BDS

TEXTBOOK OF PHYSIOLOGY

TENTH EDITION

GEORGE H. BELL
DONALD EMSLIE-SMITH
COLIN R. PATERSON

CHURCHILL LIVINGSTONE

Textbook of Physiology

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Preface to the tenth edition

The tenth edition of a textbook is, for its authors and editors at least, a special one, presenting an opportunity to make changes greater than the usual revision and re-writing necessary between successive editions. Thirty years ago, when the first edition of BDS was written, there were few university departments of biochemistry for the instruction of medical students, and few appropriate textbooks of biochemistry were available for them. Now the position is very different, and most students of physiology are taught biochemistry as a separate subject. Accordingly in this edition the physiology and biochemistry components of the previous edition have been separated. We have not hesitated however to include in this textbook biochemical information essential to the understanding of physiological events.

This edition of BDS is, like its predecessors, addressed to medical, dental and science students of physiology, both undergraduate and postgraduate. All the chapters have been revised and some have been completely re-written. Throughout, we have tried to indicate the relevance of the basic physiology to the practice of clinical medicine.

We owe a great debt to our contributors. Some are responsible for virtually whole chapters, others have made much smaller, but valuable, contributions to the chapters whose numbers are linked to their names. We are grateful, too, for their remarkable tolerance of our editorial activities.

We should like to express our gratitude to Mrs Mina Geekie and Mrs Sheena Moreland for their skilled secretarial work, to Miss Mary Benstead who has prepared many new illustrations for this edition, to Mrs Elizabeth Donnelly for help with the illustrations and to the staff of the Dundee University Library for their assistance.

We acknowledge the help and encouragement of members of the staff of Churchill Livingstone.

Dundee, 1980

G.H.B.
D.E-S.
C.R.P.

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1 Introduction

The term *physiology* refers to the functioning of a living organism or its parts. The workings of a plant or animal are explained partly by its structure but mainly by physics and chemistry. In this textbook we are not concerned specifically with biochemistry but chemical details will be discussed where necessary. A complete description of all events in the human body is not yet possible and sometimes we have to depend on experimental data derived from other mammals or even from bacteria. However, we cannot assume that what is true of other animals is also true for man.

Physiological Processes

In the more complex animals such as birds and mammals, the first characteristics of life that come to mind are warmth and movement. If a non-hibernating animal is still and cold it is assumed to be dead. By taking in food and oxidizing it an animal obtains energy which is used to produce heat or movement. The energy is obtained by the breakdown of body constituents by a process known as *catabolism*. The energy obtained by these catabolic processes may also be used for *anabolic* or synthetic processes such as those necessary for growth. Since both processes occur side by side it is convenient to use the word *metabolism* when referring to the total chemical changes occurring in the cell or in the body. So long as metabolic processes continue, however slowly, the cell is alive; their arrest is death. Since these chemical processes are under the control of enzymes the cells can move or grow only within certain limits of temperature. If the temperature is too high the enzymes are destroyed, while at low temperatures enzymic reactions are retarded and finally cease.

Living material is *organized*, that is, it has a definite structure. Moreover, particular functions, such as movement or secretion or conduction, are carried out by cells or organs whose structure is peculiarly fitted to these purposes. For a cell to survive there must be *integration* of function within it. In multicellular organisms there must be *co-ordination* of the activities of various cells, either by chemical messengers (*hormones*) or by a system of *nerves*.

Growth is a characteristic feature of living material. Growth of a single cell, however, cannot go on indefinitely because, as the cell increases in volume, its surface through which oxygen and food materials are admitted becomes so far removed from its centre that its supply of essential material is endangered. Before this stage is reached the cell divides into two daughter cells, a process known as *reproduction*.

Because a cell does not live in isolation, and can only obtain its food from outside, it must be capable of *reacting* to changes in its environment. Such changes are called *stimuli*. If a stimulus increases the rate of chemical changes in the cell it is said to *excite*; if it decreases the metabolic rate it is said to *depress* or *inhibit*.

Homeostasis. Living organisms possess two properties which at first sight seem to conflict. These are best described under the headings of *adaptation* and *homeostasis*. Simple forms of life can survive over a wide range of temperature and can adapt themselves to changes in their environment and to the foodstuffs available. Indeed, if they could not do so they would soon die. The study of adaptation forms a large part of the subject of physiology, for the cells of the body can adjust themselves to a wide variety of changes. On the other hand, many physiological reactions are directed towards preserving a constant physical and chemical internal environment. All the cells in the body except those on the surface are provided with a fluid environment of relatively constant temperature, hydrogen ion concentration and osmotic pressure. This permits many bodily activities to be carried out under optimum conditions. Small changes in the composition of the extracellular fluid produce reactions which quickly restore the internal environment to its original state. The maintenance of a constant environment for the cells is known as homeostasis.

The first requirement for homeostasis is a detector of deviation from the standard conditions; the appropriate regulator must then be 'instructed' to reduce the deviation. The new state of affairs is continuously assessed by the detector and the regulator is given fresh instructions. In other words the activity of the regulating device is constantly modified on the basis of information fed to it from the detector: such systems are termed 'feed-back' or 'control' mechanisms. Sensory receptors in muscles and joints send information to the central nervous system about length of muscles and angle of joints and movement and posture are regulated; cells sensitive to osmotic changes in the blood regulate the loss of water from the body; receptors in blood vessels detect changes in blood pressure and allow appropriate adjustments in the output of the heart and the calibre of the blood vessels. In many cases, however, the detecting mechanism has still to be discovered.

Our knowledge of the properties and functions of living cells is incomplete but we know that the laws of conservation of matter and energy apply to the animal body just as certainly as they apply to non-living material. Investigation of living matter is largely a matter of observation supplemented by the methods of physics and chemistry. Thus we may measure pressures and potentials, make chemical analyses, or trace the pathways of radioactive substances through the body. The results of these observations are correlated, interpreted in the light of previous knowledge, and used as evidence for or against a particular hypothesis.

Thus the study of physiology may be of great practical importance in leading to methods for the diagnosis and treatment of disease. At one time the organic basis for a patient's symptoms could be established only at post-mortem examination. The trend today, however, is to study the living patient in order to understand the way in which normal physiological and biochemical processes have broken down, for diseases are increasingly regarded as disordered physiological or biochemical processes which the homeostatic mechanisms have been unable to correct.

