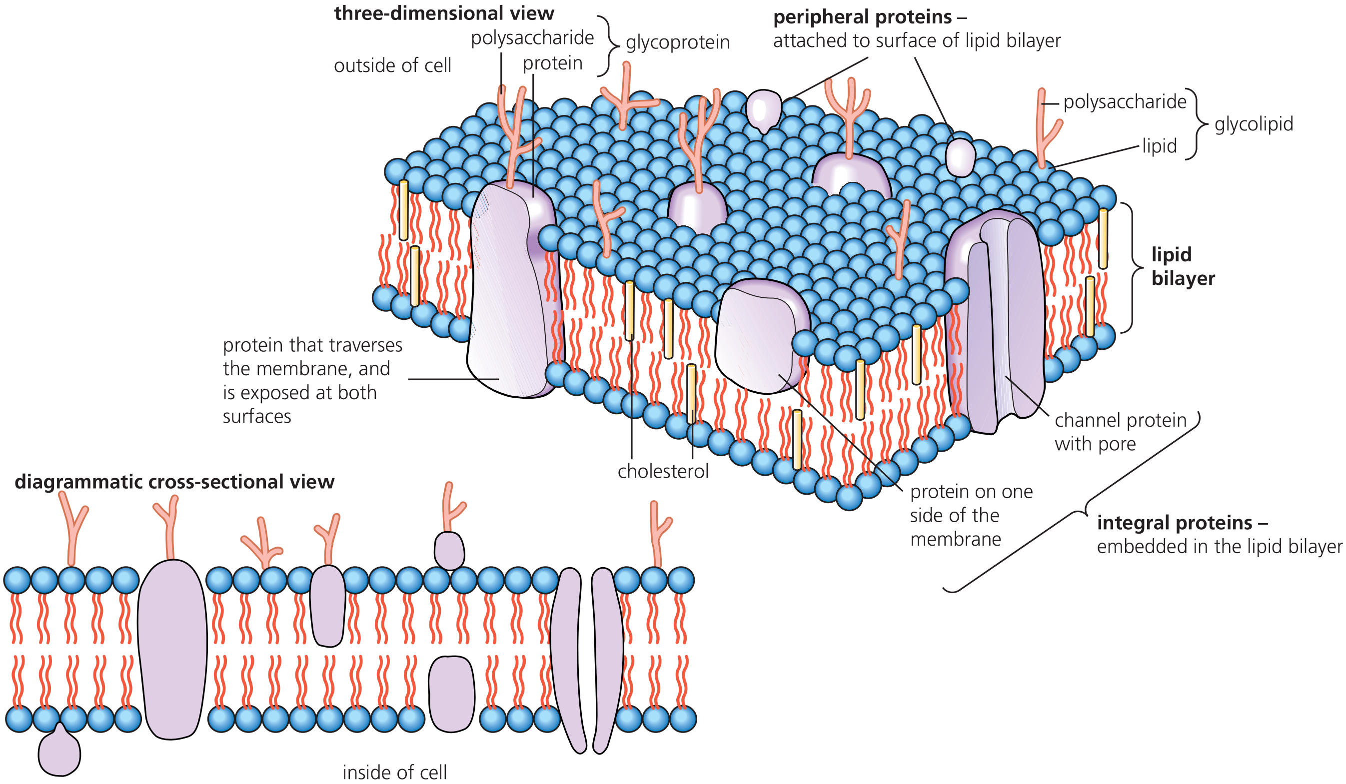


Figure 4.3 The fluid mosaic model of membrane structure

Composition of the membrane and control of how fluid it is

The phospholipids of the membrane are a mixture. Some have saturated fatty acid tails and some unsaturated fatty acid tails (Figure 2.14, page 41). An excess of unsaturated fatty acid tails makes the membrane more fluid. This is because the kinks in the tails prevent close-packing of the lipids. However, the presence of cholesterol among the phospholipid molecules has to be taken into account. The effect of cholesterol is to reduce fluidity by preventing or reducing the movements of the lipid molecules.

Membrane fluidity is an important factor. Membranes must be sufficiently fluid for many of the proteins present to move about and so to function correctly. If the temperature of a membrane falls it becomes less fluid. A point may be reached when the membrane will actually solidify. Some organisms have been found to vary the balance between saturated and unsaturated fatty acids and the amount of cholesterol in their membranes as ambient temperatures changes. In this way they maintain a properly functioning membrane, even at very low temperatures, for example.

The cell surface membrane and cell signalling

Cells respond to changes in their environment by receiving and integrating signals from other cells. They also send out messages. Most cell signals are chemical signals. For example, motile single-celled organisms detect nutrients in their environment and move towards the source. In multicellular organisms, chemical signals include growth factors and hormones that may have come from neighbouring cells or from more distant sources. Neurotransmitter signals cross a tiny gap from a neighbouring nerve cell (page 320).

Cells are able to detect these signals because of receptors in their cell surface membrane to which the 'chemical message' binds, and then trigger an internal response. Receptors are typically trans-membrane proteins, which on receipt of the signal, alert internal signalling pathways. However, some receptors occur within the cell, and possibly within the nucleus. These receptors are stimulated by signal chemicals that pass through the cell surface membrane, such as the gas nitrous oxide or a steroid hormone such as oestrogen. The activation of a receptor, whether internal or external, initiates a chain of reactions within the cell, possibly involving a second messenger. The outcome is some internal response.

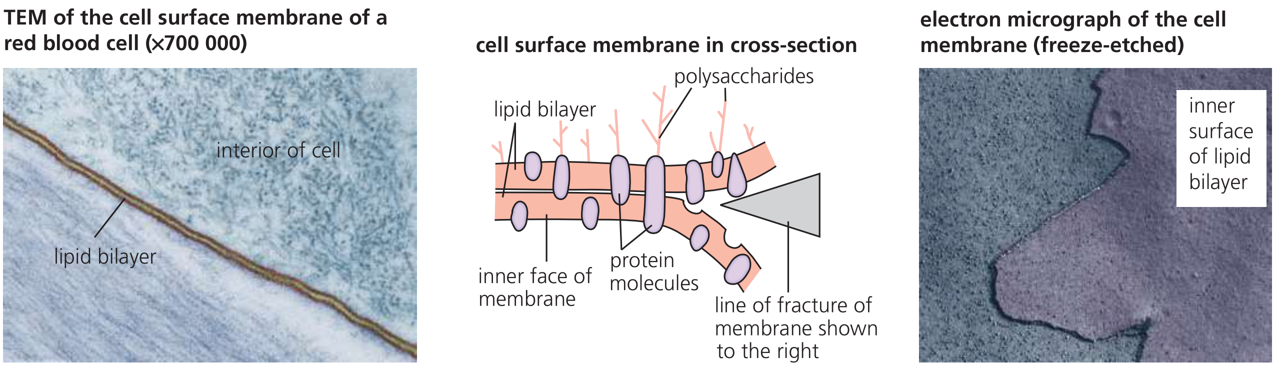


Figure 4.4 Membrane structure: evidence from the electron microscope

Summarising the rol of membrane proteins in cells

The many roles that cell membrane proteins play (as channels for transport of metabolites, as pumps for active transport, as electron carriers, carrier proteins, cells surface receptors, and as binding sites for specific hormone molecules and in antigen-antibody reactions) are outlined in Figure 4.24 on page 94.

Look at this diagram now.

The potential for complex communications between cells that may result as chemicals released from one cells combine with cell surface receptors on neighbouring cells is evident. It is the proteins of cell surface membranes that facilitate this 'cell signalling'.

4.2 Movement of substances into and out of cells

The fluid mosaic model allows an understanding of how substances enter and exit cells by a variety of different mechanisms.
Investigating the effect of increasing the size of model cells allows an understanding of the constraints of obtaining resources across the cell surface and moving substances out of cells.

By the end of this section you should be able to:

a) describe and explain the processes of diffusion, facilitated diffusion, osmosis, active transport, endocytosis and exocytosis
b) investigate simple diffusion using plant tissue and non-living materials, such as glucose solutions, Visking tubing and agar
c) calculate surface areas and volumes of simple shapes (e.g. cubes) to illustrate the principle that surface area to volume ratios decrease with increasing size
d) investigate the effect of changing surface area to volume ratio on diffusion using agar blocks of different sizes
e) investigate the effects of immersing plant tissues in solutions of different water potential, using the results to estimate the water potential of the tissues
f) explain the movement of water between cells and solutions with different water potentials and explain the different effects on plant and animal cells

Into and out of cells passes **water**, **respiratory gases** (O_2 and CO_2), **nutrients**, **essential mineral ions** and **excretory products**. Cells may secrete substances such as **hormones** and **enzymes**. They may receive **growth substances** and **hormones**, too. Plants secrete the chemicals that make up their walls through their membranes, and assemble and maintain the wall outside the membrane. Certain mammalian cells secrete **structural proteins** such as collagen in a form that can be assembled outside the cells.

In addition, the membrane at the cell surface is where the cell is identified by surrounding cells and organisms. For example, protein **receptor sites** are recognised by hormones, neurotransmitter substances (from nerve cells), as well as other chemicals, sent from other cells.

We will now look into the **mechanisms of membrane transport**. Figure 4.5 is a summary of the mechanisms of transport across membranes.

