BDS Textbook of Physiology and Biochemistry

TEXTBOOK OF PHYSIOLOGY AND BIOCHEMISTRY

GEORGE H. BELL
J. NORMAN DAVIDSON
HAROLD SCARBOROUGH

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THE AUTHORS

GEORGE H BELL

BSc, MD(Glasg), FRCP(Glasg), FRSE

Professor of Physiology in the University of Dundee;
Honorary Fellow of the Accadèmia Anatomico-Chirurgica of Perugia

J NORMAN DAVIDSON

CBE, MD, DSc, FRCP(Glasg), FRCP(Edin), FRIC, FRS

Gardiner Professor of Biochemistry in the University of Glasgow;
formerly Professor of Biochemistry in the University of London
at St Thomas's Hospital Medical School

HAROLD SCARBOROUGH

MB, PhD(Edin), FRCP(Edin), FRCP

Professor of Medicine in the
Welsh National School of Medicine of the University of Wales
and Director of the Medical Unit in the Royal Infirmary, Cardiff

PREFACE TO THE SEVENTH EDITION

IN the three years since the appearance of the sixth edition much new information in both physiology and biochemistry has come along and accordingly almost all the chapters have been revised, some of them extensively, and new pictures and diagrams have been added. Much of those parts of the book concerned with the organization and function of biological systems at the molecular and atomic level, that is cellular biochemistry or molecular biology, has been entirely rewritten.

We have accepted the recommendations of the authoritative bodies on the various conventions used in physiology and biochemistry. For spelling we have followed the Oxford English Dictionary. For anatomical terminology we have used *Gray's Anatomy* (1967), for physiological terminology Suggestions to Authors (1966), *J. Physiol.* **182**, 1–33. For biochemical terminology we have adopted the system of nomenclature and abbreviations recommended by the Combined Commission on Biochemical Nomenclature (CBN) organized at an international level jointly by the International Union of Pure and Applied Chemistry (IUPAC) and the International Union of Biochemistry (IUB). The CBN collaborates closely with the IUB Commission of Editors of Biochemical Journals (CEBJ) and with the Office of Biochemical Nomenclature (OBN) set up in the United States by the National Academy of Sciences and the National Research Council (W. E. Cohn (1967), *Journal of Chemical Documentation*, **7**, 72–73). For enzyme nomenclature we have adopted the recommendations, revised in 1964, of the Commission on Enzymes of the IUB. We have taken note of the S.I. nomenclature and abbreviations so far as possible.

The references at the end of each chapter are given in the form recommended by the Royal Society as described in Advice to Authors (Physiological Society or Biochemical Society).

As in former prefaces we willingly express our indebtedness to many colleagues. The success of this book has been in no small way due to their help and advice, both spontaneous and requested. Acknowledgement has been made of the source of all diagrams, figures and plates, but there remains much of other people's ideas the source of which it is not always possible to specify or even to identify. That does not mean that we are not grateful for it. In previous prefaces we named various colleagues who had given us the benefit of their advice. We are still grateful to them and they may still recognize their contributions in this edition. We wish to express our thanks to the following for their help with this new seventh edition: Dr E. L. Blair, Professor I. A. Boyd, Professor G. Brindley, Professor W. Burns, Dr C. Cameron, Dr Ailsa Campbell, Dr R. P. Cook, Dr Mary Coyle, Dr G. S. Dawes, Dr A. Fleck, Dr A. C. Frazer, Dr J. K. Grant, Dr J. H. Jones, Professor H. M. Keir, Dr R. D. Keynes, Dr J. C. Kernohan, Professor J. Knowelden, Dr J. A. R. Lenman, Mr G. C. Leslie, Professor R. J. Linden, Dr N. E. Loveless, Dr R. S. McNeill, Dr W. W. Park, Dr R. Passmore, Dr J. M. Patrick, Professor R. M. S. Smellie, Dr D. Emslie Smith, Dr D. A. Stansfield, Dr J. S. S. Stewart, Dr R. Y. Thomson, Dr W. Walker, Professor Sir Edward Wayne and Dr I. C. Whitfield.