The bodily activities depend so closely on one another that the workings of one part of the system cannot be comprehended without an understanding of the functioning of the whole. For example, in thinking of the activities of the heart we have to bear in mind the influence of the peripheral blood vessels, of the central nervous system, of respiration and of the chemical changes occurring in cardiac muscle. Our subject may, therefore, be likened to a circle: it is difficult to know where to enter it to begin our study, for it is only when we have completed the circle that we can fully understand it. For this reason we need to consider briefly the subject as a whole before beginning a more detailed description of its various parts.

Outline of Human Physiology

The source of all the energy required by the body for carrying out muscular activity, for respiration, for the beating of the heart and the working of the nervous system, is the food. This consists mainly of proteins, fats and carbohydrates which are oxidized in the tissues. In addition to sources of energy the food must contain inorganic substances which are necessary for example to provide material for the formation of blood and bone and to make good the loss of salts in the excreta. The food must also supply certain substances which the body cannot synthesize, such as vitamins and essential amino acids. Since fluid is lost continuously by way of the kidneys as well as by the skin and lungs, water must be drunk to make good this loss. When food is swallowed it reaches the stomach and small intestine, where it is broken down by enzymes into substances of simpler chemical constitution which are absorbed through the lining of the small intestine into the blood and distributed throughout the body.

Respiration. The oxygen required for combustion of the foodstuffs reaches the blood through the lungs. During breathing the chest expands and air flows into the lungs which are richly supplied with capillary blood vessels. Oxygen diffuses readily through the very thin walls of the capillaries and becomes attached to the haemoglobin contained in the red cells in which it is distributed throughout the body by the circulation. The carbon dioxide produced in combustion in the tissues is taken up by the blood and carried to the lungs where it escapes from the blood and is breathed out. By-products of oxidation not needed by the body reach the kidneys in the blood and are excreted into the urine.

Circulation. The heart is a two-sided muscular pump which drives the blood along the blood vessels. The left side pumps blood to the heart muscle itself, to the skeletal muscles, the brain and other organs (Fig. 1.1) The blood from these parts returns to the right heart which sends the blood to the lungs where oxygen is taken up and carbon dioxide is eliminated. The oxygenated blood then returns to the left side of the heart and is pumped out to the tissues. The blood is conveyed away from the heart at a fairly high pressure in thick-walled tubes, the arteries. These vessels branch repeatedly and become smaller in diameter, with thinner and thinner walls. In the tissues the smallest blood vessels, the capillaries, are bounded by a single layer of cells through which gases, water, or chemical substances of small molecular size move easily. The blood is drained away from the tissues at low pressure in the veins, wide vessels with relatively thin walls.

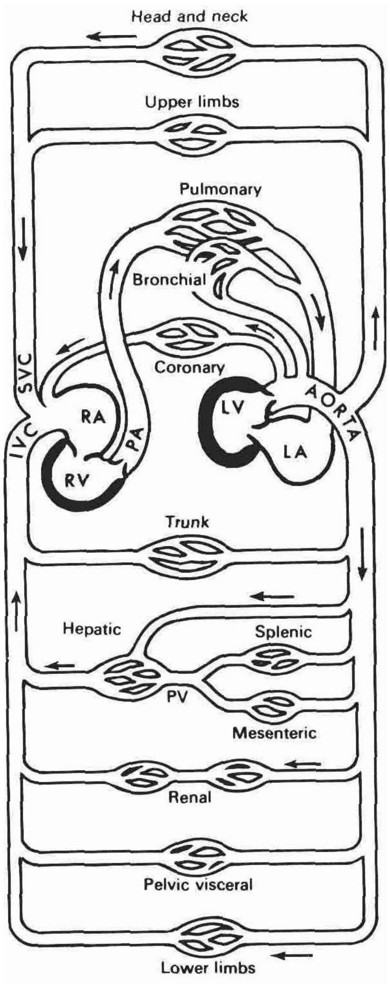

Fig. 1.1 Diagram to show the heart and circulation displayed as two ('left' and 'right') hearts and two circulations (systemic and pulmonary) arranged in series. Various important divisions of the systemic circulation are also indicated. Blood flows from arteries through capillary beds to veins. The renal circulation has two capillary beds, glomerular and tubular. PV=portal vein.

William Harvey's great discovery of the circulation of the blood is the basis of modern physiology. Harvey's work was important in a wider sense: the methods he used were essentially those of modern science—verifiable experiments yielding qualitative and quantitative data and the subsequent use of the data to develop a hypothesis. He observed, for example, that the arterial pulse occurred a very short time after the contraction of the heart and concluded that the one was responsible for the other. He noted that when an artery was cut the blood gushed out from the end nearer to the heart; the force of the gush was increased at each contraction of the ventricles. Once the blood had reached the great arteries it could not flow back into the heart because of the semilunar valves. The flow of blood in the arteries must therefore be from the heart. Similarly he made observations which indicated that blood flowed back to the heart in the veins. One of these is shown in Figure 1.2. He showed, as well, that the amount of blood ejected by a ventricle beating at its usual rate is much greater during half an hour than the total blood volume. Only a circulation could explain his findings.

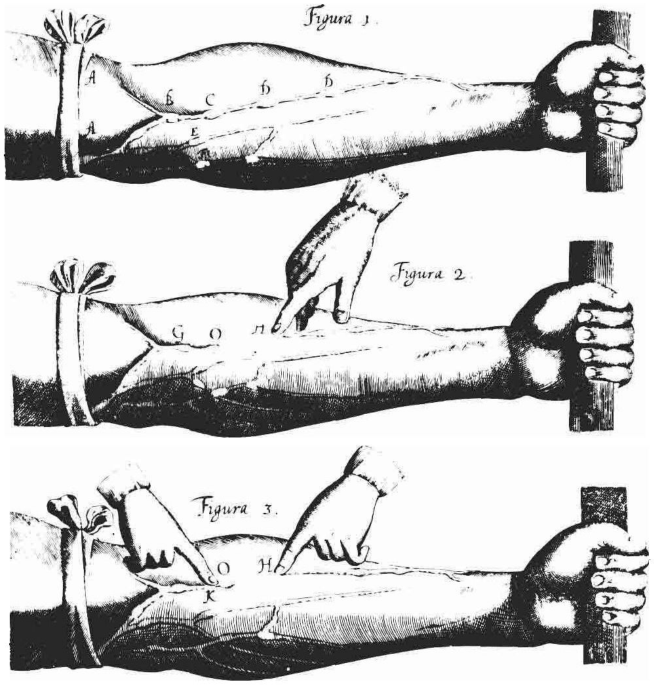

Fig. 1.2 Illustrations from Harvey's *De motu cordis* (1628). If a bandage is put around the arm tight enough to obstruct the superficial veins (but not the arteries) the veins swell. Valves can be seen as dilatations at intervals along the veins (Figura 1). If blood is milked backwards along a vein from O to H (Figura 2) none flows back through the valve at O. If then the vein is allowed to refill and the finger put back at H, blood can be milked through the valve at O but none flows back through the valve. The section H to O can be repeatedly refilled from H and emptied through O. It is clear therefore that blood in the veins can only move from the periphery toward the heart and must be derived from arterial blood.