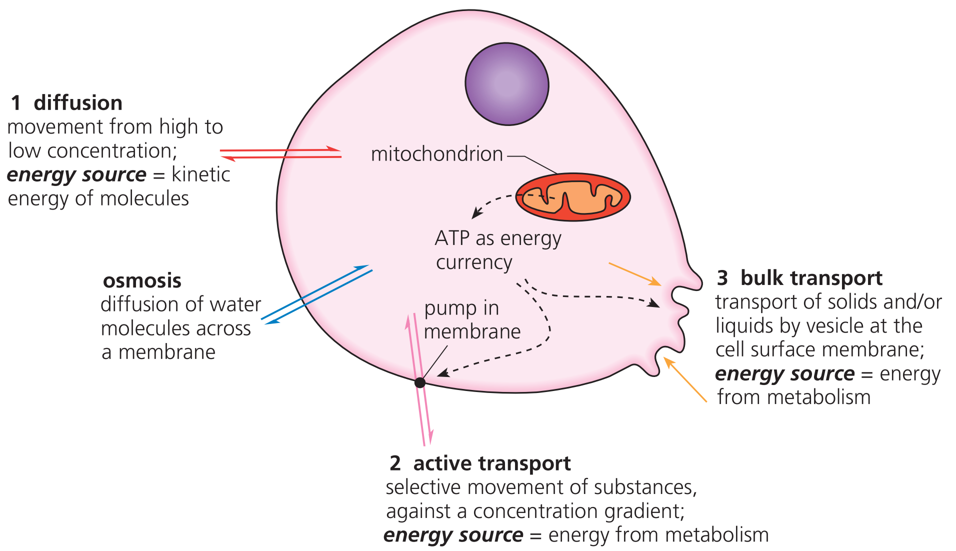


Figure 4.5 Mechanisms of movement across membranes

Diffusion: the net movement of particles such as molecules from a region where they are at a higher concentration to a region with a lower concentration, using energy from the random movements of particles. This includes diffusion of small non-polar molecules (such as oxygen and carbon dioxide) through the cell surface membrane, as well as diffusion of fat-soluble molecules (such as vitamin A) through the cell surface membrane.

Movement by diffusion

The atoms, molecules and ions of liquids and gases undergo continuous random movements. These movements result in the even distribution of the components of a gas mixture and of the atoms, molecules and ions in a solution. This is why we are able to take a tiny random sample from a solution and analyse it to find the concentration of dissolved substances in the whole solution. Every sample has the same composition as the whole. Similarly, every breath we take has the same amount of oxygen, nitrogen and carbon dioxide as the atmosphere as a whole.

Continuous random movements of all molecules ensures complete mixing and even distribution of molecules, given time, in solutions and gases. The energy for diffusion comes from the **kinetic energy** of molecules. 'Kinetic' means that a particle has this energy because it is in continuous motion.

Diffusion is the free passage of molecules (and atoms and ions) from a region of their high concentration to a region of low concentration. Where a difference in concentration has arisen in a gas or liquid, random movements carry molecules from a region of high concentration to a region of low concentration. As a result, the particles become evenly dispersed. The factors affecting the rate of diffusion are listed in Table 4.1.

Table 4.1 Factors affecting the rate of diffusion

Factors affecting the rate of diffusion	The conditions needed to achieve rapid diffusion across a surface
Concentration gradient – the greater the difference in concentration between two regions, the greater the amount that diffuses in a given time.	A fresh supply of substance needs to reach the surface and the substance that has crossed needs to be transported away.
Distance over which diffusion occurs – the shorter the distance, the greater the rate of diffusion.	The structure needs to be thin.
Area across which diffusion occurs – the larger the area, the greater the diffusion.	The surface area needs to be large.
Structure through which diffusion occurs – pores or gaps in structures may enhance diffusion.	A greater number of pores and a larger size of pores may enhance diffusion.
Size and type of diffusing molecules – smaller molecules and molecules soluble in the substance of a barrier will both diffuse more rapidly.	Oxygen may diffuse more rapidly than carbon dioxide. Fat-soluble substances diffuse more rapidly through the lipid bilayer than water-soluble substances.

Demonstrating diffusion

Diffusion in a liquid can be illustrated by adding a crystal of a coloured mineral to distilled water. Even without stirring, the ions become evenly distributed throughout the water. The process takes time, especially as the solid has first to dissolve (see Figure 4.6 on the next page).

Cell surface : volume ratio, cell size and diffusion

As a cell grows and increases in size an important difference develops between the surface area available for exchange by diffusion and the volume of the cytoplasm in which the chemical reactions of life occur. The volume increases faster than surface area; the surface area : volume ratio falls (see Figure 4.7 on the next page). So, with increasing size of a cell, less and less of the cytoplasm has access to the cell surface for exchange of gases, supply of nutrients and loss of waste products.

Put another way, we can say that the smaller the cell is, the more quickly and easily can materials be exchanged between its cytoplasm and environment by diffusion. One consequence of this is that cells cannot continue growing larger, indefinitely. When a maximum size is reached cell growth stops. The cell may then divide.

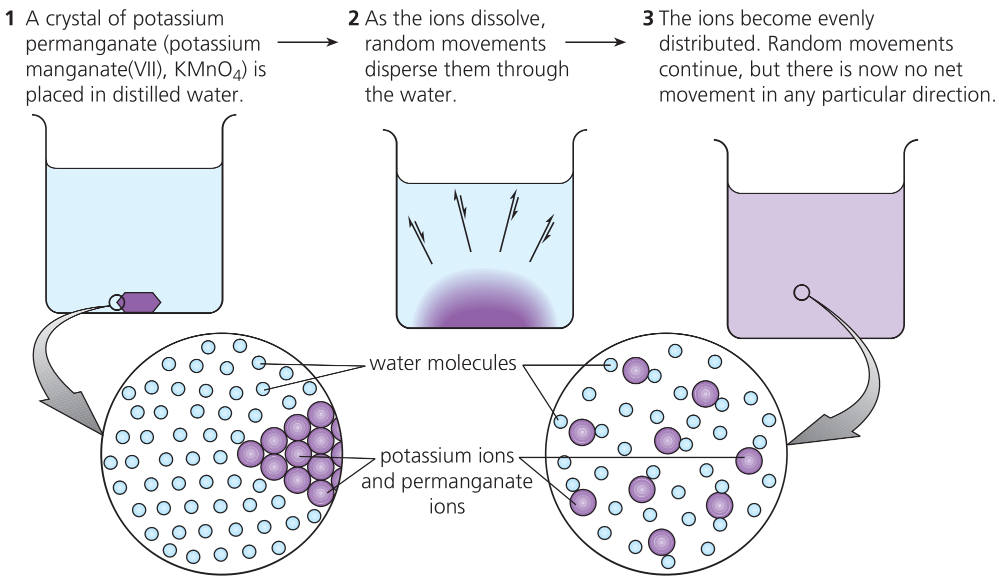
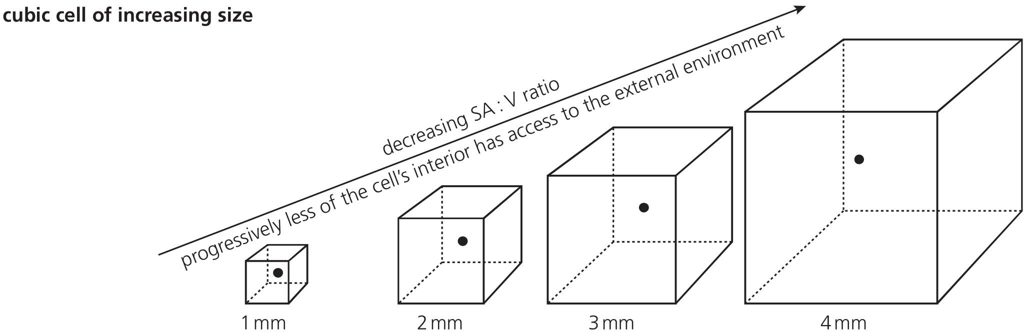


Figure 4.6 Diffusion in a liquid

Question

3 For imaginary cubic 'cells' with sides 1, 2, 4 and 6 mm:

- **a** calculate the volume, surface area and ratio of surface area to volume for each
- **b** plot a graph of the surface area of these cells against their volume
- **c** state the effect on the SA:V ratio of a cell as it increases in size
- **d** explain the effect of increasing cell size on the efficiency of diffusion in the removal of waste products from cell cytoplasm.



dimensions/mm	1 × 1 × 1	2 × 2 × 2	3 × 3 × 3	4 × 4 × 4
surface area/mm^2	6	24	54	96
volume/mm^3	1	8	27	64
surface area : volume ratio	6:1 = $^6/_1$ = 6	24:8 = $^{24}/_8$ = 3	54:27 = $^{54}/_{27}$ = 2	96:64 = $^{96}/_{64}$ = 1.5

Figure 4.7 The effect of increasing size on the surface area : volume ratio

Demonstrating the connection between surface area : volume ratio and diffusion

Working with a block of gelatine containing the acid-base indicator cresol red (coloured red in alkali, yellow in acid), small, regular-shaped blocks of known dimension can be cut, and then immersed in acid solution. The time taken for the red colour to completely disappear can be recorded in a table, against the dimensions of the blocks, listed in increasing size. The results of one such investigation are recorded in Question 4. Examine the data there, and answer the questions that follow.

Question

4 Cubes of slightly alkaline gelatin of different dimensions, containing an acid–alkali indicator (red in alkalis but yellow in acids) were prepared. The cubes were then placed in dilute acid solution and the time taken for the colour in the gelatin to change from red to yellow was measured.

Dimensions/mm	Surface area/mm^2	Volume/mm^3	Time/minutes
10 × 10 × 10	600	1000	12
5 × 5 × 5	150	125	4.5
2.5 × 2.5 × 2.5	37.5	15.6	4.0

a For each block, calculate the ratio of surface area to volume (*SA*/*V*).

b Explain why the colour changes more quickly in some blocks than others.

Diffusion in cells

Diffusion across the cell surface membrane occurs where:

- the membrane is fully permeable to the substance concerned. The lipid bilayer of the cell surface membrane is permeable to non-polar substances, including steroids and glycerol, and also oxygen and carbon dioxide in solution, all of which diffuse quickly via this route. Note that the net diffusion of different types of particle can take place in opposite directions without hindrance, too. So, at the lung surface, oxygen diffuses into the blood whilst carbon dioxide diffuses out.
- the pores in the membrane are large enough for a substance to pass through. Water diffuses across the cell surface membrane by means of the protein-lined pores of the membrane. The tiny spaces between the phospholipid molecules are another route for water molecules. This latter occurs more easily where the fluid-mosaic membrane contains phospholipids with unsaturated hydrocarbon tails, for here these hydrocarbon tails are spaced more widely. In this state, the membrane is consequently especially 'leaky' to water, for example.

