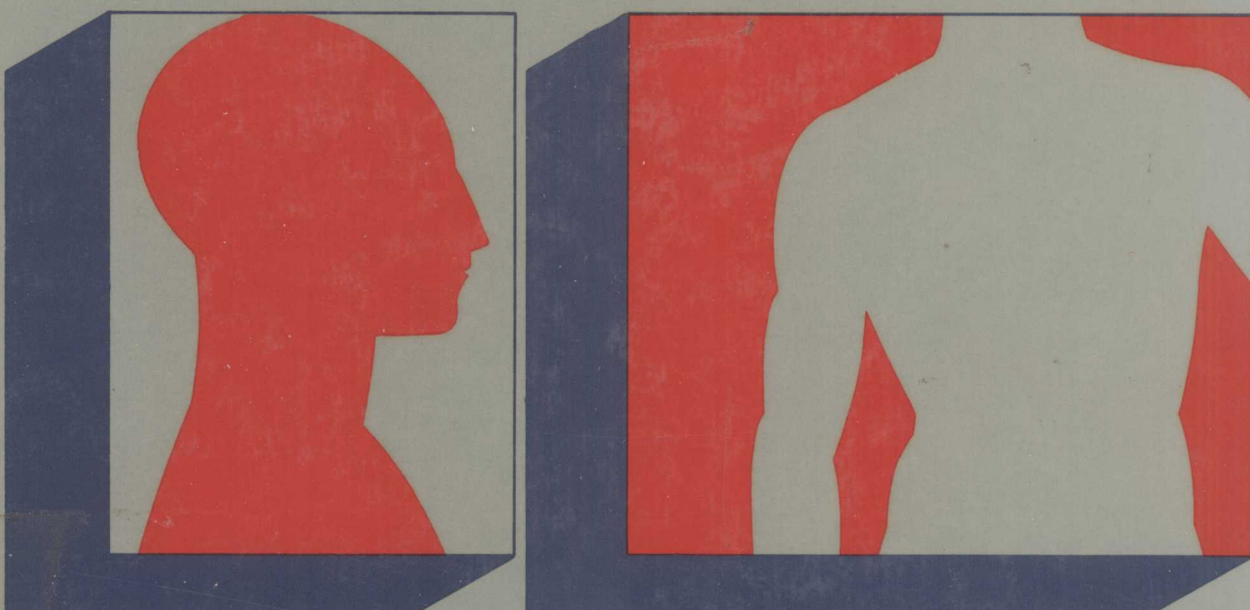
HUMAN PHYSIOLOGY

THE MECHANISMS OF BODY FUNCTION

ARTHUR J. VANDER
JAMES H. SHERMAN
DOROTHY S. LUCIANO

FOURTH EDITION



HUMAN PHYSIOLOGY
The Mechanisms of Body Function

Fourth Edition

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TO OUR PARENTS
AND TO JUDY, PEGGY, AND JOE
WITHOUT WHOSE UNDERSTANDING
IT WOULD HAVE BEEN IMPOSSIBLE.

PREFACE

The primary purpose of this book remains what it was in the first three editions: to present the fundamental mechanisms of human physiology. Our aim has been to tell a story, not to write an encyclopedia. The book is intended for undergraduate students, regardless of their scientific background. The physics and chemistry requisite for an understanding of the physiology are presented where relevant in the text. Students with little or no scientific training will find this material essential while others, more sophisticated in the physical sciences, should profit from the review of basic science oriented toward specifically biological applications. Thus this book is suitable for most introductory courses in human physiology, including those taken by students in the health professions.

The overall organization and approach of the book is based upon a group of themes which are developed in Chapter 1 and which form the framework for our descriptions: (1) all phenomena of life, no matter how complex, are ultimately describable in terms of physical and chemical laws; (2) certain fundamental features of cell function are shared by virtually all cells and, in addition, constitute the foundation upon which specialization is built; (3) the body's various coordinated functions—circulation, respiration, etc.—result from the precise control and integration of specialized cellular activities, serve to maintain relatively constant the internal composition of the body, and can be described in terms of control systems similar to those designed by engineers.

In keeping with these themes, the book progresses from the cell to the total body, utilizing at each level of increasing complexity the information and principles developed previously. Part 1 is devoted to an analysis of basic cellular physiology and the essential physics and chemistry required for its understanding. Part 2 analyzes the concept of the body's internal environment, the nature of biological control systems, and the properties of the major specialized cell types—nerve, muscle, and gland—which constitute these systems. Part 3 then analyzes the coordinated body functions in terms of the basic concepts and information developed in Parts 1 and 2. In this way we have tried to emphasize the underlying unity of biological processes.