Co-ordination. The skeletal muscles are the main effector tissues. By their contractions the position of the bones is altered during motion and respiration and speech are made possible. The highly complex movements of the limbs in walking, and of the tongue in speech, are co-ordinated by the central nervous system, consisting of the brain and spinal cord. Nerves called *efferent* or *motor* nerves leave this system and pass to all the structures of the body and control muscular movement as well as the secretion of some of the glands, the heart beat and the calibre of the blood vessels. Central control is, however, valueless unless the centre has full information about events in the body and around it. This information is conveyed to the central nervous system by the *sensory* or *afferent* nerves which carry impulses from the eye, the ear, the skin, the muscles and joints, and the heart, the lungs and the intestines. The sensory nerves are much more numerous than the motor nerves. Although many of the activities occurring in the central nervous system are exceedingly complex, relatively few rise to consciousness. We are quite unaware, for example, of the muscular adjustments needed to maintain balance or to move our eyes so that images of the external world are kept fixed on the retinae. These adjustments are called *reflex* and

In addition to the rapidly acting co-ordinating mechanism of the nervous system the body possesses a chemical (*humoral*) system which operates more slowly. For example, during the digestion of food a chemical substance (*hormone*) called secretin is produced in the mucous membrane of the duodenum, is absorbed into the blood and carried to the pancreas which responds by pouring out its digestive juices.

Reproduction. Under this heading, we consider the processes necessary for the maintenance of the species. The male cells, the *spermatozoa*, are produced in the testes and when deposited in the female genital tract one of them may fertilize an *ovum* produced in the ovary. This sets off a series of complicated changes, mainly under hormonal control, to provide for the nutrition of the fertilized cell in the uterus. At the end of pregnancy the muscular wall of the uterus contracts, the fetus is delivered and then acquires oxygen directly, by breathing air into its lungs, instead of indirectly through the *placenta*.

The Composition of Living Tissues

In addition to a large amount of water, the living body contains protein which is the main nitrogenous constituent of all living material, a variable amount of fatty material known collectively as lipid, a small amount of carbohydrate, mainly glycogen and carbohydrate-protein complexes, and mineral salts. In man the relative proportions of these constituents, especially fat and carbohydrate, vary greatly from one person to another, and in the one individual at different times in his life, according to his nutrition. Nevertheless, the composition of the human body may be represented roughly as shown in Table 1.3.

Table 1.3 Approximate composition of a man weighing 70 kg (154 lb)

	Percentage	kg
Water	70	49
Fat	15	10·5
Protein	12	8·4
Carbohydrate	0·5	0·35
Minerals	2·5	1·75
	100	70

The considerable variations in total body water between one person and another are the result of differences in fat content since the amount of water in the fat-free parts of the body is remarkably constant. In very fat people the body water may be no more than 40 per cent of the total body weight. In the fetus the relative proportion of water in the body is much higher, for example 94 per cent at the third month of fetal life.

Most tissues contain more than 70 per cent water. Exceptions are adipose tissue (50 per cent), bone (30 per cent) and teeth (5 per cent). Table 1.4 shows that by far the greatest amount of water is to be found in muscle which accounts for the largest part of the body mass.

In its capacity as a solvent, water plays a fundamental role in

Table 1.4 Percentage of the total body water which is found in the various tissues and organs

Muscle	50·8	Brain	2·7
Skeleton	12·5	Lungs	2·4
Skin	6·6	Fatty tissue	2·3
Blood	4·7	Kidneys	0·6
Intestine	3·2	Spleen	0·4
Liver	2·8	Rest of body	11·0
			100·0

fine emulsions or be rendered water-soluble in other ways, for example by combining with proteins. Some other properties of water are also important. The high heat capacity of water and its high latent heat of evaporation both contribute to the control of body temperature (Chap. 26).

Normally a large amount of water is lost from the body daily and a corresponding amount is taken in, so that water balance is maintained. The amount of water gained and lost by an adult man engaged in a sedentary occupation in a temperate climate is about 2.5 litres per day.

The elements of the human body are shown in Table 1.5.

Table 1.5 Composition of the human body (per cent by weight)

Oxygen	65	Chlorine	0·15
Carbon	18	Magnesium	0·05
Hydrogen	10	Iron	0·004
Nitrogen	3	Iodine	0·00004
Calcium	1·5	Copper	traces
Phosphorus	1·0	Manganese	traces
Potassium	0·35	Zinc	traces
Sulphur	0·25	Fluorine	traces
Sodium	0·15	Molybdenum, etc.	traces

The most abundant are carbon, oxygen and hydrogen, but minerals such as calcium and phosphorus are also plentiful. Other minerals such as iodine and iron are present only in small quantities. Nevertheless their presence in the diet is of great nutritional importance (pp. 32 to 34).