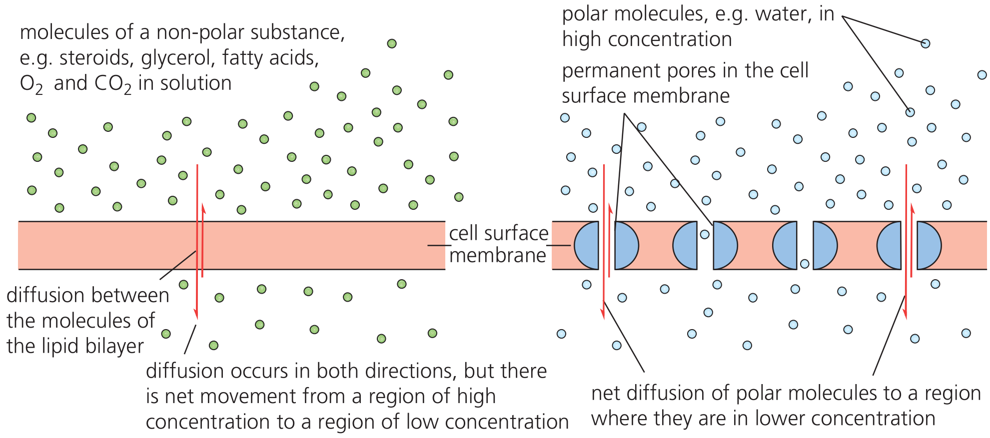


Figure 4.8 Diffusion across the cell surface membrane

Facilitated diffusion

In facilitated diffusion, a substance that otherwise is unable to diffuse across the cell surface membrane does so. This is as a result of its effect on a particular protein in the membrane. These are globular proteins that can form into pores large enough for diffusion. Those pores close up again when that substance is no longer present (Figure 4.9).

Facilitated diffusion: the diffusion of ions and polar (water-soluble) molecules through cell membranes using specific protein channels or carriers, down a concentration gradient (from regions where they are at higher concentration to regions where they are at lower concentration).

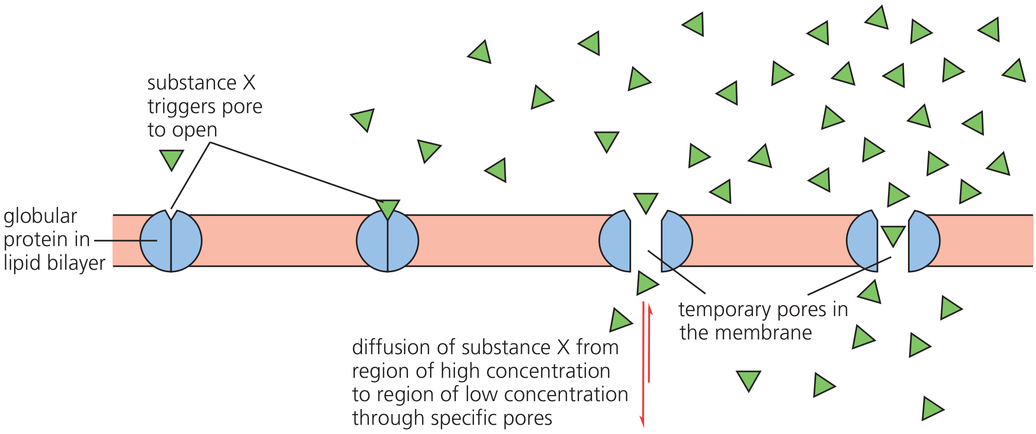


Figure 4.9 Facilitated diffusion

Alternatively a channel protein may be selective. For example, some channel proteins are 'gated' and open to allow the passage of ions only under particular conditions. There are different channels for potassium ions and sodium ions in the membrane of nerve fibres, for example (Figure 15.6, page 317).

Such proteins undergo rapid shape changes when in contact with a particular solute molecule. Facilitated diffusion follows. The movement of glucose into red blood cells occurs in this way. So does the movement of ADP into mitochondria and the movement of ATP from mitochondria into the cytosol.

Finally, we must remember that in facilitated diffusion the energy comes from the kinetic energy of the molecules involved, as is the case in all forms of diffusion. Energy from metabolism is not required.

Question

5 Distinguish between 'diffusion' and 'facilitated diffusion'.

Osmosis – a special case of diffusion

Osmosis: the diffusion of water molecules from a region where water is at a higher water potential through a partially permeable membrane to a region with a lower water potential.

First, look at the experiment shown in Figure 4.10. The bag shown here is made from a short length of dialysis tubing. Some sucrose solution is added, perhaps by using a small plastic syringe. This is an experiment that is easy to set up. When this partially filled bag is lowered into a beaker of water it quite quickly becomes stretched and turgid. Obviously there is a huge inflow of water. This is a simple but dramatic demonstration of osmosis.

Why does osmosis happen? Remember, in a sucrose solution the sucrose molecules are the solute and the water molecules are the solvent.

a solution = solute + solvent

We saw in Topic 2 that in a solution, a dissolved substance attracts polar water molecules around it (Figure 2.28, page 53). The forces holding those water molecules in this way are **hydrogen bonds**. The effect of the presence of a 'cloud' of water molecules around each solute molecule is to hamper and restrict their movements. Organic substances like sugars, amino acids, polypeptides and proteins, and inorganic ions like Na^+, K^+, Cl^- and NO_3^-, all have this effect on the water molecules around them. On the other hand, in pure water, all of the water molecules are free to move about randomly, and do so – all the time. We say that here they diffuse freely.

In the experiment in Figure 4.10, the solution of sugar was separated from pure water by a membrane – the walls of a dialysis tube. This is described as **partially permeable** because it only allows certain molecules to pass, not all of them. Water molecules move across the membrane in both directions, by diffusion. At the same time, the solute molecules with their cloud of water molecules are too large to pass through. In the mean time, there is a continuing net movement of water molecules from the region of high concentration of free water molecules (the molecules of pure water in the beaker) to the region of low concentration of free water molecules (the water molecules of the sucrose solution). This causes the bag to fill up and become stretched and turgid.

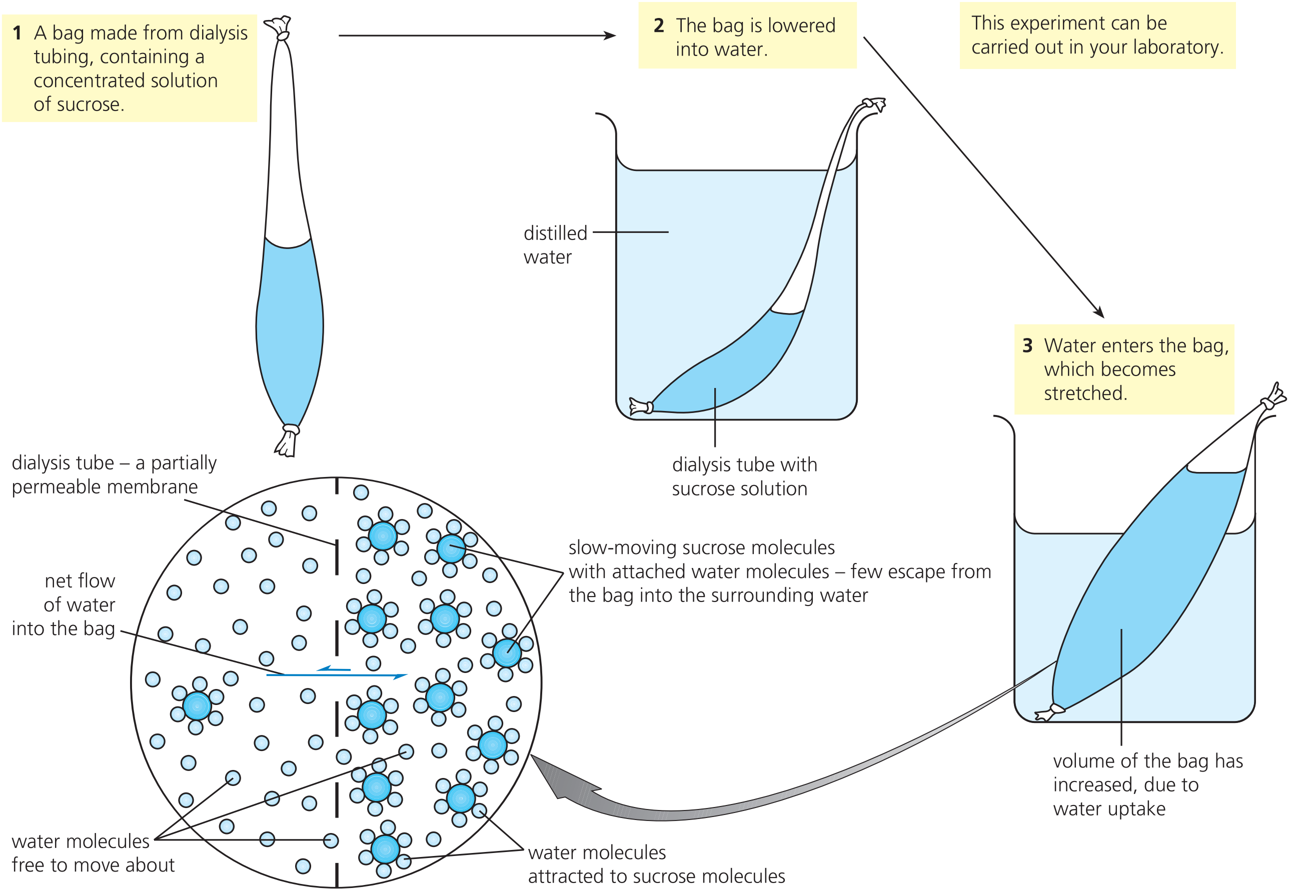


Figure 4.10 Osmosis

Water potential

The name given to the tendency of water molecules to move about is **water potential**. 'Water potential' is really a measure of the free kinetic energy of the water molecules. The Greek letter *psi* (symbol ψ) is used to represent water potential.