This approach has resulted in several characteristics of this book: (1) Cell physiology has received extensive coverage. (2) We have been willing to spend a considerable number of pages logically developing a single cellular concept (such as the origin of membrane potentials) required for the understanding of total-body physiological processes, and which we have found to offer considerable difficulties for the student. (3) We have made every effort not to mention facts simply because they happen to be known, but rather to use facts as building blocks for general principles and concepts. In this last regard, we confess that even an introductory course in physiology must teach a rather frightening number of facts, and our book is no exception. We have tried to keep in mind, however, the words of John Hunter, the eighteenth-century British anatomist and surgeon: "Too much attention can not be paid to facts; yet too many facts crowd the memory without advantage, any further than they lead us to establish principles." (4) We have employed a very large number of figures as an aid to developing concepts and explanations. These figures also provide an excellent summary of the most important material in each chapter. (5) We have not shied away from pointing out the considerable gaps in current understanding. In summary, our book may be long in areas where other texts are brief, and vice versa; moreover, our approach requires the student to think rather than simply to memorize.

In this fourth edition, the level, scope, and emphasis remain unchanged. The text has been completely updated, a process involving changes too numerous to list here. We have also done considerable rewriting in order to improve clarity of organization and presentation.

Arthur J. Vander
James H. Sherman
Dorothy S. Luciano

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A FRAMEWORK FOR HUMAN PHYSIOLOGY

1

Mechanism and Causality

A Society of Cells
Cells: The basic units
Tissues
Organs and organ systems

The Internal Environment
Body-fluid compartments

The Importance of Control

A Rationale

One cannot meaningfully analyze the complex activities of the human body without a framework upon which to build, a set of viewpoints to guide one's thinking. It is the purpose of this chapter to provide such an orientation to the subject of human physiology—the mechanisms by which the body functions.

Mechanism and Causality

The **mechanist** view of life holds that all phenomena, no matter how complex, are ultimately describable in terms of physical and chemical laws and that no "vital force" distinct from matter and energy is required to explain life. The human being is a machine—an enormously complex machine, but a machine nevertheless. This view has predominated in the twentieth century because virtually all information gathered from observation and experiment has agreed with it. But **vitalism**, the view that some force beyond physics and chemistry is required by living organisms, is not completely dead, nor is it surprising that it lingers specifically in brain physiology, where scientists are almost entirely lacking in hypotheses to explain such phenomena as thought and consciousness in physicochemical terms. We believe that even this area will ultimately yield to physicochemical analysis, but we also feel that it would be unscientific, on the basis of present knowledge, to dismiss the problem out of hand.

A common denominator of physiological processes is their contribution to survival. Unfortunately, it is easy to misunderstand the nature of this relationship. Consider, for example, the statement "During exercise a person sweats because the body needs to get rid of the excess heat generated." This type of statement is an example of **teleology**, the explanation of events in terms of purpose. But it is not an explanation at all in the scientific sense of the word. It is somewhat like saying, "The furnace is on because the house needs to be heated." Clearly, the furnace is on, not because it senses in some mystical manner the house's "needs," but because the temperature has fallen below the thermostat's set point, and the electric current in the connecting wires has turned on the heater.

Is it not true that sweating actually serves a useful purpose because the excess heat, if not eliminated, might have caused sickness or even death? Yes, it is, but this is totally different from stating that a "need" to avoid injury caused the sweating to occur. The cause of the sweating, in reality, was an automatically occurring sequence of events initiated by the increased heat generation: Increased heat generation → increased blood temperature →

increased activity of specific nerve cells in the brain → increased activity, in turn, of a series of nerve cells, the last of which stimulate the sweat glands → increased production of sweat by the sweat-gland cells. Each of these steps occurs by means of physicochemical changes in the cells involved. In science, to explain a phenomenon is to reduce it to a causally linked sequence of physicochemical events. This is the scientific meaning of causality, of the word "because."

On the other hand, that a phenomenon is beneficial to the person is of considerable interest and importance. It is attributable to evolutionary processes which result in the selecting of those responses having survival value. Evolution is the key to understanding why most bodily activities do indeed appear to be purposeful. Throughout this book we emphasize how a particular process contributes to survival, but the reader must never confuse this survival value of a process with the explanation of the mechanisms by which the process occurs.