We would like to express our gratitude for the help we have received from the library staffs of our universities and from Mr R. Callender and Miss M. Benstead, who have prepared many of the illustrations. Mrs M. I. Glenday has earned our thanks for preparing the index.

G. H. B.
J. N. D.
H. S.

September, 1968.

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CHAPTER 1

INTRODUCTION

IN the subjects of Physiology and Biochemistry we are concerned with living matter at two different levels. The biochemist studies biological systems at the level of molecules and atoms, the level of molecular biology, while the physiologist is more concerned with the intact organ, or the whole organism. Physiologists and biochemists are concerned essentially with changes in the organism as it reacts to changes in its environment. In other words, they try to take a cinematographic view of living material; however they frequently find it necessary to stop the cine-film from time to time to make a detailed examination of a single frame. For example, the chemical analysis of a tissue is a statement referring to one particular instant and a series of such analyses may indicate a progressive change from which the biochemist is able to build up a dynamic picture of the chemical activities of the tissue. Similarly the microscopic examination of a single stained section of a tissue is of value in showing its minute anatomy, but it may give little information as to its function. Such a section indeed represents only a momentary glimpse of what may be a continuously changing process. One must recognize too that disturbances of function occur that seem to have no structural basis. For example, interference with an enzyme system may produce disease, and changes in the arrangement of molecular layers may alter significantly the properties of cells and tissues.

In this book the terms 'physiology' and 'biochemistry' are used in a relatively narrow sense. We shall deal mainly with human physiology, supplementing it by descriptions of experiments on other mammals and by occasional but important references to the frog. Anyone actively engaged in the study of physiological problems is soon made painfully aware of distinct differences of function between different species and is reluctant to assume that what holds good for an animal applies without modification to man.

STRUCTURE AND FUNCTION

The single cell is the functional unit of the body and each tissue is made up of vast numbers of cells. We must not imagine, however, that a single cell is a simple uncomplicated structure. Although the ordinary light microscope may reveal little difference between one part of its cytoplasm and another, the electronmicroscope and modern biochemical techniques have revealed an amazing complexity. For this reason it is not yet possible to describe the subtle difference between a living cell and a mere aggregation of molecules.

In the case of the more complex animals such as birds and mammals, the first characteristics of life that come to mind are warmth and movement. If an 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 oxidation 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 are 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 multi-cellular 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 the supply of essential material to the latter 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 is dependent on obtaining 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 to be an *inhibitory* stimulus.

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 the *status quo*. Practically 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, the functioning of nerve cells and the working of enzymes for example, to be carried out under optimum conditions. As Claude Bernard put it: 'La fixité du milieu intérieur est la condition de la vie libre, indépendante.' Small changes in the *milieu intérieur* produce reactions which quickly restore the internal environment to its original state. Many of the adjustments of the activity of the cells and organs of the body are examples of the working of this principle which Cannon called homeostasis.

It is generally appreciated that the body regulates its internal environment with some accuracy. For example we are apt to say it keeps its hydrogen-ion concentration remarkably constant. But to leave it at that is simply to admire it from a distance without going to the trouble of making enquiries about the working of the regulatory mechanisms. The first requirement of such a mechanism 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 in modern jargon are termed 'feed-back' 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 so the output of the heart and the calibre of the blood vessels are altered to regain the *status quo*. In many cases, however, the detecting mechanism is still to be discovered—for example we do not yet know how the level of blood volume, or the level of blood sugar, are detected. Both, however, are regulated within quite narrow limits.

Although the regulation of the internal environment reaches its highest development in man, he has gone still further by attempting to control his external enviromnent. At first this involved the wearing of clothing, the building of shelters and houses, and the use of artificial heating, lighting and ventilation. These have not all proved to be unmixed blessings. Artificial lighting, for example, while it makes life more pleasant in the darkness of winter, introduces new problems of eyestrain, fatigue and extended hours of work. Later, with the advent of the industrial era, unfavourable environments were created in which men had to labour, but the dangers of many of these were mitigated by the design of machinery which could be easily and safely worked. Man now climbs high in the air and descends to great depths in the sea and a few have even ventured into space. All these adventures have provided a vast number of new biological problems. Such problems may fall properly under the heading of applied physiology but there is no definite boundary between pure and applied in this or any other science.