THE CELL

A schematic diagram of a 'typical' animal cell is shown in Figure 1.6. The cell is surrounded (or limited) by a cell

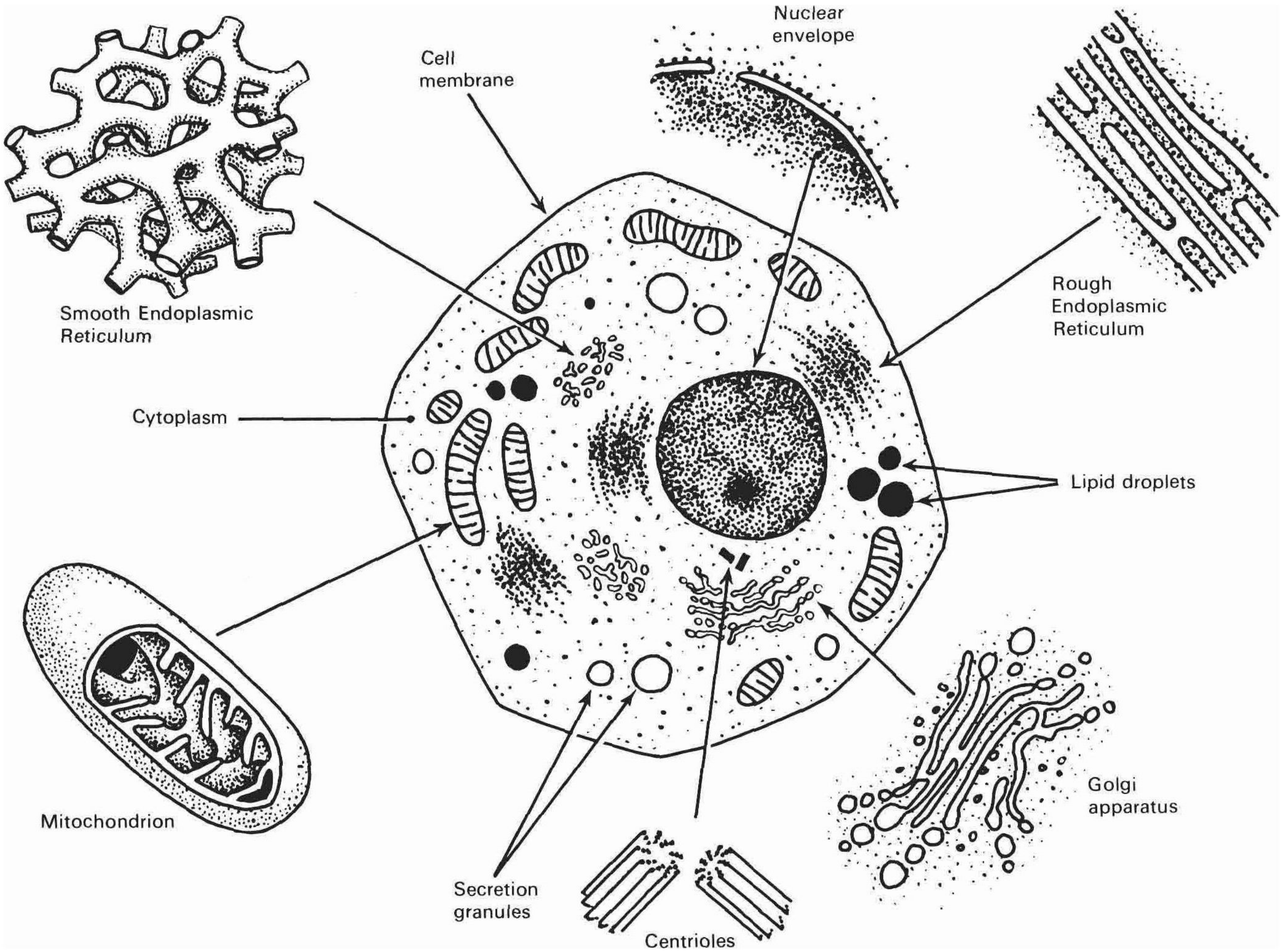

Fig. 1.6 The composition of a typical cell. The organelles as seen by electron microscopy are shown in greater detail around the outside. The interpretation of appearances shown by the electron microscope remains controversial but the appearances shown are those most widely accepted. (*After* W. Bloom & D. W. Fawcett (1975) *Textbook of Histology*. 10th edition. Philadelphia: Saunders.)

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membrane or *plasma membrane.* All cells except red cells contain a nucleus; the rest of the cell contents is known as cytoplasm which consists of a number of other organelles embedded in a liquid cell sap or *cytosol.* The cytosol contains a number of enzymes and also the low molecular weight transfer RNA.

Membranes. The plasma membrane and also the bounding membranes of the nucleus and other organelles have many features in common. All contain both phospholipids and proteins; the lipids have their hydrophilic 'heads' outermost and their hydrophobic fatty acid chains pointed toward the interior of the membrane (Fig. 1.7).

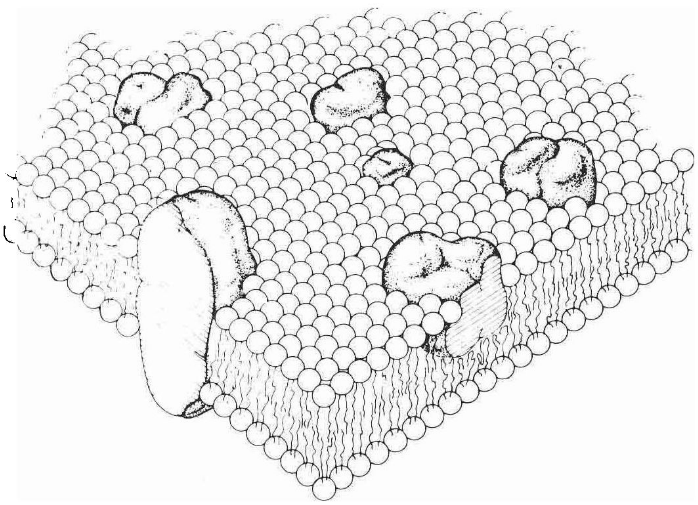

Fig. 1.7 A model to show current views of membrane structure. Irregularly shaped proteins float randomly in a lipid 'sea'. It seems likely that the proportion of protein varies greatly between membranes in different sites. (*After* P. Chapnick (1973) The skin of our cells. *The Sciences,* April 1973, 20–24.)

The ease with which a molecule can cross a membrane depends partly on its size but to a greater extent on its solubility in lipids. Thus membranes are usually impermeable to large molecules such as proteins and also to small ions, but permeable to water and small uncharged molecules like urea. Membranes are selective with regard to water-soluble substances such as sugars and amino acids. They are transported by carrier proteins which are highly specific and capable, for example, of carrying D-glucose but not L-glucose. Apart from carrier proteins the plasma membrane has special proteins which are receptors for hormones and proteins to express the person's immunological identity such as the blood group antigens on red cells and the histocompatibility antigens on other cells (Chap. 9).