A Society of Cells

Cells: The basic units

Cells are the simplest structural units into which a complex multicellular organism can be divided which still retain the functions characteristic of life. One of the unifying generalizations of biology is that certain fundamental activities are common to almost all cells and represent the minimal requirements for maintaining cell integrity and life. Thus, a human liver cell and an amoeba are remarkably similar in their means of exchanging materials with their immediate environments, of obtaining energy from organic nutrients, of synthesizing complex molecules, and of duplicating themselves.

Each human organism begins as a single cell, the fertilized ovum, which divides to form two cells, each of which divides in turn, resulting in four cells, and so on. If cell multiplication were the only event occurring, the end result would be a spherical mass of identical cells. However, during development, cells begin to exhibit a variety of specialized functions, each cell becoming specialized in the performance of a particular function, such as developing force and movement (in muscle cells) or generating electric signals (in nerve cells). The process of transforming an unspecialized cell into a specialized cell is known as **cell differentiation**. In addition to differentiating, cells migrate to new locations during development and form selective adhesions with other cells to form multicellular structures. In this manner, the cells of the body are arranged in various combinations to form a hierarchy of organized structures. Differentiated cells with similar properties aggregate to form **tissues** (nerve tissue, muscle tissue, etc.). These combine with other types of tissues to form **organs** (the heart, lungs, kidneys, etc.) which are linked together to form **organ systems** (Fig. 1-1).

About 200 distinct kinds of cells can be identified in the body in terms of detailed differences in structure and function. However, when cells are classified according to the general types of functions they perform, four broad categories emerge: (1) **muscle cells**, specialized for the production of mechanical forces which produce movement; (2) **nerve cells**, specialized for initiation and conduction of electric signals over long distances; (3) **epithelial cells**, specialized for the selective secretion and absorption of organic molecules and ions; and (4) **connective-tissue cells**, specialized for the formation and secretion of various types of extracellular connecting and supporting elements. In each of these functional categories there are several cell types that perform variations of the general class of specialized function. For example, there are three different types of muscle cells—skeletal, cardiac, and smooth muscle cells—all of which generate forces and produce movements but which differ from each other in shape, mechanisms controlling their contractile activity, and location in the various organs of the body.

Muscle cells may be attached to bones and produce movements of the limbs or trunk. They may be attached to skin (as, for example, the muscles producing facial expressions) or they may enclose hollow cavities so that their contraction expells the contents of the cavity, as in the case of the pumping of the heart or the expulsion of urine by the bladder.

