Textbook of Physiology

W. W. TUTTLE

BYRON A. SCHOTTELIUS

FIFTEENTH EDITION

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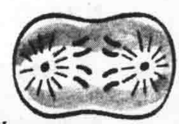

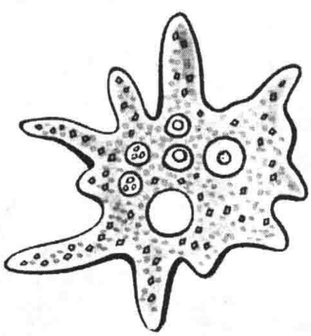

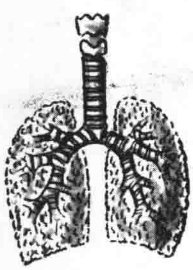

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Preface to fifteenth edition

In the preparation of this edition we have attempted to provide, as in previous editions, the requisite modern concepts in sufficient depth and breadth for a successful introduction to the study of human physiology. Moreover, considerable attention has been given to cellular and molecular biology as these contribute importantly to an understanding of mammalian physiology. To this end, a new chapter, The Cell, has been added and the material in all of the early chapters has been extensively reorganized and reinterpreted. Indeed, throughout the text, much new material has been included and old material deleted. A number of original figures appear for the first time in this edition.

By and large, the presentation is dogmatic, as befits a basic course. Detailed discussion of differing theories has been avoided, but the instructor is urged to seize this opportunity to challenge the gifted student.

We wish to acknowledge the many helpful suggestions provided us by individuals actively using previous editions either as instructors or students. Those who contributed in this way to the current edition are assured of our thanks.

We appreciate the assistance of Dr. Dorothy Schottelius in the preparation of this edition.

W. W. T.
B. A. S.

Abbreviations

ACTH *adrenocorticotrophic hormone*
ADH *antidiuretic hormone*
ADP *adenosine diphosphate*
AP *action potential*
ATP *adenosine triphosphate*
BM *basal metabolism*
CGM *central gray matter*
CNS *central nervous system*
CoA *coenzyme A*
CRF *corticotrophin-releasing factor*
DNA *deoxyribonucleic acid*
DPN *(CoI) diphosphopyridine nucleotide*
FSH *follicle-stimulating hormone*
GFR *glomerular filtration rate*
ICSH *interstitial cell-stimulating hormone*
IU *international unit*
LH *luteinizing hormone*
MSH *melanophore-stimulating hormone*
PBI *protein-bound iodine*
PD *potential difference*
RBC *red blood corpuscle*
RNA *ribonucleic acid*
RP *resting potential*

RPF *renal plasma flow*
RQ *respiratory quotient*
SDA *specific dynamic action*
STH *somatotrophic hormone*
TPN *(CoII) triphosphopyridine nucleotide*
TSH *thyroid-stimulating hormone*
WBC *white blood corpuscle*

Comparison of metric with English measures

Length

1 kilometer = 1000 meters = 0.62 mile

1 meter = 100 centimeters = 1000 millimeters = 39.37 inches = 1.09 yards

1 millimeter = $\frac{1}{25}$ inch (approximately)

1 micron, 1μ = $\frac{1}{1000}$ millimeter = $\frac{1}{25,000}$ inch

1 angstrom, 1 Å = $\frac{1}{10,000}$ micron = 1×10^{-7} millimeters

1 inch = 2.5 centimeters (approximately)

1 mile = 1.6 kilometers

Volume

1 liter = { 1000 milliliters (ml.) / 1000 cubic centimeters (c.c.) } = { 0.9 dry quart / 1.05 liquid quarts }

1 dry quart = 1.1 liters

1 liquid quart = 0.9464 liter = 946.4 ml.