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 chemical 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 physiology and biochemistry imply much more than a mere catalogue of the functions of the various parts of the body. However, neither has yet become a highly organized body of knowledge comparable to the exact sciences of physics or mathematics and many of the phenomena to be discussed can be given as yet only an incomplete explanation. Nevertheless their description must not be regarded as irrelevant since empirical findings may have immediate practical importance in 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 in modern medicine and surgery, however, is to study the living patient more and more intensely in order to understand not only his symptoms but the way in which normal physiological and biochemical processes have broken down, for disease is increasingly thought of as a disordered physiology in which the homeostatic mechanisms have been overstrained or are inadequate. The cure and prevention of numerous diseases is due to rapid advances in our knowledge of bacteriology and immunology:

to many the methods of experimental physiology are being successfully applied. Biochemical methods have been used for many years for the examination of the body fluids, to provide important diagnostic information and to control treatment. Thus, for example, much of our recent knowledge of cardiac diseases, cardiac failure and the surgical treatment of congenital cardiac malformations is based upon physiological studies made in the laboratory or in the clinic, while the modern treatment of diabetes mellitus depends almost entirely on material and methods originally developed in the laboratory.

The bodily activities are so closely dependent 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 describing the activities of the heart we have to discuss 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 in which all the parts are connected together, no one portion being more important than another. It is difficult, therefore, to know where to enter the circle to begin our study, for it is only when we have completed the circle that we can fully understand our subject. For this reason it is necessary to consider briefly the subject as a whole before beginning a more detailed description of its various parts. Riley's *Introducing Biology* will be found helpful, especially to those with little biological background (see References, p. 10).

The source of all the energy required by the body for carrying out muscular activity, for respiration, for the beating of the heart, is the food. This consists mainly of proteins, fats and carbohydrates which are oxidized (burnt) in the tissues. In addition to sources of energy the food must contain inorganic substances which are necessary to make good the loss of salts in the excreta and to provide material for formation of blood and bone. 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 relatively simple chemical constitution which are absorbed through the lining of the small intestine into the blood stream and distributed throughout the body. In the case of fats, however, absorption may occur with very little modification of the original chemical structure.

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 spongy organs richly supplied with blood vessels. Oxygen diffuses readily through the very thin walls of the capillary vessels of the lung tissue, becoming attached to the hæmoglobin 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 exhaled. By-products of oxidation not needed by the body reach the kidneys in the blood and are excreted into the urine.

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 brain, skeletal muscles, kidneys and intestine. 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, fluid, or chemical substances of small molecular size move easily. The blood is drained away from the tissues at low pressure in wide vessels (the veins) with relatively thin walls.

The skeletal muscles are the main effector tissues. By their contractions the position of the bones is altered 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 the glands, the heart beat and the calibre of the blood vessels. Central control is, however, of no value 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 and intestines. The sensory nerves are actually 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 retinæ. These adjustments are called *reflex* and the pathways involved, namely sensory nerves, central nervous system and motor nerves, are called *reflex arcs*. The lowest part of the brain, the medulla oblongata, is responsible for the muscular movements of respiration, for the control of the heart rate and the regulation of the blood vessels, and is concerned in the maintenance of posture. The cerebellum, which lies above the medulla, is concerned with co-ordination of muscular movements. The fore-part of the brain, the cerebrum, has a layer of grey matter (nerve cells) on its surface and also masses of grey matter within. The grey matter is interconnected by innumerable nerve fibres which together make up the white matter. The cerebrum is concerned in all the higher mental activities and with reading, writing and speaking, as well as in so-called voluntary movements, the perception of touch and temperature and in the special senses of vision and hearing.