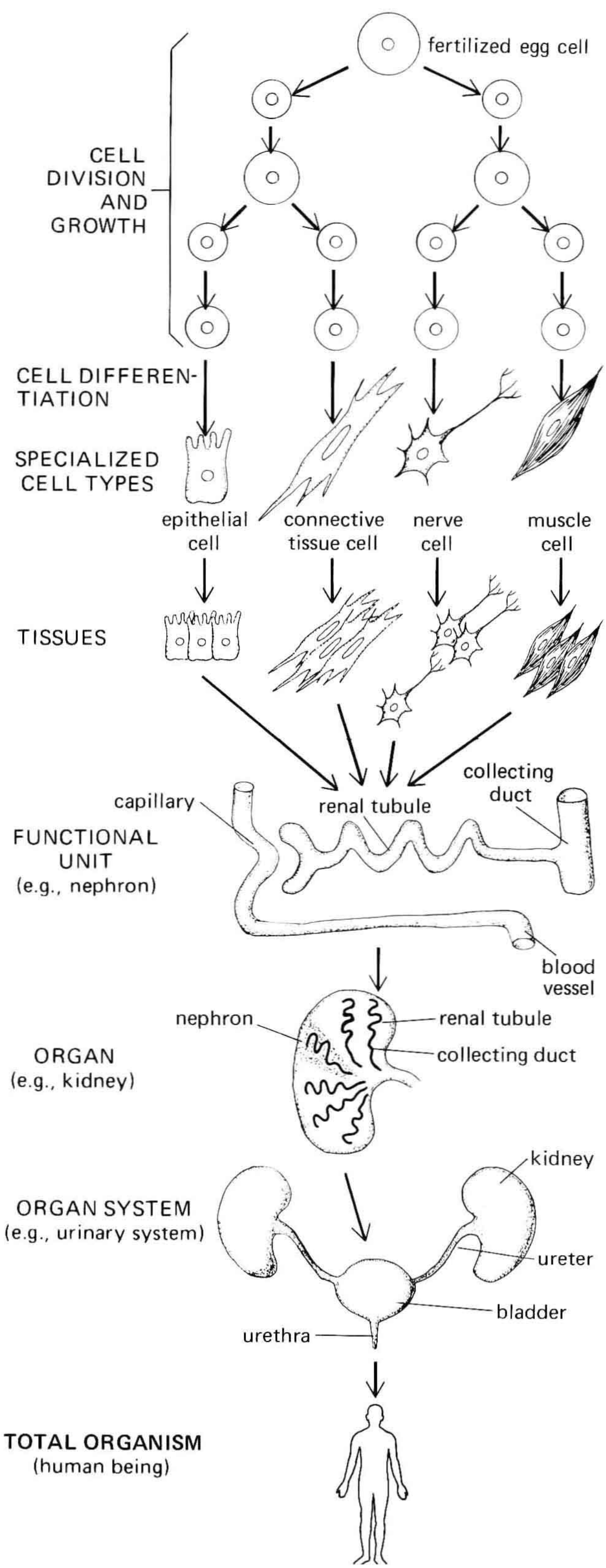

FIGURE 1-1. Levels of cellular organization.

Muscle cells also surround many of the hollow tubes in the body; their contraction changes the diameter of these tubes, as in the case of the muscle cells surrounding blood vessels.

Nerve cells have the ability to generate electric signals and the ability to propagate these signals rapidly from one area of the body to another. The signal may influence the initiation of new electric signals in other nerve cells, or it may influence secretion by a gland cell or contraction of a muscle cell. Thus, nerve cells provide a major means of controlling the activities of other cells.

Epithelial cells are located mainly at the surfaces which cover the body (or individual organs) or which line the walls of various tubular and hollow structures within the body. These cells form the boundaries between compartments and function as selective barriers regulating the exchange of molecules across them. For example, the epithelial cells at the surface of the skin form a barrier which prevents most substances in the external environment from entering the body through the skin; the epithelial linings of the lungs, gastrointestinal tract, and kidneys regulate the exchange of molecules between the blood and the external environment, i.e., across an epithelial barrier. Epithelial cells are also found in glands which form from the invagination of the epithelial surfaces (see Chap. 6 for classification of glands).

Connective-tissue cells, as their name implies, have as their major function connecting, anchoring, and supporting the structures of the body. Connective-tissue cells typically have a large amount of extracellular material between them. The cells themselves include those in the loose meshwork of cells and fibers underlying most epithelial layers and also include other cell types as diverse as fat-storing (adipose) cells, bone cells, and red and white blood cells. Many connective-tissue cells secrete into the fluid surrounding them molecules which form a matrix consisting of various types of protein **fibers** embedded in a **ground substance** made of polysaccharides and protein. This matrix may vary in consistency from a semifluid gel (in loose connective tissue) to the solid crystalline structure of bone. The extracellular fibers formed by these cells include ropelike **collagen** fibers (which have a high tensile strength and resist stretching), rubber-band-like **elastic** fibers (which provide the elastic qualities found in various organs), and fine, highly branched **reticular** fibers.

Tissues

Most specialized cells are associated with other cells of a similar kind, forming aggregates known as **tissues**. Corresponding to the four general categories of differentiated cells, there are four general classes of tissues: (1) **muscle tissue**, (2) **nerve tissue**, (3) **epithelial tissue**, and (4) **connective tissue**. It should be noted that the term "tissue" is frequently used in several different ways. It is formally defined as just described, i.e., as an aggregate of a single type of specialized cell. However, it is also commonly used to denote the general cellular fabric of any given organ or structure, e.g., kidney tissue or lung tissue, each of which in fact usually contains all four classes of tissue.

Organs and organ systems

Organs are composed of the four kinds of tissues arranged in various proportions and patterns—sheets, tubes, layers, bundles, strips, etc. For example, the kidney consists largely of (1) a series of small tubes, each composed of a single layer of epithelial cells; (2) blood vessels, whose walls consist of an epithelial lining and varying quantities of smooth muscle and connective tissue; (3) nerve fibers with endings near the muscle and epithelial cells; and (4) a loose network of connective-tissue elements that are interspersed throughout the kidney and that also form an enclosing capsule. The structure of many organs is organized into small, similar subunits often referred to as **functional units**, each performing the function of the organ. For example, the kidneys' 2 million functional units, the nephrons, are the tubules with their closely associated blood vessels. The total production of urine by the kidneys is the sum of the amounts formed by the individual nephrons.