1 fluid ounce = 29.57 milliliters

1 cubic inch = 16.38 cubic centimeters

Weight

1 microgram, 1 μg, or gamma ≐ 0.001 mg. = $\frac{1}{28,000,000}$ ounce

1 milligram = 1000 μg or gammas

1 gram = 1000 milligrams

1 kilogram = 1000 grams = 2.2+ pounds or 35.27 ounces

1 pound = 453.6 grams

1 ounce = 28.35 grams

Energy

1 kilogram-meter (kg.-m.) = 7.25 foot-pounds

1 foot-pound = 0.1381 kg.-m.

Mechanical equivalent of heat

1 large Calorie (Kilocalorie) = 426 kilogram-meters = 3,087 foot-pounds

1 kilogram-meter = 0.00234 Calories

Temperature

To convert Centigrade degrees into Fahrenheit, multiply by $\frac{9}{5}$ and add 32.

To convert Fahrenheit degrees into Centigrade, subtract 32 and multiply by $\frac{5}{9}$.

Color plates

Chapter 1

Life processes

Protoplasm

Life as a stimulus-response phenomenon

Even a cursory examination of the human body reveals a most amazing structural complexity. Its chemical constitution is equally complex. Complexity of structure, whether physical or chemical, entails complexity of operation. Hundreds of processes in the body take place simultaneously. These activities are nearly always mutually interdependent; cessation of heartbeat for four or five minutes stops the functioning of all parts. This complexity and interrelationship in function of its various parts makes the study of the living body —physiology—somewhat difficult. The study of any one part (and we can study but one part at a time) demands a knowledge of how its activity is affected by the activity of all the other parts. To overcome this difficulty it may be well at the outset to take a brief survey of the field as a whole. In this we shall consider the fundamental properties common to most, if not to all, of the various body structures and attempt to show how the more specialized functions of certain organs serve the entire body. The knowledge gained will not be extensive, but it may enable us to bring the disjointed fragments into an organized ensemble.

The human body and all the more highly organized forms of life are composed of various parts; each of these performs a definite function. Such parts are called organs; thus the stomach is spoken of as an organ of digestion and the eyes as sense organs of sight.

Two or more organs may differ somewhat in their individual functions, but collectively they may serve a definite, ultimate purpose in the body. Such an ensemble of organs is referred to as a system. Thus the mouth, esophagus, stomach, intestines, etc., constitute the digestive system; in this system each organ contributes its part to the more general function of digestion. In a similar manner we speak of the respiratory, the circulatory, the excretory, and the reproductive systems.

By closer examination it can be demonstrated that an organ is made up of two or more kinds of structures known as tissues, each performing its special duty. In the stomach, muscle tissue and gland tissue are found. The food is moved about by muscle tissue and the digestive juices are produced by the gland tissue. A tissue, in turn, is composed of a countless number of microscopic structures called cells (Chapter 2), which in any given tissue resemble each other closely. Similar to the various parts of a mechanical device, no organ in the body functions independently but only as an integral part of a highly coordinated collection of organs—the living organism.

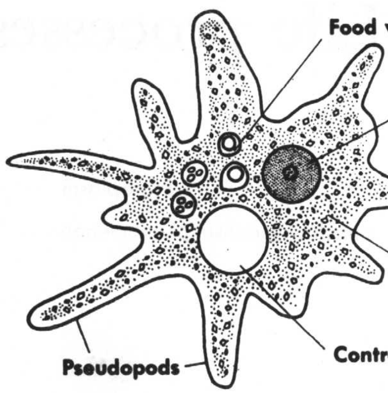

Figure 1
Amoeba proteus.

PROTOPLASM

The substance composing a cell is known as protoplasm. According to Huxley protoplasm is the physical basis of life. It is that particular form of matter which exhibits the properties and activities of life; it is living stuff.

The ameba (Figure 1), an aquatic animal about 1/100 inch in diameter, appears when viewed through the microscope as an irregular-shaped bit of matter, protoplasm. In this small mass of protoplasm it is nearly always possible to distinguish two parts, a more fluid mass, cytoplasm, surrounding a spherical and somewhat denser body, the nucleus. Hence we may define a cell as a discrete mass of protoplasm containing a nucleus. The cytoplasm is contained within a very delicate envelope, the plasma membrane. Cytoplasm often may appear as a structureless ground substance, but various minute solids in addition to the nucleus can be detected. These will be considered in Chapter 2.

