TEXTBOOK OF
Medical Physiology

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DEDICATED TO

MY FATHER

for the uncompromising principles that have guided his life

MY MOTHER

for leading her children into intellectual pursuits

MY WIFE

for her exceptional generosity to her family

MY CHILDREN

for making everything worth while

Preface

The title of this book, Medical Physiology, discloses that it is not a reference work for physiologists. Instead, it is a textbook written for students. Its purpose is to present the philosophy and logic of physiology, to demonstrate physiology as a series of regulatory systems integrated into one complete functioning organism, the human body, and to present in terms understandable to the student that important mass of physiologic knowledge needed by both physiologist and physician.

Many will look upon this one-man attempt to write a physiology text as extremely presumptuous. Yet, it has seemed to me that the advantages of single authorship greatly outweigh the disadvantages. Perhaps the most important advantage is the uniform perspective that can be achieved, a perspective that can be more nearly that of the student who desperately needs all the aid that we can give him as he is being introduced to the complexities of body function. This kind of text also has afforded an opportunity—which I hope has been realized—to attain proper balance between the respective parts of physiology, a task that is far more difficult in a collaborative work.

Development of a new textbook, particularly one employing new techniques of presentation, does not come about without many years of effort. This book is the culmination of nine years' work spent in collecting figures, amassing information, and experimenting with different teaching materials to determine which are best suited to the student. I believe strongly that no one can contribute significantly to the science of physiology unless the principles of experimentation are part of his nature, and I apply this same philosophy to the teacher—a teacher can better serve his students if he experiments with his teaching materials and is willing to cast aside his mistakes. During the past nine years I have been in the unusual position of teaching fifteen complete courses of medical physiology. This has given me the opportunity to experiment with every type of text, both American and foreign, and also to experiment with most of the material in this book. As a result of this testing process the substance of the book has been reworked several times to improve the manner of presentation and to add recent data. The purpose of all this work has been to develop a text that will convey the information necessary to the student in a way that he can understand.

Though I have a great love for physiology as a pure science, I define it as including pathologic as well as normal physiology. Much of our physiologic information has been gained from clinical patients, for each sick person is as much a source of experimental data as is an animal on a research table. Therefore, the function of the body in many diseases is described to illustrate physiologic principles, but, in presenting this pathologic physiology along with the normal, I have also had the motive of attempting to instill in the student my own love of physiology for itself as well as to provide the student with that transitional information which he needs to apply physiologic principles in other medical studies.

The great quantity of experimental data that has accumulated in the last hundred or more years has made physiology one of the most complex of all studies. This has of necessity required detailed choice of material to be included in this book. To reduce the student's burden, those parts of physiologic knowledge that I have considered most important are set in large type, while the less important matter is in small type. Unfortunately, the effort to be concise has led to more dogmatic presentation of many physiologic principles than I ordinarily would have desired. Yet, to help develop an inquiring attitude in the student, a long list of pertinent publications is presented at the end of each chapter. More effort has gone into choosing these references than is readily apparent, for they represent in general the most recent articles on each subject, and they have been especially selected for their own bibliographies to give a broad approach to the literature.

I owe much to many others who have aided in the preparation of this book. Above all I am grateful to the staff of W. B. Saunders Company for its continued help. I deeply appreciate all of the secretarial work of Mrs. Ann Wiltshire, Mrs. Irleene Buffaloe, and Miss Sue Cathey, and for the figures I am grateful to Mr. Al Teoli, Mrs. Judy Binder, Mr. Brantley Pace, and Mr. Robert Harrison. I also acknowledge with gratitude Mr. Jack Crowell's help in checking much of the proof. Finally, may I apologize to my wife and children for the several thousand hours of family association lost during the writing of this book.

ARTHUR C. GUYTON

Jackson, Mississippi

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PART I

Cellular Physiology and Introduction to Human Physiology

Chapter 1

DEVELOPMENTAL AND CELLULAR PHYSIOLOGY

Physiology is the philosophy of function in living matter, and encompassed in this philosophy is the study of physical and chemical factors responsible for the origin, development, and progression of life. Each type of life, from the monomolecular virus up to the towering tree or the complicated human being, has its own functional characteristics; therefore, the vast field of physiology may be divided into subdivisions known as viral physiology, bacterial physiology, cellular physiology, plant physiology, human physiology, and many more. The present text, which is entitled MEDICAL PHYSIOLOGY, presents the organization and function of the human body so that the student of medicine can understand the beautiful logic of the mechanisms and control systems that normally allow all the unit parts of the body to operate in harmony but under abnormal conditions to operate in disharmony, which we call "sickness."

The human body is composed of specialized organs operating in mutual support of each other, and each organ in turn is composed of millions of individual cells, each one of which is a living structure in itself. Each cell is made up of intracellular organs and supporting structures, and these are composed of individual molecules. This complicated organism is a product of evolution, which probably began with a single nucleoprotein molecule and then extended progressively through the stages of multimolecular organisms, rickettsiae, bacteria, unicellular animals, multicellular animals, and finally into the complicated structures of higher animalhood.