Finally, the last order in classification is that of the **organ system**, a collection of organs which together perform an overall function. For example, the kidneys, the urinary bladder, the tubes leading from the kidneys to the bladder, and the tube leading from the bladder to the exterior constitute the urinary system. There are ten organ systems in the body. Their components and functions are given in Table 1-1.

To sum up, the human body can be viewed as a complex society of cells of many different types which are structurally and functionally combined and interrelated in a variety of ways to carry on the functions essential to the survival of the organism as a whole. Yet the fact remains that individual cells constitute the basic units of this society, and almost all of these cells individually exhibit the fundamental activities common to all forms of life. Indeed, many of the body's different cells can be removed and maintained in test tubes as free-living cells.

There is a definite paradox in this analysis. If each individual cell performs the fundamental activities required for its own survival, what contributions do the different organ systems make? How is it that the functions of the organ systems are essential to the survival of the organism as a whole when each individual cell of the organism seems to be capable of performing its own fundamental activities? The resolution of this paradox is found in the isolation of most of the cells of a multicellular organism from the environment surrounding the

TABLE 1-1. Organ systems of the body

System	Major organs or tissues	Primary functions
Circulatory	Heart, blood vessels, blood	Rapid flow of blood throughout the body's tissues
Respiratory	Nose, pharynx, larynx, trachea, bronchi, bronchioles, lungs	Exchange of carbon dioxide and oxygen; regulation of hydrogen-ion concentration
Digestive	Mouth, pharynx, esophagus, stomach, intestines, salivary glands, pancreas, liver, gallbladder	Digestion and absorption of organic nutrients, salts, and water
Urinary	Kidneys, ureters, bladder, urethra	Regulation of plasma composition through controlled excretion of organic wastes, salts, and water
Musculoskeletal	Cartilage, bone, ligaments, tendons, joints, skeletal muscle	Support, protection, and movement of the body
Immune	White blood cells, lymph vessels and nodes, spleen, thymus, and other lymphatic tissues	Defense against foreign invaders; return of extracellular fluid to blood; formation of white blood cells
Nervous	Brain, spinal cord, peripheral nerves and ganglia, special sense organs	Regulation and coordination of many activities in the body; detection of changes in the internal and external environments; states of consciousness; learning
Endocrine	All glands secreting hormones: Pancreas, testes, ovaries, hypothalamus, kidneys, pituitary, thyroid, parathyroid, adrenal, intestinal, thymus, and pineal	Regulation and coordination of many activities in the body
Reproductive	Male: Testes, penis, and associated ducts and glands	Production of sperm; transfer of sperm to female
	Female: Ovaries, uterine tubes, uterus, vagina, mammary glands	Production of eggs; provision of a nutritive environment for the developing embryo and fetus
Integumentary	Skin	Protection against injury and dehydration; defense against foreign invaders; regulation of temperature

body (the external environment), and the presence of an internal environment.

The Internal Environment

An amoeba and a human liver cell both obtain their energy by the breakdown of certain organic nutrients; the chemical reactions involved in this intracellular process are remarkably similar in the two types of cells and involve the utilization of oxygen and the production of carbon dioxide. The amoeba picks up oxygen directly from the fluid surrounding it (its external environment) and eliminates carbon dioxide into the same fluid. But how can the liver cell obtain its oxygen and eliminate the carbon dioxide when, unlike the amoeba, it is not in direct contact with the external environment (the air surrounding the body)? Supplying oxygen to the liver is the function both of the respiratory system (comprising the lungs and the airways leading to them), which takes up oxygen from the external environment, and of the circulatory system, which distributes oxygen to all parts of the body. In addition, the circulatory system carries the carbon dioxide generated by the liver cells and all the other cells of the body to the lungs, which eliminate it to the exterior. Similarly, the digestive and circulatory systems, working together, make nutrients from the external environment available to all the body's cells. Wastes other than carbon dioxide are carried by the circulatory system from the cells which produced them to the kidneys and liver, which excrete them from the body (Fig. 1-2). The kidneys also regulate the concentrations of water and many essential minerals in the plasma. Thus the overall effect of the activities of organ systems is to create within the body the environment required for all cells to function. This is called the **internal environment**.