In addition to the rapidly acting co-ordinating and integrating mechanism of the nervous system there is a chemical (*humoral*) system which operates more slowly. For example, during the digestion of food in the duodenum a chemical substance (*hormone*) called secretin is produced in the mucous membrane, absorbed into the blood and carried to the pancreas which responds by pouring out its digestive juices. The thyroid gland in the neck produces a chemical substance which is absorbed directly from the gland into the blood stream and influences the rate of metabolic activity of the tissues.

Under the heading of reproduction, we shall have to consider the processes necessary for the maintenance of the species. The male cells, the *spermatozoa*, are produced in the testis 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 growth of the fertilized cell in the uterus. By repeated division the fertilized ovum develops into the embryo whose nutrition in the uterus is carried out by transfer of materials across the placenta. At the end of pregnancy the muscular wall of the uterus contracts, the fœtus is delivered and then acquires oxygen directly, by breathing air into its lungs, instead of indirectly through the placenta. In the meantime the mother's mammary glands have enlarged in preparation for lactation and soon after parturition they produce milk for the nourishment of the infant. Many of the organs of the infant, especially the central nervous system and the kidneys, are somewhat undeveloped at birth, but as he grows these disabilities disappear and he is then able to lead an active independent existence. An important landmark in development is puberty. At this time the gonads complete their development and in so doing produce physical and mental changes characteristic of the adult. The ovaries continue to produce ova till the menopause in the fifth decade, but the production of spermatozoa by the male persists much longer. With the approach of old age the arteries harden, the lens of the eye and probably many other tissues become less elastic, muscular power declines and there is probably some deterioration of mental activity. If the hazards of accident, infection and malignant disease are avoided, death occurs in old age by a gradual process of degeneration.

THE COMPOSITION OF LIVING TISSUES

The living body contains, in addition to a large amount of water, 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, and mineral salts. In man the relative proportions of these constituents, especially fat and carbohydrate, vary greatly from one person to another,

TABLE 1, 1

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

and in the one individual at different times in his life, according to his nutritional status. Nevertheless, the composition of the human body may be represented roughly as shown in Table 1, 1.

The chief constituent of living matter is water which is so familiar and so large a constituent of the body that its fundamental importance in both the structure and functioning of all the tissues tends to be overlooked. The subject is discussed further in Chapter 33 but some preliminary considerations are given here.

The body of a healthy adult male consists of some 65 to 70 per cent. of water and about 15 per cent. of fat; the remainder is accounted for by the solid parts of cells and supporting structures. The considerable variations in total body water as 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. This accounts for the fact that the water content of the body of the female (50 to 55 per cent.) is rather less than that of the male. In very fat people the body water may be no more than 40 per cent. of the total body weight. In the fœtus the relative proportion of water in the body is much higher, for example 94 per cent. at the third month of fœtal life. The reasons for these differences are not known.

TABLE 1, 2

Water Content of Human Tissues

Analytical Figures from one Male Human Body, age 35

Tissue	Per cent. of total Body Wt.	Water Content per cent.
Skin	7·81	64·68
Skeleton	14·84	31·81
Teeth	0·06	5·00
Striated muscle	31·56	79·52
Brain, spinal cord, and nerve trunks	2·52	73·33
Liver	3·41	71·46
Heart	0·69	73·69
Lungs	4·15	83·74
Spleen	0·19	78·69
Kidneys	0·51	79·47
Pancreas	0·16	73·08
Alimentary tract	2·07	79·07
Adipose tissue	13·63	50·09
Remaining tissues—		
Liquid	3·79	93·33
Solid	13·63	70·40
Contents of alimentary tract	0·80	..
Bile	0·15	..
Hair	0·03	..
Total body, weighing 70·55 kg.	100·00	67·85

After H. H. Mitchell, T. S. Hamilton, F. R. Steggerda & H. W. Bean (1945), *J. biol. Chem.* **158**, 625.