The membranes surrounding subcellular organelles also have a selective permeability and enclose discrete compartments, each with its own complement of enzymes, substrates and co-factors. This arrangement ensures that different metabolic processes within the cell proceed optimally. For example, the ideal conditions for fatty acid synthesis are not the same as for fatty acid breakdown; the former takes place in the cytosol while the latter occurs within the inner membrane of mitochondria.

Because lipids are electrical insulators there may be

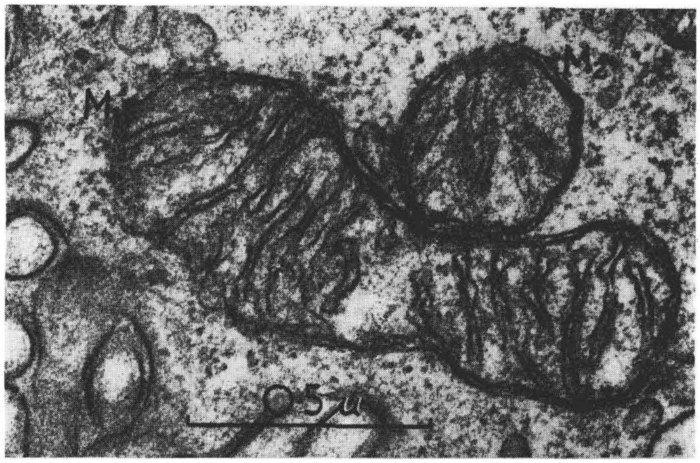

Fig. 1.8 Mitochondria in longitudinal section (M_1) and in cross section M_2 lying close to the surface membrane of the cell. (*By courtesy of P. G. Toner and G. M. Wyburn.*)

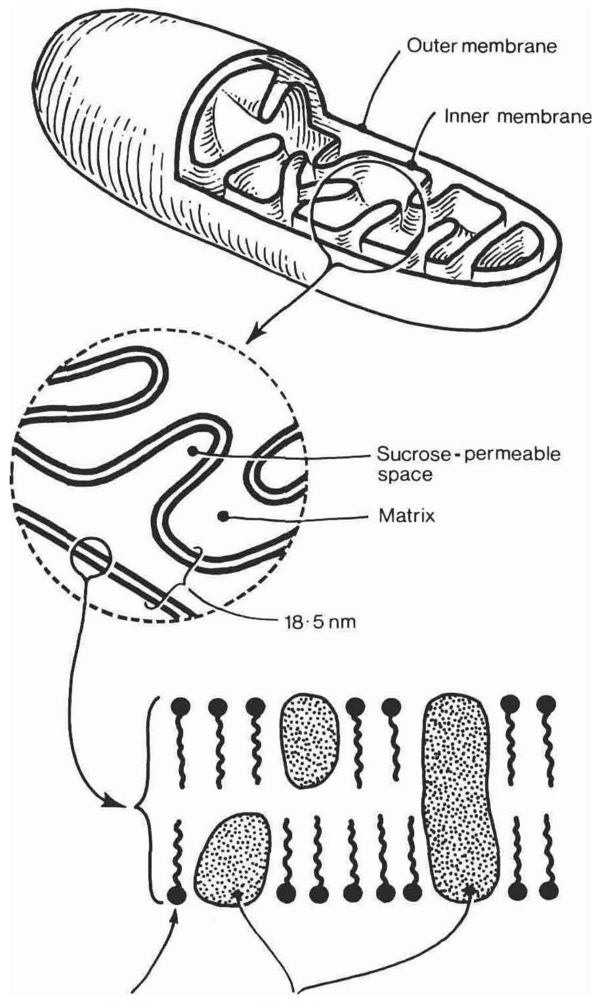

Fig. 1.9 Sketch of mitochondrion to show the double wall. The inner membrane, which is folded to give the cristae, separates the outer *sucrose permeable space* from the inner *matrix.* The bottom diagram shows an enlarged view of the double membrane which, like the cell membrane, consists of lipids and proteins. The proteins of the inner membrane include the enzymes of the electron transport system.

considerable differences in electrical voltage across a membrane.

The organelles. The *nucleus* contains a mesh-work of densely staining DNA, the chromatin of the histologist. Before a cell divides, the chromatin condenses to form the *chromosomes* which contain almost all the DNA of the cell. The nucleus is surrounded by a double membrane pierced at intervals by pores, and contains one or more dense, spherical bodies termed *nucleoli* which are rich in RNA and are the sites of synthesis of the ribosomal RNA responsible for protein synthesis.

Surrounding the nucleus is the *cytoplasm* in which are found various organelles such as secretion granules, lysosomes and mitochondria (Fig. 1.8). Each *mitochondrion* is bounded by a double membrane, the inner layer of which is folded to produce the *cristae* which divide the interior into compartments. Each membrane consists of a lipid bilayer containing proteins (Fig. 1.9). The mitochondria (of which there are about 400 in a liver cell) contain the enzymes responsible for oxidative phosphorylation, and are the site of the production of high energy compounds (such as adenosine triphosphate, ATP) in the cell. They have been termed the 'power houses of the cell'. But probably an equally important function of mitochondria is the regulation of the calcium concentration within the cell by the uptake and release of calcium ions. Thus the activity and metabolism of many cells, especially cardiac cells, are regulated to some extent by their mitochondria.

The cytoplasm also contains a complex meshwork of canals and vesicles known as the *endoplasmic reticulum* (Fig. 1.10) with membranes about 5 nm thick. Two kinds of endoplasmic reticulum can be distinguished under the electron microscope, rough endoplasmic reticulum (RER) and smooth endoplasmic reticulum (SER). These tubules appear to form a series of canals leading from the exterior of the cell to the nucleus. The SER contains enzymes responsible for metabolic pathways such as those for the detoxication of foreign substances and for the synthesis of hormones and glycoproteins. In the RER the surface of the tubules and vesicles is studded with small round electron-dense particles (diameter 10 to 20 nm) known as *ribosomes*. These consist of about equal amounts of protein and RNA and, together with transfer RNA, messenger RNA, activated amino acids, enzymes and other factors, are responsible for protein synthesis. Ribosomes also occur free in the cytoplasm, unattached to reticular membranes. Indeed, in some cells (intestinal epithelium, tumour cells) the endoplasmic reticulum is scanty and most of the ribosomes are unattached. During the mechanical disruption of cells, the endoplasmic reticulum also is disrupted and, after isolation by differential centrifugation, is obtained in the form of fragments of membrane, each bearing some ribosomes. These fragments of membrane are known as *microsomes* (diameter 60 to 150 nm) and the ribosomes may be released from them by a suitable surface active agent such as sodium deoxycholate. The ribosomes may then be purified and analysed.