The internal environment is not merely a theoretical physiological concept. It can be identified quite specifically in anatomical terms: The body's

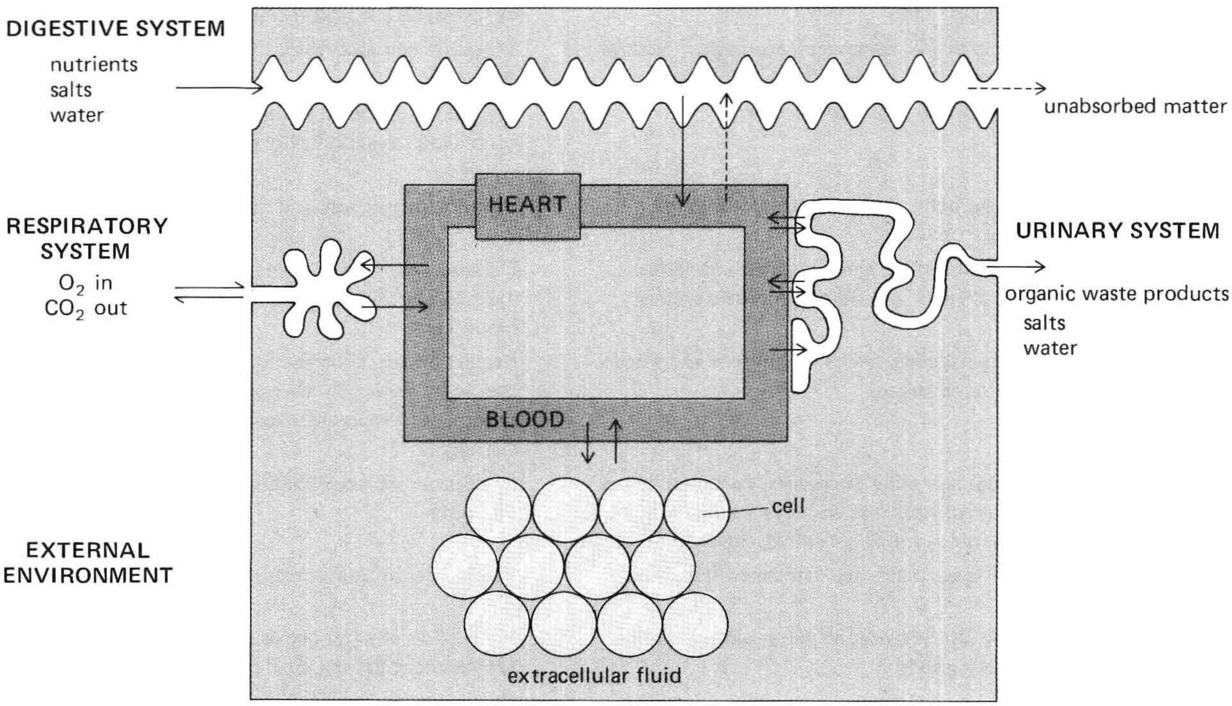

FIGURE 1-2. Exchanges of matter occur between the external environment and the circulatory system via the digestive system, respiratory system, and urinary system.

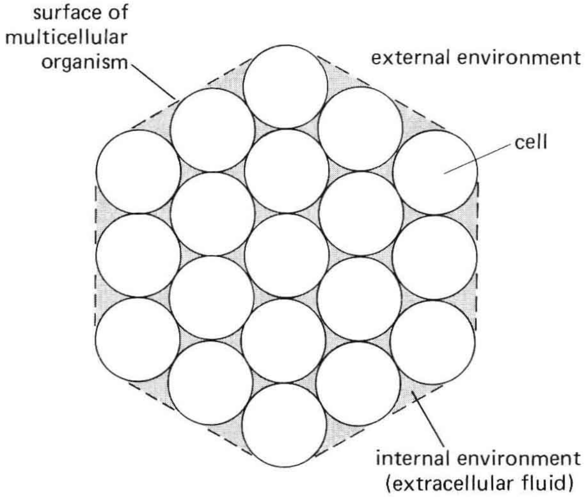

FIGURE 1-3. Extracellular fluid is the internal environment of the body.

internal environment is the **extracellular fluid** (literally, fluid outside the cells), which bathes each of the body's cells (Figs. 1-2 and 1-3). In other words, the environment in which each cell lives is not the "external environment" surrounding the entire body but the local extracellular fluid surrounding that cell. It is from this fluid that the cells receive oxygen and nutrients and into which they excrete wastes. A multicellular organism can survive only as long as it is able to maintain the composition of its internal environment in a state compatible with the survival of its individual cells. The French physiologist Claude Bernard first clearly described in 1857 the central importance of the extracellular fluid of the body: "It is the fixity of the internal environment which is the condition of free and independent life. . . . All the vital mechanisms, however varied they may be, have only one object, that of preserving constant the conditions of life in the internal environment." This concept of an internal environment and the necessity of maintaining its composition relatively constant is the single most important unifying idea to be kept in mind while attempting to unravel and understand the functions of the body's organ systems and their interrelationships.