That protoplasm is not a solid in the ordinary meaning of this term is evident from the mechanical changes it can, in many instances, undergo with such great ease. Examined microscopically, protoplasm generally appears as a semifluid transparent substance having a fair degree of viscosity. The physical structure of the semifluid material of cytoplasm has been variously described as reticular (network), granular, alveolar (honeycomb), and fibrillar (threadlike). In certain cells the rupturing of the cell membrane causes the protoplasm to flow out and to form globules.

Chemical composition of protoplasm

The chemical investigation of protoplasm as such is impossible because analysis destroys life; the results are those of a dead body. One thing, however, is certain and fundamental: protoplasm is not an individual chemical substance such as sodium chloride or sugar. It is composed of a large number of chemical compounds, among which we find proteins, fats, carbohydrates, water, and various minerals. The elements most frequently present in the various compounds found in protoplasm are carbon, oxygen, nitrogen, hydrogen, phosphorus, sulfur, sodium, potassium, calcium, magnesium, chlorine, iodine, iron, and copper; none of these elements is peculiar to protoplasm. A detailed discussion of the compounds in which the aforementioned elements occur belongs more properly in a later chapter; here we must content ourselves with a few cursory, but necessary, observations.

Water. From 50 to 90% of protoplasm is water. Deprived of this water, nearly all protoplasms die quickly; a few forms (notably plant seeds) pass into a condition of latent (inactive) life from which they can be revived by the addition of water. In cell water we find dissolved some crystalloids but colloids (gel-like substances) are more abundant.

It is difficult to picture to ourselves a piece of machinery such as our muscles being composed of 75% water; it does not suggest the necessary firmness, stability, and rigidity customary in machines. However, the ease with which a contracting muscle changes its shape is evidence of the semifluidity of its protoplasm. The viscosity of protoplasm varies from one type of cell to another. Soon after death the fluid material of protoplasm becomes firmer in texture.

Certain parts of our body exhibit firmness and solidity to a high degree, e.g., tendons, ligaments, cartilages, and bones. This, however, does not indicate that the protoplasm lacks a high percentage of water, for these structures are formed of a large amount of solid material deposited between the living cells.

Inorganic materials. Among the most important of the inorganic salts are the soluble chlorides, sulfates, phosphates, and carbonates of sodium, potassium, calcium, and magnesium. The amount of each of these salts present in protoplasm varies with the different kinds of cells, but, like water, they are indispensable for life. Each salt plays its particular role in the activity of the protoplasm.

Proteins. As familiar examples of proteins, egg albumin (white of egg), the curd of sour milk, and gelatin may be mentioned. Proteins are one of the most complex substances with which the biochemist deals. They are complex because the molecules contain at least five, and frequently more than five, elements, and the size of the molecule is exceedingly large.

There are many kinds of proteins that differ from each other in composition, solubility, and chemical reactions. Some are soluble in dilute salt solutions (as in milk, blood, and lymph). Only a few are soluble in water. Nearly all proteins are undialyzable; i.e., they cannot pass through vegetable or animal membranes (such as the urinary bladder, lungs, and pericardium), and they therefore belong to the class of compounds frequently called colloids—the gluelike and jellylike compounds.

Proteins in solution are easily precipitated by certain reagents, such as alcohol, and are coagulated by heat (e.g., egg albumin) so that the previously soluble protein is rendered insoluble.

Carbohydrates. Carbohydrates are composed of carbon, hydrogen, and oxygen. They include the simple sugars, e.g., glucose, the double sugars, of which sucrose and lactose are well-known examples, and the so-called starches, among which are the ordinary starches and a substance known as glycogen. It is especially in the form of glycogen (sometimes called animal starch) that we find the carbohydrates in animal cells.