The cytoplasm of most cells also contains small organelles known as *lysosomes* (formerly known as microbodies) which are essentially little sacks of hydrolytic enzymes which can break down large molecules. The enzymes include peptidases (cathepsins) which break down proteins, ribonuclease, deoxyribonuclease, β-glucuronidase and acid phosphatase. These enzymes are thought to be responsible for the dissolution of damaged or dead cells during the process of autolysis. They also play an important role in the phagocytes, the cells which ingest and destroy foreign particles such as bacteria (Chap. 9). Peroxisomes are small organelles which contain catalase and take up hydrogen peroxide.

Some cells contain a *Golgi apparatus* which is concerned with the packaging of proteins produced by the RER before their excretion from the cell. It is generally thought that the Golgi apparatus is continuous with the RER and also with other organelles, particularly lysosomes.

Also in the cytoplasm are microfilaments and microtubules which are 25 nm in diameter and have walls consisting mainly of very fine helical filaments of the protein 6-*S* tubulin. The microtubules (Fig. 1.11) are concerned with movements of the cell and also movements of organelles within the cell; they

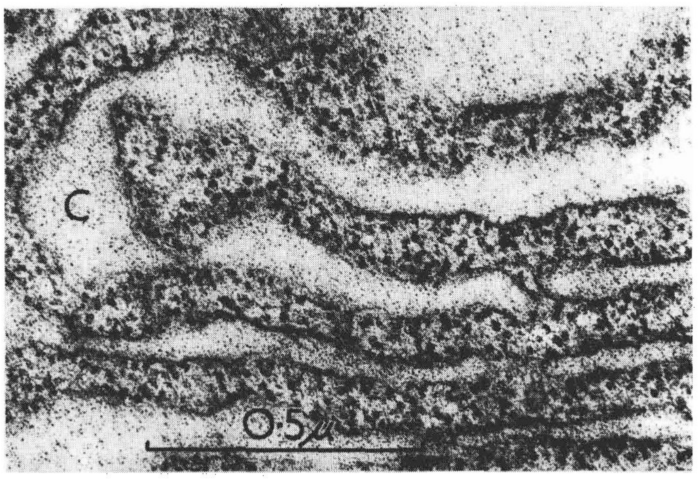

Fig. 1.10 Cisternae of granular endoplasmic reticulum showing cavities (C) bounded by membranes. Ribosomes are attached to the outer, or cytoplasmic, surfaces of the cisternae and also lie free in the cytoplasm. (*By courtesy of P. G. Toner and G. M. Wyburn.*)

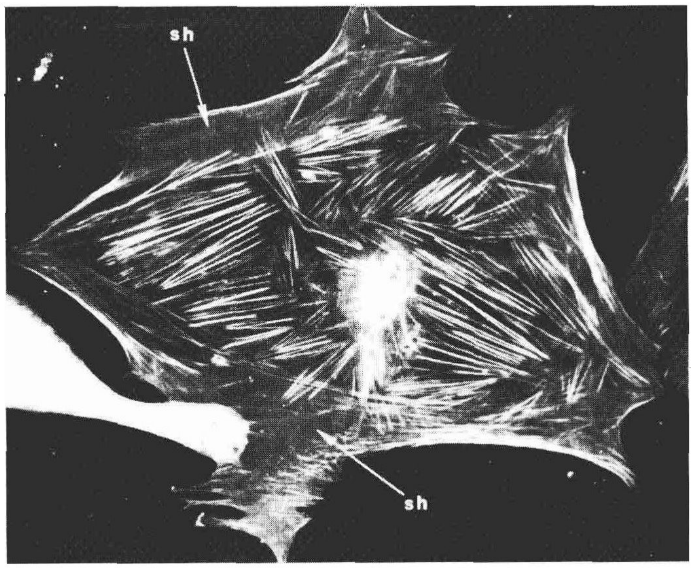

Fig. 1.11 Fibroblast from human skin with immunofluorescent staining to show actin in microfilaments. sh indicates sheath-like structures whose function is unknown. From Lazardides, E. (1975) *Journal of Cell Biology*, 65, 549–561.

form the spindle of the mitotic apparatus which draws apart the chromosomes in anaphase during cell division.

Coated vesicles (60 to 110 nm) found in many cells transport cell membrane from one place to another in the form of small bags inside the cell. The crystalline coat of these vesicles is of a protein called *clathrin* in the form of an open polyhedral lattice. In nerve cells the coated vesicles recycle the membrane used to carry packets of transmitter substance. In oocytes the vesicles gather up pieces of yolk protein.

It is easy to get the idea from a histological section that cells are fixed immobile structures but immuno-fluorescence methods have shown that many cells as well as muscle cells contain filaments of the muscle proteins actin, myosin and tropomyosin. Both microfilaments and microtubules are likely to be involved in normal cell movement.

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2 Food, Energy and Nutrition

The food we eat is composed of animal and plant tissues or products derived from them. Its oxidation provides the energy needed for the maintenance of body temperature, for muscular activity including that of the heart and for metabolism including synthetic processes. In addition, food provides materials which cannot be synthesized in the body.

THE COMPOSITION OF FOODS

Milk

The human infant starts life on a diet consisting solely of milk. Human and cow's milk differ in composition and average values are given in Table 2.1. Cow's milk varies with the season, the breed of the cow and its feeding. Artificial milks used for infant feeding often differ markedly from human milk.