To summarize, the total activities of every individual cell in the body fall into two categories: (1) Each cell performs for itself all those fundamental basic cellular processes (movement of materials across its membrane, extraction of energy, protein synthesis, etc.) which represent the minimal requirements for maintaining its individual integrity and life; and (2) each cell simultaneously performs one or more specialized activities which, in concert with the activities performed by the other cells of its tissue or organ system, contribute to the survival of the total organism by helping maintain the stable internal environment (extracellular fluid) required by all cells. These specialized activities together constitute the coordinated body processes (circulation, respiration, digestion, etc.) typical of multicellular organisms like human beings.

Clearly, the society of cells which constitutes a human body bears many striking similarities to a society of persons (although the analogy must not be pushed too far). Each person in a complex society must perform individually a set of fundamental activities (eating, excreting, sleeping, etc.), which is virtually the same for all persons. In addition, because the complex organization of a society makes it virtually impossible for any individual within the society to raise his or her own food, arrange for the disposal of wastes, and so on, each individual participates in the performance of one of these supply-and-disposal operations required for the survival of all. A specialized activity, therefore, becomes an additional part of one's daily routine, but it never allows the individual to cease or to reduce the fundamental activities required for survival.

Body-fluid compartments

Extracellular fluid is located in two so-called compartments. Approximately 80 percent of the extracellular fluid surrounds the body's cells (excluding the blood cells). Because it lies between cells, it is also known as **intercellular** or, more often, **interstitial fluid**. The remaining 20 percent of the extracellular fluid is the fluid portion of the blood, the **plasma**. The blood (plasma and blood cells suspended in the plasma) is continuously circulated by the action of the heart to all parts of the body. As will be seen in Chap. 11, the plasma exchanges oxygen, nutrients, wastes, and other metabolic products with the interstitial fluid as the blood passes through the capillaries of the body. Because of the transcapillary exchanges between plasma and interstitial fluid, solute concentrations are virtually identical in the two fluids, except for protein concentration. With this major exception, the entire extracellular fluid may be considered to have a homogeneous composition which is very different from that of the **intracellular fluid** (the fluid inside the cells). These differences will be described in Chap. 6.

To generalize one step further, the human body can be viewed as containing three fluid compartments: (1) blood plasma, (2) interstitial fluid, and (3) intracellular fluid (Fig. 1-4). The major molecular component of all three compartments is water, which accounts for about 60 percent of the normal body weight, and amounts to about 42 liters (L) in a standard man. Two-thirds of the total body water (28 L) is intracellular fluid. The remaining one-third of the total body water (14 L) is the extracellular fluids, 80 percent as interstitial fluid (11 L) and 20 percent as plasma (3 L).

The above figures for the volumes of fluids in the various compartments of the body are those of a 70-kg (154-lb) man. Obviously, body measurements vary between different individuals. Some measurements vary directly with body weight and can be expressed as a percentage of the total body weight, whereas others depend on age, sex, and state of health as well as body weight. The typical values for a healthy, 70-kg, 21-year-old male have been used for years as representative measurements for an individual. This standard was chosen because most of the data collected over the years on normal, healthy individuals has come from measurements made on male medical students. Measurements on females of the same age, corrected for differences in total body weight, give values of a similar magnitude, although slight sex-specific differences do exist. Thus, a female has a slightly lower total body-water content than a male of the same weight because her body is composed of a higher percentage of fat-storing (adipose) tissue, which contains less water than other tissues. Unless otherwise stated, quantitative values given in this text refer to a healthy, 70-kg, 21-year-old male.