Water moves from a region of higher water potential to a region of lower water potential. We say water moves down a **water potential gradient**. Equilibrium is reached only if or when the water potential is the same in both regions. At this point, there would be no net movement of water from one region to another, but random movements of water molecules continue, of course.

Next we will examine the effects of dissolved solutes, and then of mechanical pressure on water potential, before returning to a re-statement of water potential.

Questions

6 What is meant when we say a membrane is partially permeable?

7 When a concentrated solution of glucose is separated from a dilute solution of glucose by a partially permeable membrane, which solution will show a net gain of water molecules? Why do we speak of a 'net' gain?

8 Jam is made of equal weights of fruit and sucrose. What happens to a fungal spore that germinates after landing on jam?

This experiment can be carried out in your laboratory.

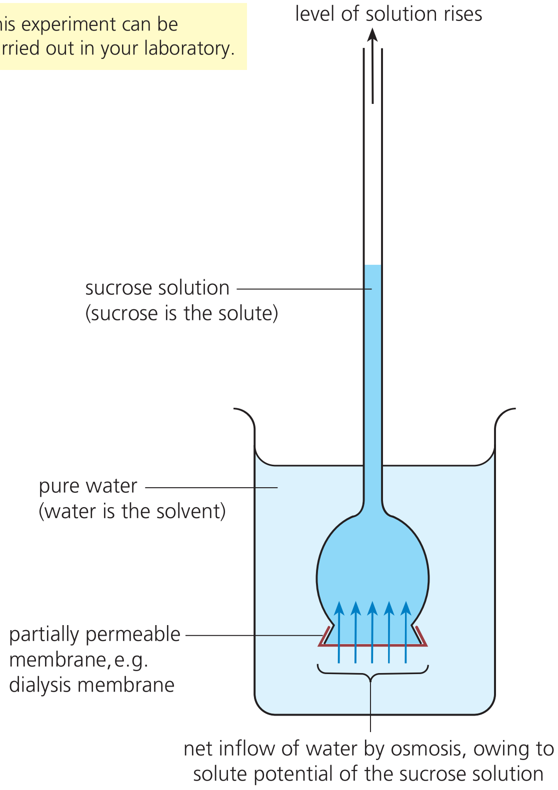


Figure 4.11 An osmometer

The concentration of solute molecules and water potential

Pure water obviously has the highest water potential. By convention, this is set at zero. Once a solute is dissolved in water, the water molecules are immediately less likely to diffuse (they are less mobile). So the effect of dissolving solute in water is to lower its water potential. Consequently solutions at atmospheric pressure must have a negative value of water potential (since pure water is set at zero). Also, the stronger the solution (i.e. the more solute dissolved per volume of water) the larger the number of water molecules that are slowed up and held almost stationery. So, in a very concentrated solution, very many more of the water molecules have restricted movements than do in a dilute solution.

The amount of dissolved solute present in a solution is known as the **solute potential** of the solution. It is given the symbol ψ_s. A simple osmometer is shown in Figure 4.11. We use an osmometer to demonstrate the solute potential of a solution. Once the osmometer is lowered into the beaker of water, very many more water molecules diffuse across the membrane into the solution than move in the opposite direction. The solution is diluted and it rises up the attached tube. An osmometer like this could be used to compare the solute potentials of solutions with different concentrations.

Pressure potential

The other factor that may influence osmosis is mechanical pressure acting on the solution. This factor is given the name **pressure potential**. It is represented by the symbol ψ_p.

If a pressure greater than atmospheric pressure is applied to a solution, then this is an example of a pressure potential being created in a solution. In the demonstration in Figure 4.12 a short length of dialysis tubing has been set up to show how the pressure potential of a solution can become large enough to stop the osmotic uptake of water altogether.

Question

9 When a concentrated solution of sucrose is separated from a dilute solution of sucrose by a partially permeable membrane, which solution:

a has a higher concentration of water molecules

b has lower water potential

c will experience a net gain of water molecules?

This experiment can be carried out in your laboratory.

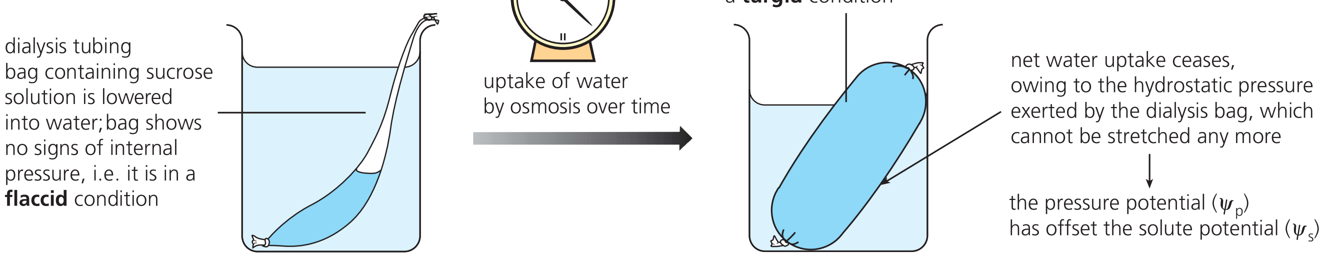


Figure 4.12 Pressure potential at work

Water potential = solute potential + pressure potential

The concept of 'water potential' allows the effects of the two factors acting on water in a system (such as a dialysis tubing 'bag' or a living cell) to be brought together in a single equation:

$$\text{water potential} = \text{solute potential} + \text{pressure potential}$$
$$\psi = \psi_s + \psi_p$$

We have seen that the water potential of a solution is the name we give to this tendency of water molecules to enter or leave solutions by osmosis, and that the Greek letter psi (symbol ψ) is used to represent the water potential.

Since 'water potential' is really a measure of the free kinetic energy of the water molecules, pure water obviously has the highest water potential. By definition, this is set at zero. We have also seen that once a solute is dissolved in water, the water molecules are immediately less likely to diffuse (they are less mobile). So, the effect of dissolving a solute in water is to lower its water potential. Consequently solutions at atmospheric pressure have a negative value of water potential. For example, a solution containing:

3.42 g of sucrose in a 100 cm^3 has a water potential of –270 kPa, and
34.2 g of sucrose in a 100 cm^3 has a water potential of –3510 kPa.

Do negative values like these give you problems?

Not really, perhaps. You use them in daily life. Imagine an international weather forecast that reports the temperature in Siberia has changed from –10 °C to –25 °C. You immediately know this means it's much colder there. In other words, –25 °C is a much lower temperature than –10 °C, even though 25 is a larger number than 10.

In the same way –3510 kPa is a smaller water potential than –270 kPa, although 3510 is larger number than 270.

Questions

10 When a concentrated solution of glucose is separated from a dilute solution of glucose by a partially permeable membrane, which solution:

a has a higher water potential

b has a higher concentration of water molecules

c will show a net gain of water molecules?

Osmosis in cells and organisms

Since water makes up 70–90 per cent of living cells and cell surface membranes are partially permeable membranes, osmosis is very important in living things. We can illustrate this first in plant cells.

Osmosis in plants

We need to think about the effects of osmosis in an individual plant cell first (Figure 4.13). There are two factors to consider.

- In a plant cell there is a cellulose cell wall. This is not present in an animal cell.
- In any cell the net direction of water movement depends upon whether the water potential of the cell solution is more or less negative than the water potential of the external solution.

When the external solution is **less negative** (that is, there is little or no dissolved solutes), there is a net flow of water **into** the cell. The cell solution becomes diluted. The volume of the cell is expanded by water uptake. As a result, the cytoplasm may come to press hard against the cell wall. If this happens the cell is described as **turgid**. The pressure potential that has developed (due to the stretching of the wall) offsets the solute potential of the cell solution completely and further net uptake of water stops. Incidentally, the cell wall has actually protected the delicate cell contents from damage due to osmosis.

When the external solution is **more negative** (that is, much dissolved solutes), there is a net flow of water **out** of the cell. The cell solution becomes more concentrated. As the volume of cell solution decreases, the cytoplasm starts to pull away from parts of the cell wall (contact with the cell wall is maintained at points where there are cytoplasmic connections between cells). The cells are said to be **plasmolysed** (*lysis* means splitting) and are **flaccid**.