Lipids. Lipids, a class of compounds that includes the common fats, are composed mainly of carbon, hydrogen, and oxygen. They are present in protoplasm either as simple compounds or in complex combination with other substances (e.g., lipoproteins). A large proportion of the energy requirement of living tissues is met by these important fuels. Usually energy production involves the oxidation of a balanced mixture of carbohydrates and lipids; indeed, lipid metabolism is linked to carbohydrate metabolism.

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In protoplasm are found the compounds just discussed and many others. However, protoplasm must not be regarded as merely a mixture of these ingredients, for we find practically the same substances in the fluid portion of the blood, to which we do not ascribe the properties of life. In protoplasm these compounds are properly organized to form an exceedingly complex and labile structure; little is definitely known in regard to the nature of the union holding them together. Each of the ingredients in the protoplasmic structure no doubt plays a specific part. The protein material, which forms the most abundant solid constituent of protoplasm, may be regarded as forming the structural basis of the cell.

Physiological properties of protoplasm

In addition to the chemical and physical properties common to all inanimate objects (such as color, cohesiveness, elasticity, acidity, specific gravity, etc.), protoplasm exhibits what are generally termed physiological properties or phenomena. Among these are *contractility, irritability, conductivity, metabolism, excretion, growth,* and *reproduction.* As implied in Huxley's definition, the physiological properties are the very expression of life. However this does not necessarily mean that they are not ultimately dependent upon the chemical and physical properties of protoplasm.

Contractility. One of the most conspicuous characteristics of an animal is its power to move some parts of its body or to change its own position with respect to its surroundings. This is in sharp contrast with the immobility of inanimate objects. Upon observing an ameba for some length of time, it is noticed that at a certain point a projection arises. The protoplasm seems to stream in this direction so that the projection or pseudopod enlarges; at the same time the protoplasm at some other portion of the body can be seen to withdraw. Several of these pseudopods are shown in Figure 1. By thus changing its shape, the ameba moves from place to place. The power of protoplasm to change its form is called contractility.

Not all cells in a highly specialized animal body possess the property of contractility. In the human body two structures in particular are endowed with contractility: muscles and certain leukocytes (white blood cells). By the simultaneous contraction of thousands of cells, a muscle shortens in length and increases in thickness. The leukocyte shows its contractility by the formation and withdrawal of pseudopods, similar to the ameba.

Irritability or excitability. Another matter of general observation is the ease with which slight changes in the environment can induce changes in the activity of a living organism. When an ameba that has been quiescent for a considerable length of time is disturbed by placing a drop of dilute acid near it or by heating the water in which it lives, a change in its form is soon observed. The animal by its contractility responded to the disturbance. The power of protoplasm to respond to an environmental change is known as irritability; the change in the environment is called a stimulus. Among the more commonly experienced environmental changes that befall us, may be mentioned thermal (heat and cold), photic (light), acoustic (sound), chemical, and mechanical (such as impact, pressure, and pull).

A stimulus sets up a change in the protoplasm that is known as the excitatory state. This, in turn, evokes the activity characteristic of the protoplasm that is being stimulated; e.g., the protoplasm of a muscle contracts, that of the salivary gland secretes saliva, and that of the tear glands forms tears. However, the various forms of protoplasm may differ, and whatever property or power these forms may or may not have, all protoplasm possesses the characteristic of irritability. Irritability is a fundamental property common to all protoplasm, and, in consequence, it is employed as a diagnostic property by which the living is distinguished from the dead. A freshly excised muscle of a frog is alive since it responds upon being stimulated. But the excised muscle soon dies. How can we know whether this has occurred? Death may be determined by whether or not it responds to stimulation. When the form of stimulation to which a particular organ is highly irritable has been ascertained and when the organ loses its irritability to this stimulation and no treatment can regain it, we say that the organ is dead.