Evolution is to physiology what recorded history is to the social organization of mankind, for each stage in the phylogenetic development of man is a logical outgrowth of the previous stage. Many of the physiologic mechanisms of complex animalhood and planthood are inherited from the earliest forms of life. Therefore, for a complete understanding of how the human being is organized and how his organs operate, it is quite necessary to review from the beginning the physiologic developments in each stage of life.

PHYSIOLOGY OF PRE-CELLULAR DEVELOPMENT

The Origin of Life—Spontaneous Chemical Evolution

The most plausible theory for the origin of life is that of *spontaneous chemical evolution*. In the early, highly reactive atmosphere of the earth, there existed large quantities of hydrogen, carbon, nitrogen, and oxygen—the essential building stones of all living matter on earth. These substances, in the presence of heat and metallic catalysts and under the influence of sunlight, can be converted very easily into many different organic compounds. Indeed, by spectrographic analysis of light rays from the incandescent stars, organic substances such as methane have been discovered on the surfaces of these stars even though no life exists there, and the atmosphere of our near neighbor, Venus, has a high percentage of formaldehyde, a very reactive organic compound which can be polymerized with ease into sugars. Also, ammonia is often catalyzed into existence by the reaction of steam and metallic nitrides, which undoubtedly existed on the earth's early surface. It is not a long step from formaldehyde, the simple sugars, methane, and ammonia to the various simple amino acids such as glycine and alanine, and it is quite easy to understand how amino acids, by the process of peptide linkage, could have combined to form simple or even complicated proteins while the earth was still young. Thus, because proteins are the basic substances of life, the origin of life could have come about very easily as a result of spontaneous chemical evolution.

Reproduction as the Secret of Life

Though it is quite easy to understand how even complex molecules such as proteins undoubtedly were spontaneously generated on the highly reactive surface of the early earth, nevertheless, remaining to be developed was the key to the progression of life—that is, *reproduction.*

One of the most familiar studies in chemistry is that of catalysts, and many proteins are a type of catalyst called "enzymes." A few catalysts are *autocatalytic,* for they catalyze the formation of more molecules of their own type. Among the simplest of the autocatalytic agents is iron oxide, or what is commonly known as rust. When rust once appears on new iron, it autocatalyzes the development of more iron oxide.

Of special interest to students of life are the *nucleoproteins,* which are complicated conjugated proteins and which often are autocatalysts. Once autocatalytic nucleoproteins have been formed and are mixed with appropriate organic chemical compounds for building stones, these nucleoproteins can catalyze the formation of other nucleoproteins having molecular structures that duplicate their own. Thus, in the early development of the world, only one such reproducible nucleoprotein spontaneously generated in the reactive atmosphere was all that would have been needed to start the unbroken chain of life, for thereafter continuous formation of new living structures could have proceeded indefinitely.

If this theory of the origin of life is correct, the original living nucleoprotein was very similar to some of the present well known viruses, for the small viruses are probably single nucleoprotein molecules. For instance, chemical tests show the tobacco mosaic virus to be a nucleoprotein molecule with a molecular weight of approximately 40,000,000.

Communal Organization of Nucleoproteins to Form Complex Structures

Mutation and the Formation of Multimolecular Organisms. In order for the original living nucleoprotein to develop into the animal and plant kingdoms, another essential milestone had to be passed: that is, the reproducing nucleoprotein molecules had to change their molecular structures progressively and yet continue to reproduce the new molecules indefinitely. Such changes are known as "mutations."

Though some molecules of nucleoprotein are theoretically capable of living separately from each other, these molecules tend to aggregate and, as new offspring molecules are formed, the offspring become part of the aggregate. Some of the offspring of the original living nucleoprotein undoubtedly mutated to become new nucleoproteins which remained in the aggregate. Also, some of the new nucleoproteins were undoubtedly able to perform certain chemical functions more efficiently than could the original nucleoprotein, whereas the original nucleoprotein was still able to perform other chemical functions more efficiently than could the new ones. For instance, it is possible that one nucleoprotein would have been able to catalyze the formation of sugar from formaldehyde very easily while another might have been able to catalyze the formation of ammonia from water and nitrides. Therefore, the aggregate structure probably had an even better chance of surviving and reproducing than had the separate nucleoprotein molecules, thus originating a multimolecular organism. By further mutation and further aggregation of molecules, still many more different and progressively more complex types of multimolecular organisms could have developed on the early earth, and such are still developing almost infinitely in the form of the viruses.

Development of Specialized Functions in Viruses and the Development of Rickettsiae and Bacteria. As the structure of viruses became more complex, and their sizes became larger as shown in Figure 1, some of the molecules presumably became specialized as *enzymes,* some became specialized for the formation of a surface barrier or what might be called a *primitive membrane,* and others perhaps specialized for the purpose of controlling reproduction. Finally, the aggregating mixture of nucleoproteins attracted around it quantities of electrolytes, sugars, fats, and many other substances. At this stage of development, the viruses became *rickettsiae,* and, with still further growth and organization, these became *bacteria.*

It was in the stage of bacteria that tre-