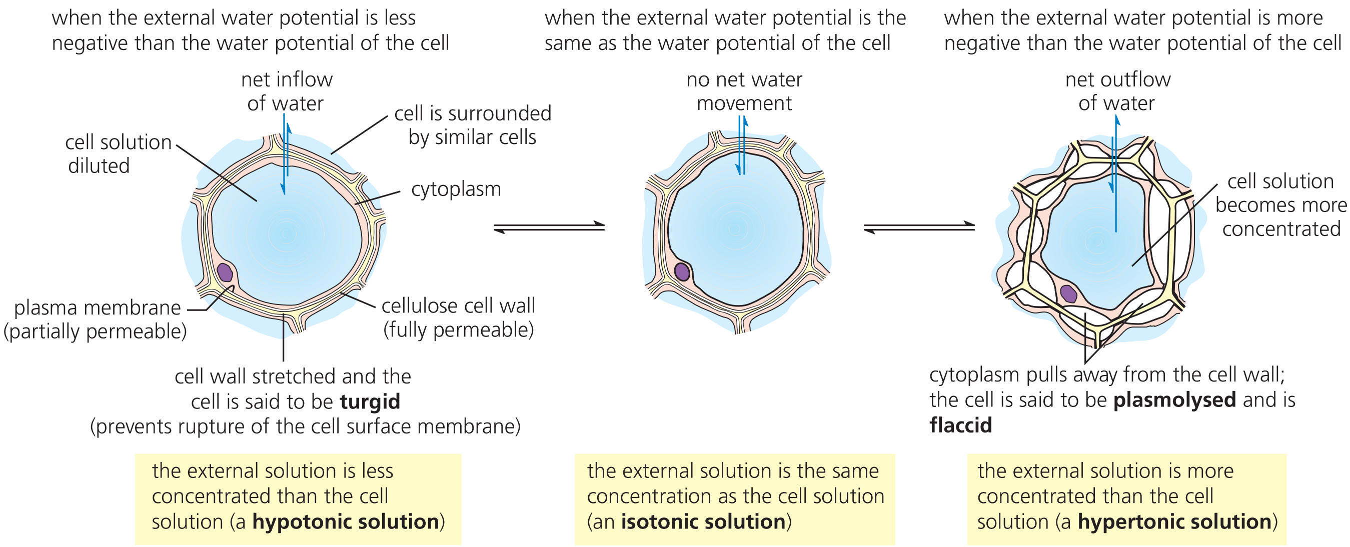


Figure 4.13 A plant cell in changing external solutions

Estimation of the water potential of plant tissue

The net direction of water movement in a cell depends on whether the water potential (ψ) of the cell solution is more negative or less negative than the water potential of the external solution. We exploit this in our measurement of the water potential of plant tissues. Representative samples of tissue are bathed in solutions of a range of water potentials so that the solution which causes no net movement of water can be found. This technique may be applied to plant tissue from which you can cut reproducible-sized cylinders that will fit into a test tube or boiling tube. The tissue should be fully turgid at the outset; soak in water to ensure this. Examples of suitable tissues would include beetroot, potato tuber and carrot root. Cut the cylinders with a cork borer, wash them in tap water, and finally measure their length (or cut them all to a standard length) (Figure 4.14).

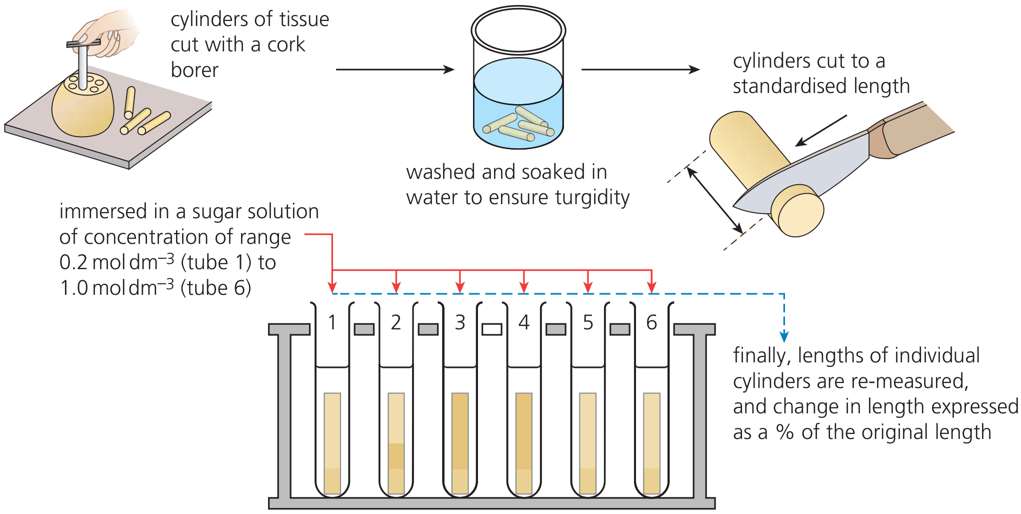


Figure 4.14 Measuring water potential of plant tissue

Table 4.2 The water potential of sucrose solutions

Sucrose (mol dm^{-3})	Water potential (kPa)
0.2	–540
0.4	–1120
0.6	–1800
0.8	–2580
1.0	–3510

Steps to the experiment:

- Immerse (at least) one cylinder in each of the range of five sucrose solutions, 0.2 mol dm^{-3} to 1.0 mol dm^{-3} in a tube. Leave them immersed for one day. Set up a table to record the lengths of the tissue cylinders from each of the five tubes.
- Re-measure the length of each cylinder and record this in your table. Calculate the change in length as a percentage of the original length.
- Plot a graph of the percentage change in length against the molarity of the sucrose solution. Read off the molarity of sucrose that causes no change in length of the tissue.
- Using the conversion table below, quote the water potential of the tissue you have investigated.

In evaluating the experiment, consider the significant potential causes of error or inaccuracy in the technique. *What improvements could you make?*

Movement of water between plant cells

We have seen that water flows from a less negative to a more negative water potential. For example, consider two adjacent cells that have initial solute potentials and pressure potentials (values in kilopascals) as shown:

cell A	cell B
$\Psi s = -1400$	$\Psi s = -2100$
$\Psi p = 600$	$\Psi p = 900$

The water potential of each cell can be calculated ($\psi = \psi_s + \psi_p$):

$$\psi \text{ of cell A} = -800\,\text{kPa}$$

$$\psi \text{ of cell B} = -1200\,\text{kPa}$$

So net water flow is from cell A to cell B until an equilibrium in water potentials is established.

When we discuss water movement through plants (Topic 7, page 135) we will see the flow of water from cell to cell in roots. From root hair cells, where water uptake occurs from a soil solution (of high water potential, i.e. less negative ψ), to the cells at the centre of the root (of lower water potential, i.e. more negative ψ).

Plasmolysis in plant cells

Plasmolysis is most easily observed in cells with a coloured vacuolar solution. Examples include beetroot tissue or the epidermis of rhubarb leaf stalks. There may be others local to you (Figure 4.15).

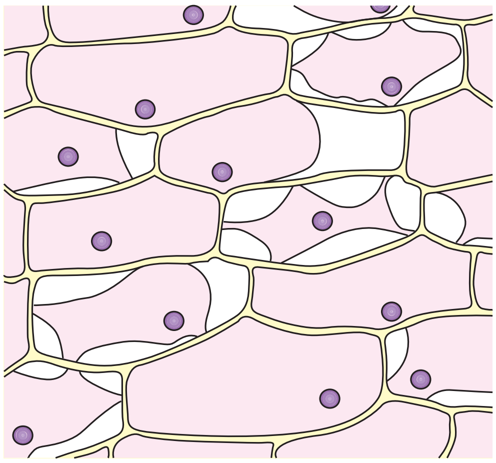


Figure 4.15 Plasmolysed plant cells

In the plasmolysed cell, the wall exerts no pressure at all. As a plasmolysed cell starts to take up water the contents enlarge. At the point where the cytoplasm starts to push against the wall, a slight pressure potential is produced (Figure 4.16). As water uptake continues, the pressure potential eventually becomes large enough to reduce the cell's water potential to zero. At that point, water uptake stops.

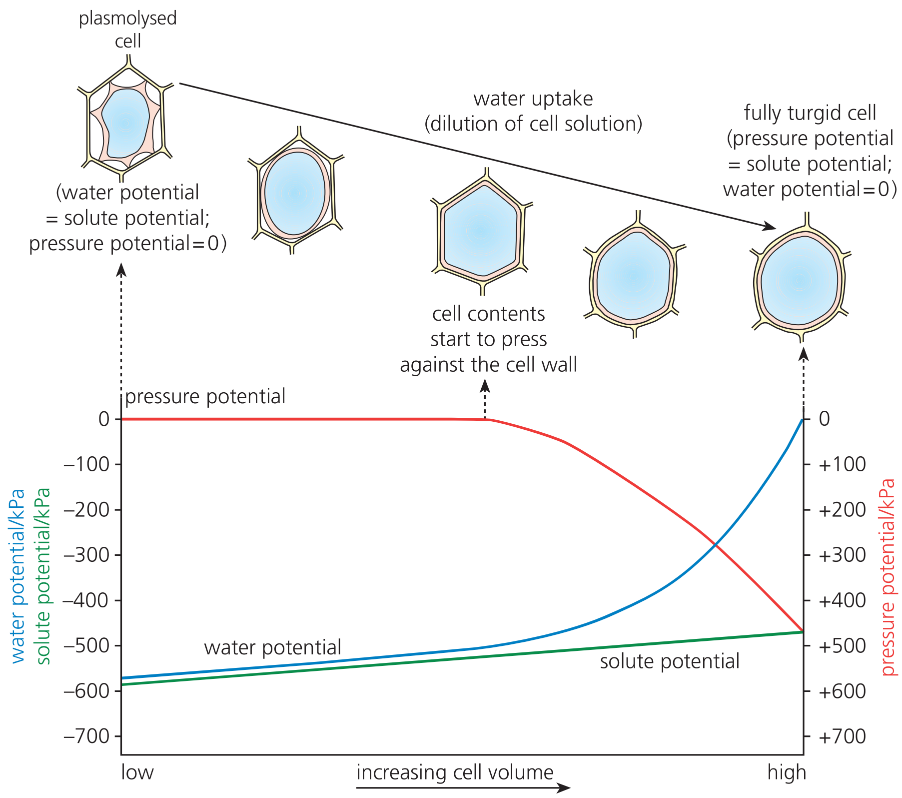


Figure 4.16 Changing water potential of a plant cell

Plasmolysis and wilting

Typically, the cytoplasm of plant cells is undamaged by a period of plasmolysis. Cells promptly recover when water becomes available. In non-woody plants (they are called **herbaceous plants**, to tell them apart from trees and shrubs) a state of turgor is the normal condition. The turgidity of all the cells plays a key part in the support of the plant body. If herbaceous plants become short of water for a prolonged period, the plant wilts. Ultimately, a wilted plant will die if it does not receive water.

well-watered potted plant with turgid cells

water loss continues; many cells of the leaves and stem become plasmolysed; flaccid cells provide no support

Figure 4.17 Wilting

Questions

11 As an herbaceous plant wilts, its cells change from being turgid to flaccid. In this situation, what happens to:

a the solute potential of the vacuolar solution in the cells

b the pressure potential of these cells?