Another outstanding characteristic of life may be noted here incidentally. When a stimulus calling forth a change in protoplasm ceases, protoplasm returns to its former state. Quite appropriately some authors speak of the resiliency of protoplasm.

Conductivity. The application of a stimulus to a certain part of the body may cause activity in a distant part; e.g., the stimulation of the olfactory organs by the odor of fragrant food causes the salivary glands to become more active. The olfactory organs and the salivary glands are interconnected by nerves. It must be evident that the stimulation of the receptors of smell generates nerve impulses which eventually are transmitted to the glands and excite them to activity.

The ability of protoplasm to convey an impulse is known as conductivity. Like irritability, conductivity is present in all cells, but both properties find their highest development in nerve tissue. So far as we know, nerve impulses never originate in the absence of adequate stimulation.

Automatism or spontaneity. Frequently it happens that a quiescent ameba forms a pseudopod, apparently without any stimulus having been applied. Some authorities claim that this phenomenon shows the power of protoplasm to initiate its own activity; i.e., it has the property of spontaneity. Although it may be very difficult or sometimes impossible to discover any form of stimulation that may have acted upon the ameba, yet for other reasons we cannot grant the existence of this property. One fundamental law of the universe is Newton's law of inertia which states that a body at rest remains at rest until acted upon by some external force. Is is more than likely that the ameba is no exception to this law. In the human body actions also are induced by stimulation.

It is, however, customary to apply the term *automaticity* to an organ which, after removal from the body, continues its usual activity without any apparent external stimulation. Automaticity holds true for the excised heart of a frog but never for an excised skeletal muscle. Automatic action is the result of an internal stimulus.

Energy transformations—metabolism. Protoplasm is constantly active. This activity shows itself not only in the changing of its form but also in the production of heat and electrical potential and in chemical changes. All matter resists undergoing changes; i.e., it has inertia. Therefore to produce a change this inertia must be overcome; it is accomplished by energy.

Energy may be defined as the ability to do work or to produce a change. There are many forms of energy, such as heat, light, sound, mechanical, electrical, chemical, etc. It is customary to speak of two modes of energy, that of motion or kinetic energy and that of position or potential energy.

Kinetic energy. The energy of motion may be in the form of mechanical energy of a moving body, e.g., the energy of wind and waves, of flowing blood, and of a moving part of an animal. Heat is the energy of the movements of individual molecules. The movement of electrons gives rise to the electric energy of a current.

Potential energy. Potential energy may be regarded as stored energy. No change is produced by it, but there is latent power which under proper conditions is capable of doing work. A suspended weight, a coiled spring, and a stretched rubber band all possess potential energy.

Conservation and transformation of energy. The amount of energy in the universe is said to be constant—energy can be neither created nor destroyed. This is the law* of the conservation of energy.† However, energy can be changed from one form into another. Thus the energy of an electric current can be transformed into heat, light, or sound. We may also transform kinetic into potential energy; e.g., a weight is raised from the ground to a certain height and placed on a support. In doing this the energy of motion obtained from the arm of an individual or from any other source is transformed into potential energy of position; it is said to be latent in the weight. It is energy of position by virtue of the attraction existing between the earth and the weight; this attraction was overcome by the force that separated these two bodies. It is energy due to separation. When the support upon which the weight rests is removed, the potential energy of position is transformed into mechanical kinetic energy of motion. When the weight strikes the earth, the energy of the moving body is transformed into sound and heat energy.

Chemical potential energy. In the same manner we may speak of the energy of position, or separation, in chemical phenomena. By passing an electric current through water, the water is decomposed into hydrogen and oxygen. The energy of the electric current disappears, and we find it associated with the hydrogen and oxygen atoms. Because of the attraction between the separated atoms, there exists potential energy of position or separation, known as chemical potential energy. Under proper conditions, such as the introduction of a spark, the hydrogen and oxygen unite, and the chemical potential energy is transformed into kinetic energy of heat, light, sound, mechanical energy, etc. As much energy is liberated by the union of the gases in the formation of water as is needed to separate an equal quantity of the water into the two gases.