Table 2.1 Composition of human and cow's milk per 100 g

	Human milk	*Fresh summer cow's milk*
Energy value	289 kJ	272 kJ
Water	87·1 g	87·6 g
Protein	1·3 g	3·3 g
Casein: whey proteins	1:3	4:1
Fat	4·1 g	3·8 g
Carbohydrate (lactose)	7·2 g	4·7 g
Calcium	34 mg	120 mg
Iron	70 μg	50 μg
Phosphorus	14 mg	95 mg
Sodium	14 mg	50 mg
Potassium	58 mg	150 mg
Citrate	80 mg	150 mg
Retinol and carotene	35 and 22 μg	35 and 22 μg
Thiamin	20 μg	40 μg
Riboflavin	30 μg	190 μg
Niacin	220 μg	80 μg
Ascorbic acid	3·7 mg	2 mg
Vitamin D sulphate	0·9 μg	0·03 μg

This and the subsequent food tables are derived from *McCance and Widdowson's The Composition of Foods* 4th edition (1978) by Paul, A. A. & Southgate, D. A. T. London: H.M.S.O.

The chief proteins of milk are casein and the whey proteins, α-lactalbumin and β-lactoglobulin. Casein, a phosphoprotein, occurs as calcium caseinate. When acid is added to milk casein is rendered insoluble and the milk curdles. Milk goes 'sour' and curdles if kept at room temperature because bacteria in it multiply and produce lactic acid. When milk comes into contact with the enzymes rennin or pepsin *coagulation* or *clotting* occurs and a clot of calcium caseinate separates. On standing the clot contracts, expressing a clear fluid known as whey. The clot retains all the milk fat.

Milk is an excellent source of protein, calcium and phosphorus but it is deficient in iron. However, infants are born with a store of iron sufficient to prevent anaemia unless the period of suckling is more than about four months.

Milk is an important source of vitamins A and D and riboflavin; it is a poor source of vitamins C and K. Human breast milk contains sufficient vitamin D as water-soluble vitamin D sulphate to meet the needs of the young infant. Breast-fed infants rarely suffer from rickets.

Raw milk is perishable because it provides an ideal substrate for the growth of micro-organisms. Freshly drawn milk may contain bacteria, some of them pathogens, and it may be further infected during handling before reaching the dairy or factory. Thus to ensure that a bacteriologically safe product of good keeping quality is delivered to the consumer it is necessary to destroy the pathogens by appropriate heat treatment and to reduce the population of the other bacteria. Most milk destined for the liquid market is pasteurized by the high temperature short time (HTST) process in which it is heated to 71 to 73°C for not less than 15 seconds. Pasteurized milk should contain no pathogenic micro-organisms and the content of other micro-organisms should be so low that the milk will remain fresh for several days if kept cool. Pasteurization has little effect on the nutritional value of milk, the only significant change being a loss of about one-quarter of the vitamin C.

For longer term storage milk is sterilized by being heated to 130 to 150°C for one second and filled aseptically into cartons. The resulting product, ultra heat treated (UHT) milk, has suffered little loss of nutritive value and keeps for up to six months without refrigeration.

Dried milk. In the preparation of dried milk, water is removed either by spray-drying or by roller-drying. The resulting product is of high nutritive value but it cannot be stored for very long periods since the fat tends to be oxidized and become rancid. Dried skim milk is a valuable source of protein and calcium but it is, of course, almost free from fat and the fat-soluble vitamins A and D.

Condensed milk. This is prepared by removing part of the water in a vacuum. The concentrate is then sterilized at a high temperature in tins (*evaporated milk*), or it is treated with sugar (about 40 per cent) to prevent the growth of bacteria (*sweetened condensed milk*).

Cream and butter. In the preparation of *cream* the fat is separated from milk either by gentle centrifugation or by allowing it to rise to the surface. Cream contains a high proportion (40 to 50 per cent) of fat. Milk from which the cream has been removed is known as *skim milk.*

Table 2.2 Composition of dairy produce per 100 g

	Protein g	Fat g	Carbo-hydrate g	kJ	Calcium mg	Iron mg
Cow's milk, whole	3·3	3·8	4·7	272	120	0·05
Cow's milk, skimmed	3·4	0·1	5·0	142	130	0·05
Butter	0·4	82	0·0	3041	15	0·16
Margarine vitaminized	0·1	81	0·1	3000	4	0·3
Cheese, cheddar type	26	33·5	0·0	1682	800	0·4

When cream is submitted to prolonged shaking (churning) the fat globules coalesce to form a solid mass of *butter* which is, like cream, an important source of the fat-soluble vitamins, especially vitamin A. It contains 65 per cent saturated fats. The residual fluid, known as buttermilk, has a composition similar to that of skim milk and is a rich source of protein, lactose and the inorganic salts of milk.

Cheese. This is made by coagulating the proteins of milk with rennet (an enzyme preparation from calf stomach) at 30°C. Most of the fat is included in the coagulated mass which is pressed out and allowed to 'ripen' under the influence of bacteria. The characteristic texture and taste of the finished cheese depends on the particular bacteria and moulds involved in the ripening process. During the ripening process tyramine may be formed from tyrosine; some varieties may contain more than 0·5 mg of tyramine per g. Cheese is a good source of protein, fat, and mineral elements such as calcium.

Margarine

Margarine is prepared from blends of vegetable oils and animal fats. The mixture after hydrogenation acquires a consistency similar to that of butter. Soft margarines contain 25 to 50 per cent of polyunsaturated fatty acids. Butter has only 2 per cent. Vitamins A and D are added to margarine in Britain.

Meat, Fish and Eggs

Meat is essentially skeletal muscle (Table 2.3). When fresh meat is allowed to hang glycogen disappears and acids such as lactic acid are produced which tend to soften the muscle fibres and make the meat more tender.

Other parts of animals usually described as offal are used for food. Liver and kidney are both rich in nucleoprotein and contain less fat than most meat. Liver is rich in vitamin A and in iron. 'Sweetbreads' (pancreas and thymus) are rich in nucleoprotein.

Fish is an important source of animal protein (Table 2.3). White fish such as cod, haddock and plaice contain only a small proportion (less than 2 per cent) of fat but fat fish, herring, mackerel and salmon, contain 5 to 18 per cent of fat and can provide useful amounts of the fat-soluble vitamins A and D.

Eggs are a good source of proteins, vitamins and minerals. One average egg (6·25 g) supplies 327 kJ, 6·4 g protein, 5·9 g fat, 30 mg calcium, 1·6 mg iron (all of which is available), 80 μg retinol, 1 μg vitamin D, 0·06 mg thiamin and about 260 mg riboflavin.

Meat substitutes, mostly based on soya beans, have recently become available. Their amino acid content is different from that of beef. The methionine content is low but is compensated by a higher content of cystine. These soya products contain little fat.

