# MEDICAL PHYSIOLOGY AND BIOPHYSICS

RUCH & FULTON

# MEDICAL PHYSIOLOGY AND BIOPHYSICS

# Edited by

# THEODORE C. RUCH, Ph.D.

PROFESSOR AND EXECUTIVE OFFICER

DEPARTMENT OF PHYSIOLOGY AND BIOPHYSICS

UNIVERSITY OF WASHINGTON SCHOOL OF MEDICINE

#### and

# JOHN F. FULTON, M.D.

LATE STERLING PROFESSOR OF THE HISTORY OF MEDICINE  ${\tt YALE~UNIVERSITY~SCHOOL~OF~MEDICINE}$ 

Eighteenth Edition

OF

HOWELL'S TEXTBOOK OF PHYSIOLOGY

# W. B. SAUNDERS COMPANY

Philadelphia and London

#### Reprinted October, 1960, January, 1961 and August, 1961

© 1960, by W. B. Saunders Company.

Copyright under the International Copyright Union

Copyright, 1905, by W. B. Saunders and Company. Copyright, 1907, 1909, 1911, 1913, 1915, 1918, 1921, 1924, 1927, 1930, 1936, 1940, 1946, 1949 and 1955, by W. B. Saunders Company

All copyright renewals registered

All Rights Reserved. This book is protected by copyright. No part of it may be duplicated or reproduced in any manner without written permission from the publisher.

Made in the United States of America. Press of W. B. Saunders Company

LIBRARY OF CONGRESS CATALOG CARD NUMBER: 60-7819

### AN AMERICAN TEXT-BOOK OF PHYSIOLOGY

edited by William H. Howell, Ph.D., M.D. W. B. Saunders and Company 1896

# A TEXT-BOOK OF PHYSIOLOGY FOR MEDICAL STUDENTS AND PHYSICIANS

written by William H. Howell, Ph.D., M.D., LL.D. W. B. Saunders and Company 1905

# HOWELL'S TEXTBOOK OF PHYSIOLOGY 15th Edition

edited by John F. Fulton, M.D. W. B. Saunders Company 1946

### A TEXTBOOK OF PHYSIOLOGY

16th and 17th Editions

edited by John F. Fulton, M.D. W. B. Saunders Company 1949 and 1955

# Contributors

#### DONALD H. BARRON, Ph.D.

Professor of Physiology, Yale University School of Medicine

#### ROSEMARY BIGGS, B.Sc., Ph.D., M.D.

Scientific Officer, Medical Research Council, Blood Coagulation Research Unit, Churchill Hospital, Oxford, England

#### JOHN R. BROBECK, Ph.D., M.D.

Professor of Physiology, University of Pennsylvania School of Medicine

#### ALAN C. BURTON, Ph.D.

Professor of Biophysics, University of Western Ontario Faculty of Medicine

#### LOREN D. CARLSON, Ph.D.

Chairman, Department of Physiology, University of Kentucky College of Medicine

#### PAUL F. FENTON, Ph.D.

Professor of Biology, Brown University

#### THOMAS R. FORBES, A.B., Ph.D.

Associate Professor of Anatomy and Associate Dean, Yale University School of Medicine

# RAÚL HERNÁNDEZ-PEÓN, M.D.

Director, Unit for Brain Research, Medical Center, Mexico City

#### DAVID I. HITCHCOCK, Ph.D.

Associate Professor of Physiology, Yale University School of Medicine

#### CHARLES W. HOOKER, Ph.D.

Professor of Anatomy, University of North Carolina

#### ALAN KOCH, Ph.D.

Research Instructor in Physiology and Biophysics, University of Washington School of Medicine

#### ROBERT B. LIVINGSTON, M.D.

Director of Basic Research, National Institute of Mental Health and National Institute of Neurological Diseases and Blindness, United States Public Health Service, Bethesda, Maryland; Lecturer in Anatomy and Physiology (Professor), University of California at Los Angeles Medical Center

#### JOHN L. PATTERSON, JR., M.S., M.D.

Research Professor of Medicine, Medical College of Virginia

#### HARRY D. PATTON, Ph.D., M.D.

Professor of Physiology and Biophysics, University of Washington School of Medicine

#### THEODORE C. RUCH, Ph.D.

Professor and Executive Officer, Department of Physiology and Biophysics, University of Washington School of Medicine

#### ROBERT F. RUSHMER, M.D.

Professor of Physiology and Biophysics, University of Washington School of Medicine; Senior Consultant, Madigan General Hospital, Fort Lewis, Washington

#### JANE A. RUSSELL, Ph.D.

Associate Professor of Biochemistry, Emory University

#### ALLEN M. SCHER, B.A., Ph.D.

Associate Professor of Physiology, University of Washington School of Medicine

#### ARNOLD L. TOWE, B.A., Ph.D.

Assistant Professor of Physiology and Biophysics, University of Washington School of Medicine

#### FRANK W. WEYMOUTH, Ph.D.

Professor of Physiology, Emeritus, Stanford University; Professor of Physiological Optics, Los Angeles College of Optometry