In the elemental state carbon and oxygen contain chemical potential energy; at the proper temperature (the kindling temperature) they unite and the energy becomes kinetic, in the form of heat and light. The uniting of oxygen with another element or with a compound is called oxidation, e.g., ordinary burning. Except for carbon monoxide, carbon dioxide, and the carbonate salts of metals, any compound containing

*A law is not a rule or regulation according to which something happens; neither does a law explain why it happens. Rather it is a statement of a relationship man has discovered between two or more phenomena; under the same conditions they are invariably reproducible. The discovery of such relationships is the goal of scientific research; isolated facts are of little value.

†According to the modern conception of the universe (the relativity theory) this statement is not strictly correct, for matter and energy are regarded as two phases of a single principle—energy-matter. Matter may be changed into energy, as occurs in the disintegration of radium and uranium. But in everyday chemical reactions this is too slight to be considered.

carbon is known as an organic compound, as distinct from an inorganic compound. All organic compounds that contain carbon and hydrogen or carbon, hydrogen, and oxygen are oxidizable; i.e., they have affinity for more oxygen. In consequence they contain potential energy. Among these compounds are alcohol, coal, and foods such as lipids, carbohydrates, and proteins.

Source of energy for animal life. The potential energy in the food utilized by the animal is in all cases derived directly or indirectly from the plant world. Plants are able to synthesize, or build up, simple inorganic compounds such as water, carbon dioxide, nitrates, sulfates, and phosphates into highly complex organic substances (e.g., sugars, starches, lipids, and proteins). Since these last-named substances contain much potential energy, although the materials from which they are derived are practically devoid of energy, energy from some external source must be drawn upon and stored. This source is the radiant energy of the sun. In the chlorophyll, or green pigment, of plants radiant energy produces a series of chemical changes in the inorganic compounds mentioned and thereby transforms them into organic substances such as glucose. The radiant energy is transformed into chemical potential energy and becomes latent in the products formed (e.g., glucose).

This process of photosynthesis may be expressed as follows:

$$CO_2 + H_2O + \text{Radiant energy} \rightarrow$$
$$CH_2O + O_2 + \text{Chemical potential energy}$$

Several CH_2O molecules combine to form $C_6H_{12}O_6$, which is glucose. This simple sugar is regarded as the basic material from which other carbohydrates, fats, and proteins are constructed. It is the storing (conserving) of energy that makes the process of photosynthesis the fundamental process upon which the existence of all life depends. Being unable to perform this synthesis, the animal takes into its body (directly in herbivorous animals and indirectly in carnivorous animals) the plant-made and energy-rich carbohydrates, fats, and proteins. Green plants are the great living synthetic mechanisms; all animals are predatory.

Catabolism. Protoplasm is a living machine. Similar to inanimate machines such as electric motors, it does not create energy. Protoplasm is an energy-transforming mechanism. Hence, to be active it must be supplied with energy. The source of this lies in the chemical potential energy of carbohydrates, lipids, and proteins. These substances, as will be discussed later, are not only found in our food but are also constituents of protoplasm itself. Although it is generally helpful to speak of the food in the protoplasm as fuel and of the protoplasm as the machine, in reality no sharp distinction can be drawn. To be utilized for vital processes (e.g., the contraction of a muscle) the chemical potential energy in the food or protoplasm must be released.

The release of potential energy is known as catabolism. Subsequent chapters are devoted to a more detailed account of the energy transformations in our body, but in order to understand any protoplasmic activity it will be necessary to anticipate this by a brief preliminary study.

Liberation of energy. When a large organic molecule is split into two or more smaller molecules, the products formed contain less potential energy than the original molecule; hence some energy must have been set free; e.g., during yeast fermentation the large molecule of glucose, $C_6H_{12}O_6$, is broken up into 2 molecules of carbon dioxide, CO_2, and 2 molecules of ethyl alcohol,