Cereals

The main constituents of cereals (and therefore flour) are starch (about 70 per cent), water (about 15 per cent) and protein (about 11 per cent) (Table 2.4). The amount of fat varies widely (0·5 to 8 per cent) from one cereal to another, being particularly high in oatmeal. The inorganic matter, about 2 per cent, consists chiefly of calcium, phosphorus and iron.

The endosperm in the centre of the wheat grain (Fig. 2.5) is mainly starch with some protein, but the outer layer of the endosperm contains the important proteins glutelin and gliadin as well as minerals and nicotinic acid. The germ is particularly rich in vitamins of the B group.

Table 2.3 Composition of meat, fish and eggs per 100 g edible portion

	Protein g	Fat g	Carbo-hydrate g	kJ	Calcium mg	Iron mg
Beef, sirloin, roast, lean only	27·6	9·1	0·0	806	10	2·1
Lamb leg, roast, lean only	29·4	8·1	0·0	800	8	2·7
Bacon back, fried, lean and fat	24·9	40·6	0·0	1926	13	1·3
Liver, calf, fried	26·9	13·2	7·3	1063	15	7·5
Cod, grilled	20·8	1·3	0·0	402	10	0·4
Haddock, smoked, steamed	23·3	0·9	0·0	429	58	1·0
Herring, fried	23·1	15·1	1·5	975	39	1·0
Eggs, whole, fresh	12·3	10·9	0·0	612	52	2·0

Table 2.4 Composition of some cereal products per 100 g

	Protein g	Fat g	Carbo-hydrate g	kJ	Calcium mg	Iron mg
Bread, brown	8·9	2·2	44·7	948	100	2·5
Bread, white	7·8	1·7	49·7	991	100	1·7
Flour, fortified 72 per cent extraction for making white bread	11·3	1·2	74·8	1433	140	2·2
Oatmeal, raw	12·4	8·7	72·8	1698	55	4·1
Biscuits, water	10·8	12·5	75·8	1859	120	1·6
Rice, polished, boiled	2·2	0·3	29·6	522	1	0·2

In the process of milling the degree of extraction, that is, the percentage of the whole grain retained in the flour, can be varied widely. 'Wholemeal' (92 per cent extraction) or flour of 100 per cent extraction contains a large proportion of indigestible fibrous matter. When the extraction is less than 80 per cent the loss in minerals and vitamins is considerable.

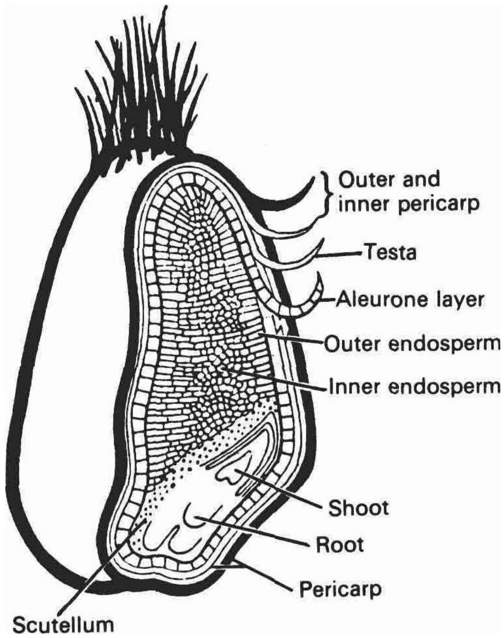

Fig. 2.5 Longitudinal section through a grain of wheat. (*From* R. A. McCance (1946) *Lancet,* i, 77.)

White flour (72 per cent extraction) has the advantage of good keeping qualities but much of the minerals, vitamins and proteins have been removed with the bran and embryo. In Britain white flour is therefore fortified with calcium, iron and thiamin.

'Brown bread' is usually made from white flour to which a proportion of bran has been added. It has a higher vitamin content than has white bread, has more flavour and contains more fibre (p. 21).

Bread. When wheat flour is kneaded with water a sticky mass of dough is formed by promotion of disulphide bond interchange in soluble proteins. Traditionally the dough is made to rise by the action of yeast on the starch in the dough but now rapid mechanical agitation is applied to produce the same effect. During baking the starch grains are ruptured and some of the starch is converted into soluble starch and dextrins; caramelized products are formed in the crust. When bread is toasted it loses water, it is caramelized further and the starch on the surface is largely converted into degradation products which give toast its brown colour. The composition of bread is given in Table 2.4.

Gluten is the mixture of proteins, mainly gliadins and glutelins, present in wheat, barley and rye and the flours made from these cereals produce a dough on the addition of water. Cornflour (wheat starch), oatmeal and flour made from maize contain less gluten and therefore can be made into bread only with difficulty. The intestinal mucosa of patients with coeliac disease is damaged by the α-gliadin of wheat but its mode of action is not fully understood.

Fruit and Vegetables

Most green vegetables contain much indigestible fibrous material. They are good sources of minerals and of ascorbic acid and carotene, the precursor of vitamin A (Table 2.6).

Potatoes contain mainly starch in the form of granules which swell up and burst on cooking. Potatoes are traditionally described as 'fattening' but since they contain 80 per cent water they are low in energy value compared with many other carbohydrate foods; removal of boiled potatoes from the diet leads only to a modest reduction in the energy intake. Potatoes provide about one quarter of the ascorbic acid intake, a small amount of good quality protein, and useful amounts of iron and fluorine. If cooked in fat the energy value goes up about three fold (see Table 2.6).

The pulses (beans, peas, lentils) are good sources of protein (20 to 25 per cent in the dried state). In the fresh form but not when dried they supply ascorbic acid and carotene.

Most fruits are of little nutritive value except as sources of ascorbic acid. When ripe they contain varying amounts of sugar; the banana is unique in supplying starch as well.

Sugar manufactured from cane or sugar beet is almost pure sucrose. Since it contains no vitamins or minerals it is said to provide 'empty' calories. Recently, because of its relative cheapness, large quantities of *isoglucose* have been used in some kinds of food processing in which liquid sugar is needed. It is a mixture of glucose and fructose formed by the action of the enzyme isomerase on glucose derived from the starch of maize.

Chocolate and cocoa have a relatively high protein, fat and carbohydrate content and have thus a high energy value, but the energy value of tea and coffee depends entirely on the

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