#### WALTER WOODBURY, Ph.D.

Associate Professor of Physiology and Biophysics, University of Washington School of Medicine

#### HELEN M. PAYLING WRIGHT, B.Sc., Ph.D., L.M.S.S.A.

Research Assistant, University College Hospital, London

#### ALLAN C. YOUNG, Ph.D.

Associate Professor of Physiology and Biophysics, University of Washington School of Medicine

# Preface to the Eighteenth Edition

This Book, which has been a significant force in medical education for nearly three quarters of a century, has received a new title for this edition. The new title was chosen to represent the editors' conviction that physiology should be developed and taught "in depth." Such depth is attained by ranging from fundamental approaches derived directly from the university disciplines, especially physics, through classic physiology to clinical physiology. The first of these orientations is conveyed, somewhat inadequately, by adding the word "biophysics" to the title—inadequately because psychology as well as physics, physical chemistry and mathematics is becoming increasingly important to physiology.

No incompatibility is seen between emphasizing fundamental approaches and the inclusion of more clinical physiology. This has not been done by adding paragraphs of dilute clinical medicine at the end of each chapter. Instead, whether it be a sentence, a paragraph or a chapter devoted to pathologic physiology, the criterion has been: does physiology illuminate the pathologic state or, conversely, does the abnormal function point up the normal physiology? The emphasis on the clinical applications of physiology has been considerably increased in this edition, but space limitations prevent a complete and systematic presentation. Whole textbooks are devoted to pathologic physiology and some believe, with reason, that the first course cannot adequately cover both normal and pathologic physiology. Even so, such a course gains by the inclusion of some clinical physiology, and the student and the physician gain by having both side by side rather than separated in time and space.

In the 18th edition we have sought to maintain an important feature of previous editions, the authority which comes with drawing authors from various laboratories. At the same time we have attempted to gain a uniformity of level, point of view and style by having many excellent chapters of the 17th edition rewritten or revised by a geographically related group of authors and by editing for content and expression considerably more than is usual for textbooks with many authors. Thanks are therefore due to past as well as present contributors for taking time from busy lives in the interest of producing an authoritative book suitable for medical students. I would like also to acknowledge my debt to Professor John F. Fulton, not only for the fine heritage of scholarship represented by the 17th edition but also for his good counsel and active participation in the planning and execution of this edition.

Many chapters are completely or extensively rewritten. In this category are nearly all of the chapters on nerve, muscle, reflexes and motor systems of the brain; the chapters on blood, hemodynamics, the cardiac cycle, the electrocardiogram and the control of cardiac output; and all but one of the chapters on respiration. In addition, renal physiology has been freshly described, using the terminology and concepts of physical chemistry and emphasizing the concepts of active transport. The chapters on the endocrines and reproductive physiology have been thoroughly revised in the

light of recent advances in these fields. All chapters, whether newly written or revised, have been carefully edited by Maryeva W. Terry and many of the figures have been drawn or redrawn by Helen N. Halsey; to them the authors and editors owe a great debt.

Three excellent chapters have been dropped from this edition on the grounds that their subject matter has largely passed into the realm of biochemistry and are adequately handled in textbooks of that field. On the other hand, two chapters have been added, one on the biophysics of the cell membrane and the other on the neurophysiology of emotion. These two new chapters—standing at the opposite ends of the physiologic spectrum, subcellular analysis and physiologic integration—indicate that physiology is indeed rapidly growing in depth and breadth, and owes much of its recent advance to a solid base in the university disciplines.

T. C. Ruch

# Preface to the First Edition

In the preparation of this book the author has endeavored to keep in mind two guiding principles: first, the importance of simplicity and lucidity in the presentation of facts and theories; and, second, the need of a judicious limitation of the material selected. In regard to the second point every specialist is aware of the bewildering number of researches that have been and are being published in physiology and the closely related sciences, and the difficulty of justly estimating the value of conflicting results. He who seeks for the truth in any matter under discussion is oftentimes forced to be satisfied with a suspension of judgment, and the writer who attempts to formulate our present knowledge upon almost any part of the subject is in many instances obliged to present the literature as it exists and let the reader make his own deductions. This latter method is doubtless the most satisfactory and the most suitable for large treatises prepared for the use of the specialist or advanced student, but for beginners it is absolutely necessary to follow a different plan. The amount of material and the discussion of details of controversies must be brought within reasonable limits. The author must assume the responsibility of sifting the evidence and emphasizing those conclusions that seem to be most justified by experiment and observation. As far as material is concerned, it is evident that the selection of what to give and what to omit is a matter of judgment and experience upon the part of the writer, but the present author is convinced that the necessary reduction in material should be made by a process of elimination rather than by condensation. The latter method is suitable for the specialist with his background of knowledge and experience, but it is entirely unfitted for the elementary student. For the latter, brief comprehensive statements are oftentimes misleading, or fail at least to make a clear impression. Those subjects that are presented to him must be given with a certain degree of fullness if he is expected to obtain a serviceable conception of the facts, and it follows that a treatment of the wide subject of physiology is possible, when undertaken with this intention, only by the adoption of a system of selection and elimination.