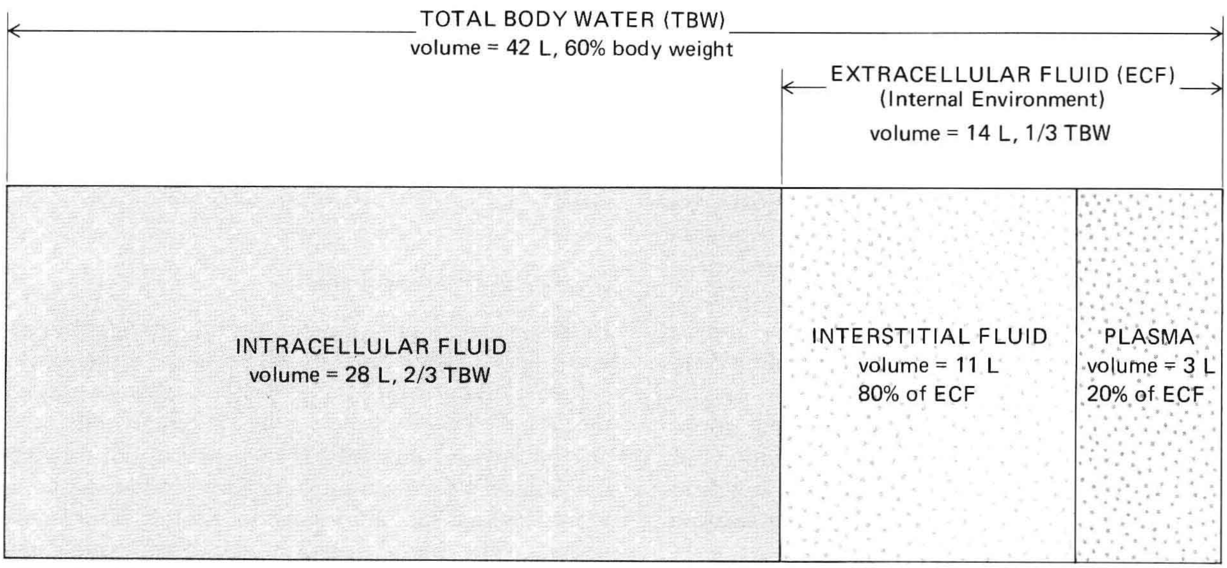

FIGURE 1-4 Fluid compartments of the body. Volumes are for a "standard" 70-kg man.

The Importance of Control

Implicit in life is control. Regardless of its level of organizational complexity, no living system can exist without precise mechanisms for controlling its various activities.

Every one of the fundamental processes performed by any single cell (an amoeba or a liver cell) must be carefully regulated. What determines how much sugar enters a cell? Once inside the cell, what proportion of this sugar is to be utilized for energy or transformed into fat or protein? How much protein of each type is to be synthesized, and when? How large is the cell to grow, and when is it to divide? The list is almost endless. Thus, an understanding of cellular physiology requires knowledge not only of the basic processes but also of the mechanisms which control them. Indeed, the two are inseparable.

In any multicellular organism like a human being, these basic intracellular regulators remain, but the existence of a multitude of different cells organized into specialized tissues and organs obviously imposes the requirement for overall regulatory mechanisms. Information about all important aspects of the external and internal environments must be monitored continuously; on the basis of the content of this information, "instructions" must be sent to the various tissue and organ cells (particularly muscle and gland cells) directing them to increase or decrease their activities.

This processing of information is performed primarily by the nervous and hormonal systems. Thus these two systems contribute to the survival of the organism by controlling the activities of the various bodily components so that any change (or impending change) in the body's internal environment automatically initiates a chain of events wiping out the change or leading to a state of readiness should the impending change actually occur. For example, when (for any reason) the concentration of oxygen in the blood significantly decreases below normal, the nervous system detects the change and increases its output to the skeletal muscles responsible for breathing movements. The result is a compensatory increase in oxygen uptake by the body and a restoration of normal internal oxygen concentration.

A Rationale

With this introductory framework in mind, the overall organization and approach of this book should easily be understood. Because the fundamental features of cell function are shared by virtually all cells and, in addition, constitute the foundation upon which specialization develops, we devote the first part of this book to an analysis of basic cellular physiology. Much of this cell biology is now referred to as **molecular biology** in recognition of the ultimate goal of explaining cellular processes in terms of interactions between molecules.

At the other end of the organizational spectrum, the third part of the book describes how the body's various coordinated functions (circulation, respiration, etc.) result from precisely controlled and integrated activities of specialized cells grouped together in tissues and organs. The theme of these descriptions is that each of these coordinated functions (with the obvious exception of reproduction) serves to keep some important aspect of the body's internal environment relatively constant.

The second part of the book provides the principles and information required to bridge the gap between these two organizational levels, the cell and the body. Control systems are analyzed first in general terms to emphasize that the basic principles governing virtually all control systems are the same, but the bulk of Part 2 is concerned with the major components of the body's control systems (nerve cells, muscle cells, and gland cells). Once acquainted with the cast of major characters—nerve, muscle, and gland cells—and the theme—the maintenance of a stable internal environment through the interactions of these components—the reader will be free to follow the specific plot lines—circulation, respiration, etc.—of Part 3.

PART · ONE

BASIC CELL FUNCTIONS