An estimation of the water content of the various tissues of a 70 kg. man is shown in Table 1, 2. Most tissues contain more than 70 per cent. water; a red blood cell contains 71·7 per cent. water, and even the skeleton and adipose tissue contain quite large amounts. The latter, of course, does not consist entirely of fat; it contains connective tissue, for example, which has water in it and the spaces between the fat cells also contain water. Table 1, 3, 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 (Chapter 2) water plays a fundamental role in cellular reactions. A very large number of substances are soluble in water and many others, such as fats and fat-soluble compounds, can be carried in fine emulsions or be rendered water-soluble by combination with hydrophilic substances. Certain other properties of water are also of importance. Owing to the high heat capacity of water, large changes in heat production can take place in the body with very little alteration in body temperature. Since the latent heat of evaporation of water is high, the loss of a small amount of water in evaporated sweat means a relatively large loss of heat. Moreover the high latent heat of solidification is a protection against the freezing of the tissues.

TABLE 1, 3

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

After E. P. Cathcart (1926), *Glasg. med. J.* **106**, 3.

In the normal course of events a large amount of water is lost from the body daily and a corresponding amount is taken in, so that water balance is maintained. As shown in Table 1, 4, the amount of water gained and lost by an adult man engaged in a sedentary occupation in a temperate climate is about 2½ litres per day.

Water is gained by the body from two main sources. Most of it is taken in by the mouth in the form of food and drink, but a small amount of water is normally formed in the tissues as the result of the oxidation of the hydrogen of foodstuffs. The amount of water ingested in the diet varies, of course, over very wide limits according to habit, climate and occupation. Studies in man with deuterium oxide (heavy water, Chapter 9) have shown that the absorption of water from the stomach is approximately 2·5 per cent. of the dose per minute whereas from the small intestine it is much more rapid, about 26 per cent. of the dose per minute. Patients with injuries of the limbs absorb water from the alimentary tract more slowly than normal, and in patients with abdominal injuries water absorption is grossly delayed.

The amount of metabolic water formed in the tissues as the result of the oxidation processes described in Chapter 10 is about 300 ml. in man, that is about 14 per cent. of his total daily fluid intake. This water is formed in the cells and is of great value to the organism, since its formation is not accompanied by the great osmotic changes associated with the intake of large amounts of fluid. It is of the utmost importance to the hibernating animal which lives for long periods on metabolic water, and to organisms such as the clothes moth which do not normally have ready access to water.

Table 1, 4, gives no idea of the great turnover of fluid which takes place in

TABLE 1, 4

Water Balance of an Adult Man in a Temperate Climate

Daily Intake		Daily Output	
Drink	1300 ml.	Urine	1500 ml.
Food	850 ml.	Expired air	400 ml.
Formed in body by oxidation	350 ml.	Skin	500 ml.
		Fæces	100 ml.
Total . .	2500 ml.	Total . .	2500 ml.

the body in the course of a day. In twenty-four hours a man secretes 1 to 1·5 l. of saliva; 1 to 2 l. of gastric juice; 0·5 to 1 l. of bile; 0·6 to 0·8 l. of pancreatic juice and 3 l. of intestinal juice. All this fluid, with the exception of about 100 ml. which escapes in the fæces, is reabsorbed.

The composition of the human body in terms of elements is shown in Table

TABLE 1, 5

Composition of the Human Body (*after Sherman*)

	Wet weight basis per cent.		Wet weight basis per cent.
Oxygen . .	65	Chlorine . .	0.15
Carbon . . .	18	Magnesium . .	0·05
Hydrogen . .	10	Iron . . .	0·004
Nitrogen . .	3	Iodine . .	0·00004
Calcium . .	1·5	Copper . . }	
Phosphorus . .	1·0	Manganese . }	
Potassium . .	0·35	Zinc . . }	traces
Sulphur. . .	0·25	Fluorine . }	
Sodium . .	0·15	Molybdenum, etc. }	

1, 5. The most abundant elements are of course 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 the greatest nutritional importance. The requirement of a mineral element varies according to age and activity, and is greater in the

A*