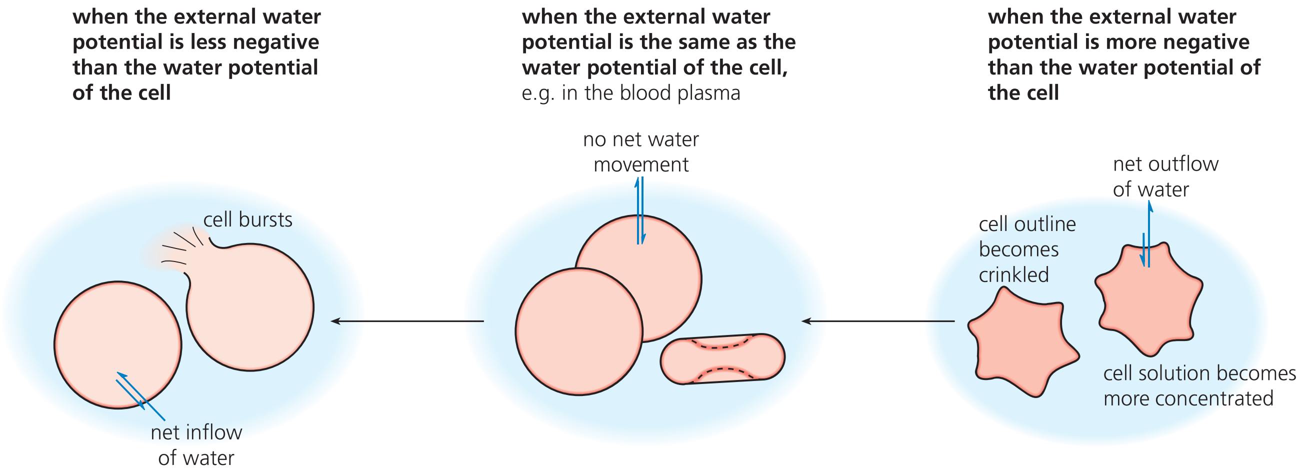
Osmosis in animals

An animal cell lacks the protection of a cellulose cell wall. Consequently, compared with a plant cell, it is very easily damaged by changes in the external solution. If a typical animal cell is placed in pure water, the cell surface membrane will break apart quite quickly. The cell will have been destroyed by the pressure potential generated.

Figure 4.18 shows what happens to an animal cell (a red blood cell) when the external solution has a water potential that is both less negative and more negative than the cell solution.

In most animals (certainly in mammals) these problems are avoided because the osmotic concentration of body fluids – the blood plasma and tissue fluid – is very precisely regulated. The water potential is regulated both inside and outside body cells (to maintain isotonic conditions). This process is known as **osmoregulation** (Topic 14).

Figure 4.18 A red blood cell in changing external solutions



Questions

12 What is the outcome of immersing an animal cell in a solution of substantially lower water potential than that of the cell? What would be the effect on a plant cell?

13 Two adjacent animal cells, M and N, are part of a compact tissue. They have:

cell M	
ψ_s	–580 kPa
ψ_p	410 kPa
cell N	
ψ_s	–640 kPa
ψ_p	420 kPa

Will net water flow be from cell M to cell N? Explain your answer.

Aquatic, unicellular animals

Many unicellular animals live in aquatic environments and survive even though their surroundings have a water potential substantially less negative than the cell solution. All the time, water is flowing into these cells by osmosis. They are in constant danger that their membrane will burst because of high internal pressure. In fact the problem is overcome – or rather, prevented.

The protozoan *Amoeba* is one example. The cytoplasm of an amoeba contains a tiny water pump, known as a **contractile vacuole**. This works continuously to pump out the excess water. How important the contractile vacuole is to the organism is fatally demonstrated if the cytoplasm is temporarily anaesthetised – the *Amoeba* quickly bursts.

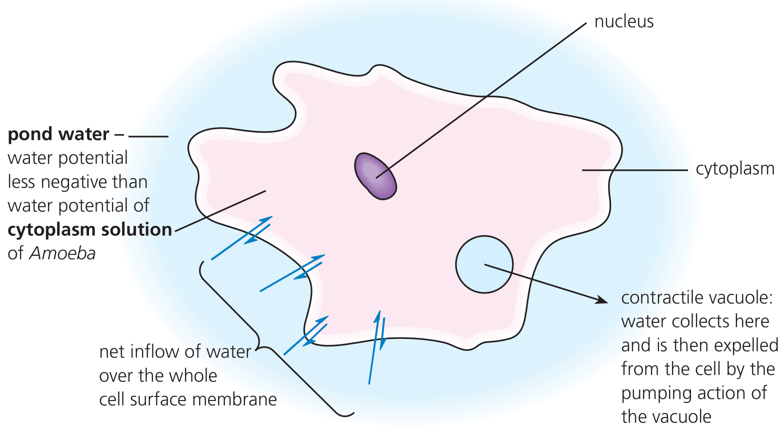


Figure 4.19 The role of the contractile vacuole in *Amoeba*

Extension

Polar water molecules and the lipid bilayer – a recap

We have seen that water enters and leaves cells by osmosis, yet the lipid bilayer of the cell surface membrane is at least theoretically impermeable to polar water molecules. However, water molecules are very small and it is likely that there are many tiny spaces open between the giant molecules of the lipid bilayer. Remember, the lipid molecules are also constantly moving about. In addition, quite small, protein-lined pores exist in the membrane and are permanently open. These proteins allow unrestricted water movement because the pore is lined by hydrophilic amino acid residues.

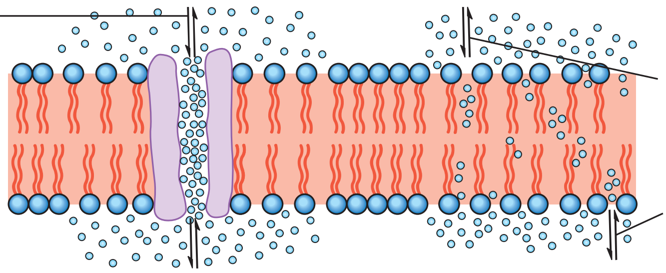


Figure 4.20 How polar water molecules cross the lipid bilayer

Movement by active transport

Active transport is the selective movement of molecules across a membrane. In active transport, metabolic energy produced by the cell and held as ATP is used to drive the transport of molecules and ions across membranes. Active transport has characteristic features distinctly different from those of movement by diffusion. These are as follows.

1 Active transport may occur against a concentration gradient

Molecules can be moved by active transport from a region of low concentration to a region of higher concentration. The cytosol of a cell normally holds some reserves of molecules valuable in metabolism, like nitrate ions in plant cells or calcium ions in muscle fibres. The reserves of useful molecules and ions do not escape; the cell surface membrane retains them inside the cell. However, when more useful molecules or ions become available for uptake, they are actively absorbed into the cells. This uptake occurs even though the concentration outside is lower than the concentration inside.

2 Active uptake is a highly selective process

For example, in a situation where potassium chloride, consisting of potassium (K^+) and chloride (Cl^-) ions, is available to an animal cell, it is the potassium ions that are more likely to be absorbed, since they are needed by the cell. Where sodium nitrate, consisting of sodium (Na^+) and nitrate (NO_3^-) ions, is available to a plant cell, it is likely that more of the nitrate ions are absorbed than the sodium ions, since this too reflects the needs of these cells.

3 Active transport involves special molecules of the membrane called 'pumps'
The pump molecule picks up particular molecules and transports them to the other side of the membrane where they are then released. The pump molecules are globular proteins that traverse the lipid bilayer. Movements by these pump molecules require reaction with ATP. By means of this reaction, metabolic energy is supplied to the process. Most membrane pumps are specific to particular molecules. This is the way *selective* transport is brought about. If the pump molecule for a particular substance is not present, the substance will not be transported.

Active transport is a feature of most living cells. We meet examples of active transport in the gut where absorption occurs, in the active uptake of ions by plant roots, in the kidney tubules where urine is formed, and in nerves fibres where an impulse is propagated. We discuss some of these examples later.

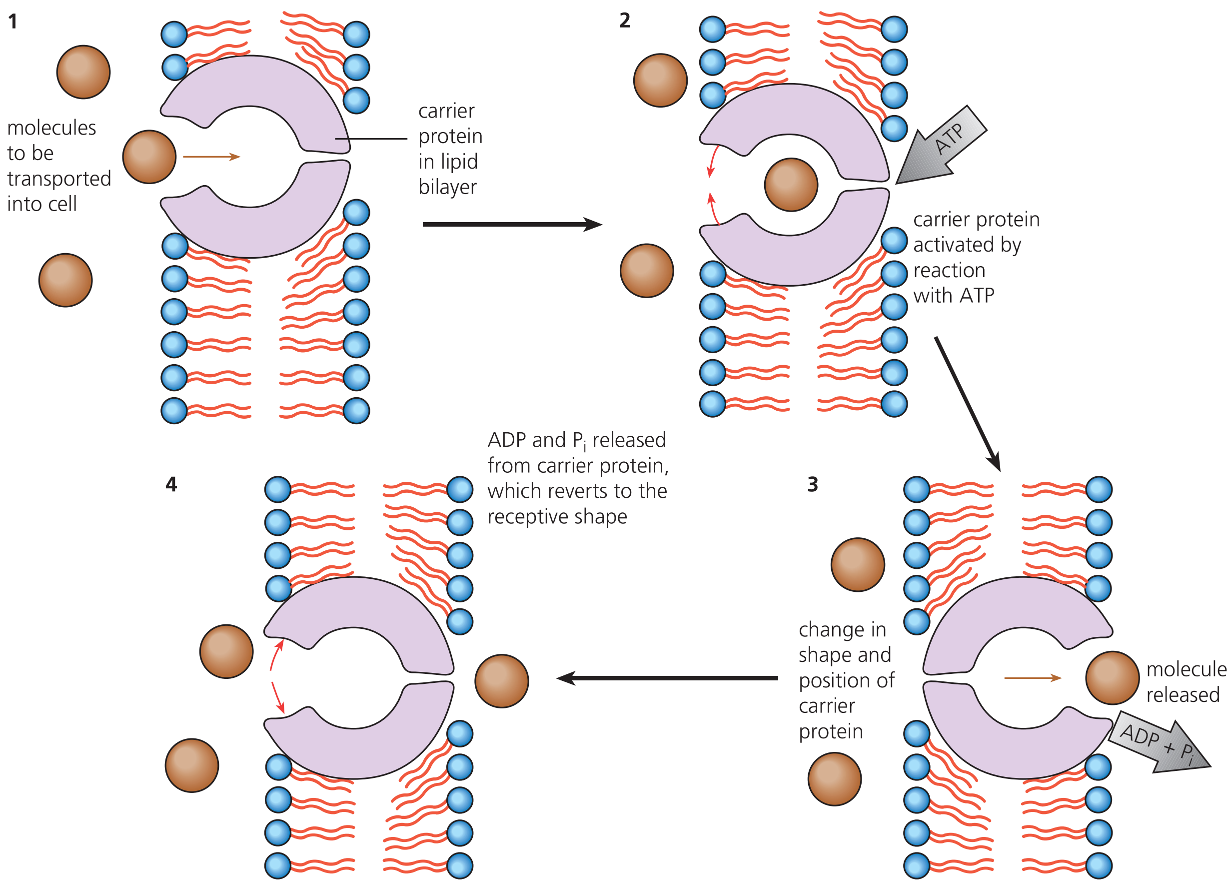


Figure 4.21 Active transport of a single substance

The protein pumps of cell surface membranes are of different types. Some transport a particular molecule or ion in one direction (Figure 4.21). Occasionally, two substances are transported in the same direction; for example, Na^+ and glucose. Others transport two substances (like Na^+ and K^+) in opposite directions (Figure 4.22).

A case study: the structure and function of sodium–potassium pumps in axons

A nerve impulse is transmitted along the axon of a nerve cell by a momentary reversal in electrical potential difference in the axon membrane, brought about by rapid movements of sodium and potassium ions. You can see the structure of a nerve cell and its axon in Figure 15.3, page 313.

Sodium–potassium pumps are globular proteins that span the axon membrane. In the preparation of the axon for the passage of the next nerve impulse, there is active transport of potassium (K^+) ions in across the membrane and sodium (Na^+) ions out across the membrane. This activity of the Na^+–K^+ pump involves transfer of energy from ATP. The outcome is that potassium and sodium ions gradually concentrate on opposite sides of the membrane. The steps to the cyclic action of these pumps are:

1 With the interior surface of the pump open to the interior of the axon, three sodium ions are loaded by attaching to specific binding sites.
2 The reaction of the globular protein with ATP now occurs, resulting in the attachment of a phosphate group to the pump protein. This triggers the pump protein to close to the interior of the axon and open to the exterior.
3 The three sodium ions are now released, and simultaneously, two potassium ions are loaded by attaching to specific binding sites.
4 With the potassium ions loaded, the phosphate group detaches. This triggers a reversal of the shape of the pump protein; it now opens to the interior, again, and the potassium ions are released.
5 The cycle is now repeated again.

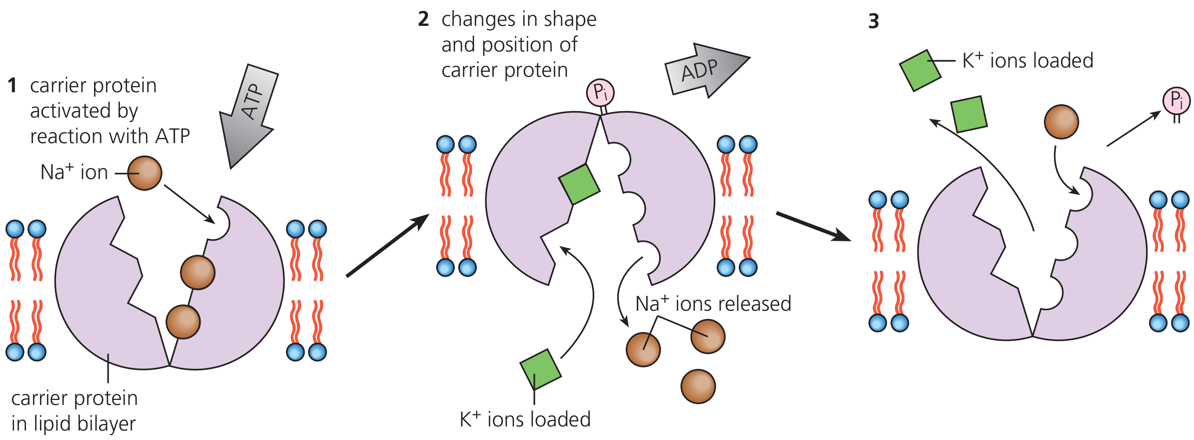


Figure 4.22 The sodium–potassium ion pump

Question

14 Samples of five plant tissue disks were incubated in dilute sodium chloride solution at different temperatures. After 24 hours it was found that the uptake of ions from the solutions were (in arbitrary units):

	Sodium ions	Chloride ions
Tissue at 5°C	80	40
Tissue at 25°C	160	80

Comment on how absorption of sodium chloride occurs, giving your reasons.

Movement by bulk transport

Bulk transport occurs by movements of **vesicles** of matter (solids or liquids) across the cell surface membrane. The flexibility of the fluid mosaic membrane makes this activity possible, and energy from metabolism (ATP) is required. Figure 4.23 shows this form of transport across a cell surface membrane, in action.

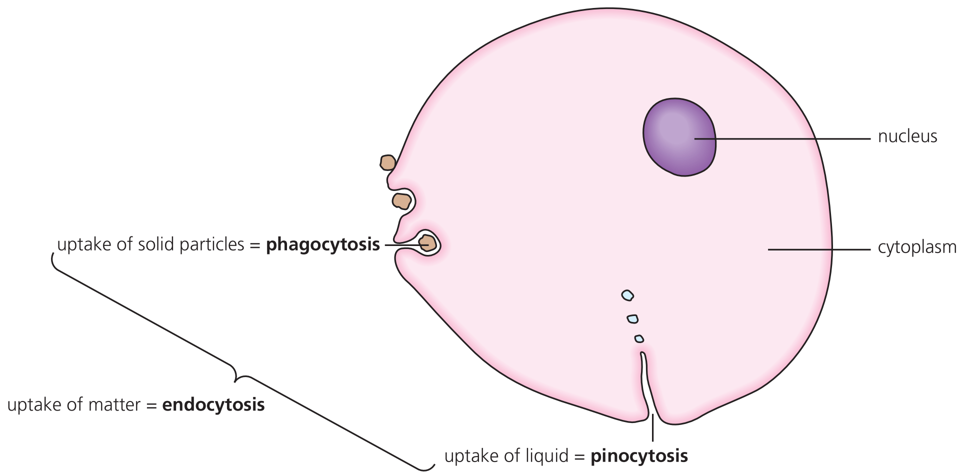


Figure 4.23 Movement by bulk transport

Exocytosis is the process by which cells export products such as enzymes by means of vesicles. We have seen that vesicles may be budded off from the **Golgi apparatus** (Figure 1.16, page 18). The vesicles are then guided to the cell surface membrane by the network of microtubules in the cytosol. Here they merge with the membrane and their contents are discharged to the outside of the cell.

Alternatively, waste matter may be disposed of at the cell surface, in a similar way.

By the reverse process, **endocytosis**, substances may be imported into the cell. Here, fresh vesicles are formed at the cell surface. This occurs when part of the cell surface membrane forms a 'cup' around a particle or a drop of fluid, and encloses it to form a vesicle. This vesicle is then brought into the cytosol.

The wholesale import of solid matter in this way is termed **phagocytosis**. In the human body, there is a huge force of phagocytic cells, called the **macrophages**. Some of these mop up debris of damaged or dying cells and break it down. For example, we dispose of about 3×10^{11} red blood cells each day! All of these are ingested and disposed of by macrophages.

Pinocytosis is bulk import of fluids and occurs in the same way. Bulk uptake of lipids by cells lining the gut occurs as part of the digestion process, for example.

Questions

15 Phagocytic cells are also found in the airways of the lungs. What is their role and how do they carry it out?

16 Distinguish between the following pairs.

- **a** proteins and lipids in cell membranes
- **b** active transport and bulk transport
- **c** hypotonic and hypertonic solutions
- **d** endocytosis and exocytosis

Exocytosis: secretion of materials out of cells by cytoplasmic vesicles fusing with the cell surface membrane and releasing the contents of the vesicle into the fluid around the cell, using ATP to move the cytoplasm.

Endocytosis: uptake of materials into cells by inward foldings of the cell surface membrane to form sacs of membrane that separate from the membrane to form vesicles within the cytoplasm, using energy from ATP to move the cytoplasm around. The process may involve liquid solutions or suspensions (pinocytosis) or solid macromolecules or cells (phagocytosis).

A summary of the functions of membrane proteins

We can now see that the proteins of the cell surface membrane, scattered about and across the lipid bilayer as they are, show diversity in function – all highly significant in the life of a cell. These functions are summarised in Figure 4.24.

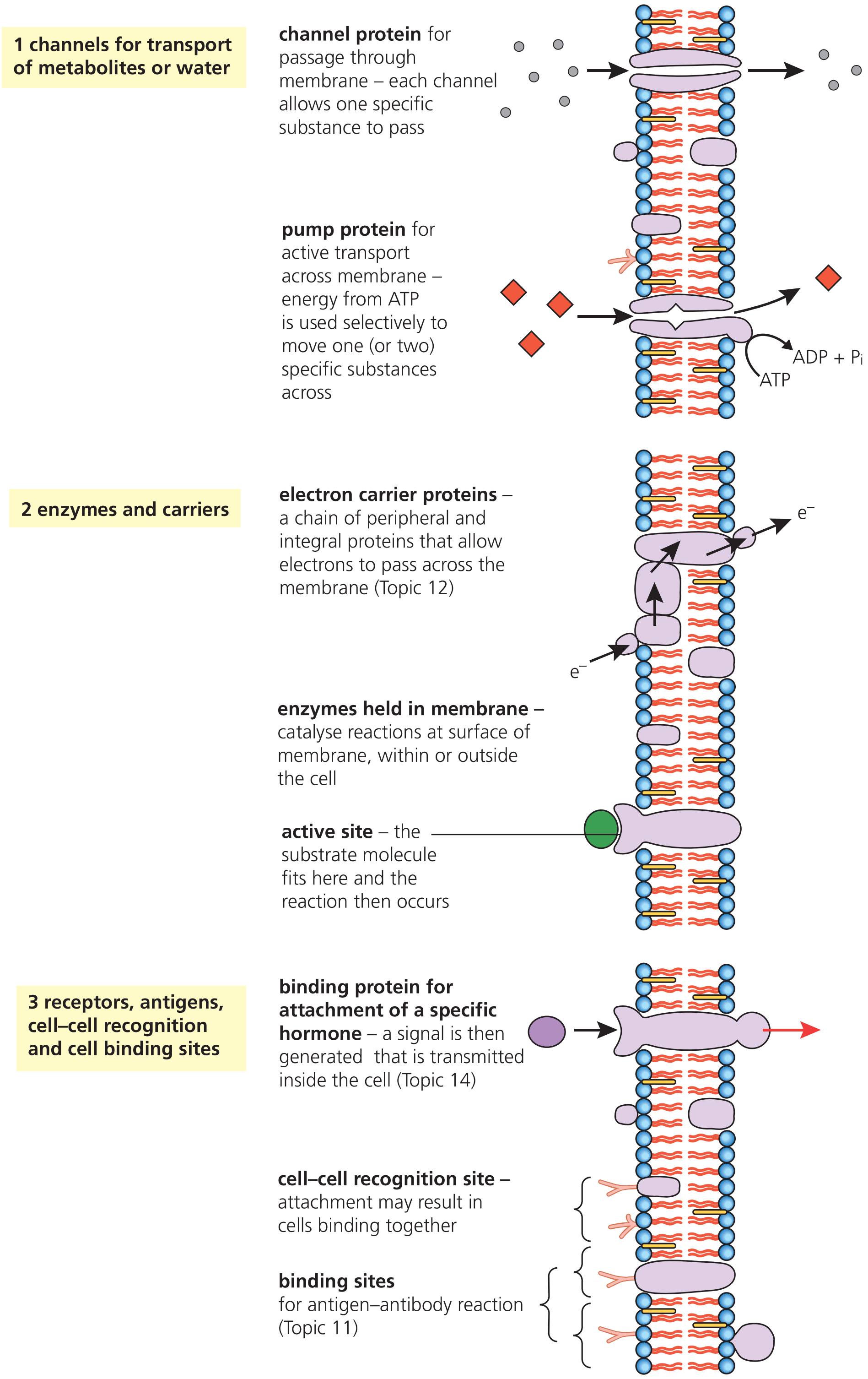


Figure 4.24 The functions of membrane proteins – a summary

Summary

- The **cell surface membrane** is an **organelle** that surrounds and **contains the cell contents**. Across it there is a continuous **movement of the molecules** needed by cells or being disposed of by them.
- The membrane consists of **lipids and proteins** with a small amount of **carbohydrate**. The lipids are **phospholipids**, molecules with a hydrophilic head and a hydrophobic tail, organised into a bilayer with the heads on the outsides. The proteins are **globular proteins** arranged in, across and on the surface of the lipid bilayer. Short carbohydrate chains are attached to some of the proteins and lipids on the outside. In addition, a variable quantity of molecules of **cholesterol** occurs, inserted between some of the lipid molecules.
- The membrane is described as **a fluid mosaic**, as the components (particularly the lipids) move about laterally, relative to each other, and the proteins appear to be randomly scattered about. The cholesterol regulates membrane fluidity.
- There are three **mechanisms of transport** across membranes. In **diffusion** (and **osmosis**, a special case of diffusion) the energy comes from the kinetic energy of matter. In **active transport** (i.e. pumping) and in **bulk transport**, the energy is provided indirectly from cell metabolism, via ATP.
- **Diffusion** occurs from a region of high concentration to a region of low concentration. The lipid bilayer of the cell surface membrane acts as a barrier, at least to polar substances. Polar substances such as water diffuse through tiny pores or small spaces in the bilayer. Some molecules react with a membrane protein to open a specific channel (**facilitated diffusion**).
- The name given to the tendency of water molecules to move about is **water potential**. The Greek letter *psi* (symbol ψ) is used to represent water potential. Water moves from a region of higher water potential to a region of lower water potential – down a **water potential gradient**. Equilibrium is reached only if or when the water potential is the same in both regions. At this point, there would be no net movement of water from one region to another, but random movements of water molecules continue.
- **Solute molecules** in solution are surrounded by water molecules held by **hydrogen bonds**. In a concentrated solution, few water molecules are free to move. Therefore there is net diffusion of **free water molecules** in pure water or a dilute solution (free water molecules in high concentration), through a **partially permeable membrane** (such as the cell surface membrane), into a more concentrated solution (where free water molecules are in low concentration) – a process known as **osmosis**.
- **Active uptake** is a **selective process** and involves the accumulation of ions and organic substances **against a concentration gradient**. The process is powered by metabolic energy and involves highly specific **protein molecules in the membrane** that act as **pumps**.
- Bulk transport is the movement of the contents of **vesicles** (tiny, membrane-bound sacs) of matter, solid or liquid, into (**endocytosis**) or out of (**exocytosis**) the cell.

Examination style questions

1 Fig. 1.1 is a diagram of a cell surface membrane.

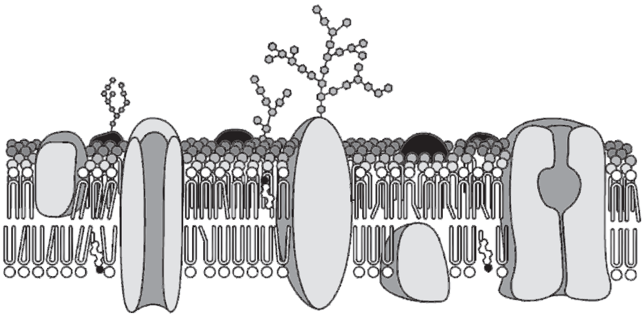


Fig. 1.1

a) Use a label line and the appropriate letter to label each of the following on a copy of Fig. 1.1.

P protein for active uptake of potassium ions

Q protein for facilitated diffusion of polar molecules

R receptor site for a hormone

S hydrophilic heads of phospholipids on the internal surface of the membrane

T molecule that modifies the fluidity of the membrane [5]

b) Some cells take in bacteria by endocytosis.

Explain how endocytosis occurs at a cell surface membrane. [3]

[Total: 8]

(Cambridge International AS and A Level Biology 9700, Paper 21 Q1 November 2011)

2 Fig. 2.1 shows a flatworm which lives in ponds, streams and rivers. The dimensions of the flatworm are 12.5 mm long by 3.0 mm wide. Its volume was estimated as 12.6 mm^3. Flatworms do not have a transport system for the respiratory gases, oxygen and carbon dioxide.

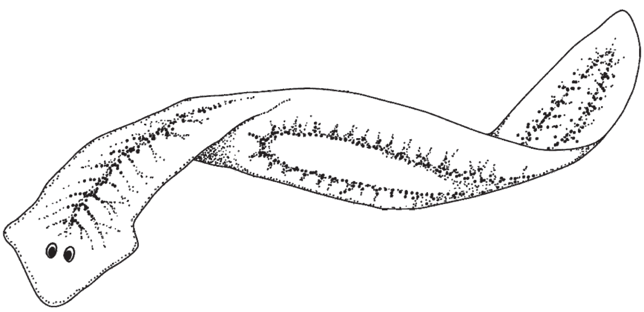


Fig. 2.1

a) With reference to Fig. 2.1 and the information above, explain how flatworms survive without a transport system for respiratory gases. [4]

b) This flatworm lives in freshwater which has a low concentration of sodium ions. The flatworm's body fluids have a higher concentration of sodium ions than the surrounding water.

i) Suggest how the flatworm retains sodium ions in its body fluids. [2]

ii) State **one** role of sodium ions in organisms. [1]

[Total: 7]

(Cambridge International AS and A Level Biology 9700, Paper 22 Q3 June 2009)

3 Thirty strips of plant tissue of measured, standard length were cut, quickly washed, and then blotted dry. To each of three small beakers were added 10 strips and the tissue samples were immersed in sucrose solution of different concentrations. After a period of 30 minutes, the tissue strips were removed and their length remeasured. The results were as follows:

Beaker	1	2	3
Sucrose solution (mol dm^3)	0.1	0.4	0.8
Change in length of tissue strips	increase	no change	decrease

a) Why were the tissue strips briefly washed and blotted dry before measurement? [1]

b) Why did the experimenter use a sample of 10 strips in each treatment? [2]

c) Explain what events in the cells of the tissue strips in beaker 1 during the experiment bring about their change in length. [6]

d) Explain what events in the cells of the tissue strips in beaker 3 during the experiment bring about their change in length. [6]

e) What can you conclude from the results from the tissue sample in beaker 2? [3]

f) For what reason is osmosis described as a special case of diffusion? [2]

[Total: 20]

4 Design and outline a laboratory experiment to investigate the effect of temperature on the cell surface membrane. Use samples of plant tissue that contains an intensely red, water-soluble pigment in the cell vacuoles (such as beetroot).

a) What steps would you take to ensure the significance of your results?

b) What outcomes to your experiment do you expect?