The fundamental facts of physiology, its principles and modes of reasoning, are not difficult to understand. The obstacle that is most frequently encountered by the student lies in the complexity of the subject—the large number of more or less disconnected facts and theories which must be considered in a discussion of the structure, physics, and chemistry of such an intricate organism as the human body. But once a selection has been made of those facts and principles which it is most desirable that the student should know, there is no intrinsic difficulty to prevent them from being stated so clearly that they may be comprehended by anyone who possesses an elementary knowledge of anatomy, physics, and chemistry. It is doubtless the art of presentation that makes a textbook successful or unsuccessful. It must be admitted, however, that certain parts of physiology, at this particular period in its development, offer peculiar difficulties to the writers of textbooks. During recent years chemical work in the fields of digestion and nutrition has been very full, and as a result theories hitherto generally accepted have been subjected to criticism and alteration, particularly as the important advances in theoretical chemistry and physics have greatly modified the attitude and point of view

of the investigators in physiology. Some former views have been unsettled and much information has been collected which at present it is difficult to formulate and apply to the explanation of the normal processes of the animal body. It would seem that in some of the fundamental problems of metabolism physiological investigation has pushed its experimental results to a point at which, for further progress, a deeper knowledge of the chemistry of the body is especially needed. Certainly the amount of work of a chemical character that bears directly or indirectly on the problems of physiology has shown a remarkable increase within the last decade. Amid the conflicting results of this literature it is difficult or impossible to follow always the true trend of development. The best that the textbook can hope to accomplish in such cases is to give as clear a picture as possible of the tendencies of the time.

Some critics have contended that only those facts or conclusions about which there is no difference of opinion should be presented to medical students. Those who are acquainted with the subject, however, understand that books written from this standpoint contain much that represents the uncertain compromises of past generations, and that the need of revision is felt as frequently for such books as for those constcruted on more liberal principles. There does not seem to be any sound reason why a textbook for medical students should aim to present only those conclusions that have crystallized out of the controversies of other times, and ignore entirely the live issues of the day which are of so much interest and importance not only to physiology, but to all branches of medicine. With this idea in mind the author has endeavored to make the student realize that physiology is a growing subject, continually widening its knowledge and readjusting its theories. It is important that the student should grasp this conception, because, in the first place, it is true; and, in the second place, it may save him later from disappointment and distrust in science if he recognizes that many of our conclusions are not the final truth, but provisional only, representing the best that can be done with the knowledge at our command. To emphasize this fact as well as to add somewhat to the interest of the reader short historical résumés have been introduced from time to time, although the question of space alone has prevented any extensive use of such material. It is a feature, however, that a teacher might develop with profit. Some knowledge of the gradual evolution of our present beliefs is useful in demonstrating the enduring value of experimental work as compared with mere theorizing, and also in engendering a certain appreciation and respect for knowledge that has been gained so slowly by the exertions of successive generations of able investigators.

A word may be said regarding the references to literature inserted in the book. It is perfectly obvious that a complete or approximately complete bibliography is neither appropriate nor useful, however agreeable it may be to give every worker full recognition of the results of his labors. But for the sake of those who may for any reason wish to follow any particular subject more in detail some references have been given, and these have been selected usually with the idea of citing those works which themselves contain a more or less extensive discussion and literature. Occasionally also references have been made to works of historical importance or to separate papers that contain the experimental evidence for some special view.

W. H. HOWELL

# Contents

#### Section I. BIOPHYSICS OF THE CELL MEMBRANE

Chapter 1	
THE CELL MEMBRANE: IONIC AND POTENTIAL GRADIENTS AND ACTIVE TRANSPORT	2
By J. Walter Woodbury	
Electric Potentials and Ion Concentrations in Muscle  Passive Forces Affecting Ion Movements.  Electrostatics  Ionic Equilibrium  Active Sodium Transport.  Generation and Maintenance of Ion and Potential Differences.	3 7 11 15 18 22
Section II. NERVE AND MUSCLE	
Chapter 2	
ACTION POTENTIAL; CABLE AND EXCITABLE PROPERTIES OF THE CELL MEMBRANE.	32
By J. Walter Woodbury and Harry D. Patton	
Electrical Phenomena at Rest and in Action.  Biophysics of Nerve Conduction.	34 44
Chapter 3	
SPECIAL PROPERTIES OF NERVE TRUNKS AND TRACTS	66
By Harry D. Patton	
Potentials in a Volume Conductor.	83
By J. Walter Woodbury	
Properties of Spinal Tracts	91
Chapter 4	
MUSCLE	96
By J. Walter Woodbury AND Theodore C. Ruch	
Changes Accompanying Muscular Response,  The Motor Unit and Gradation of Muscular Activity  xi	97 109

xii	CONTENTS

Neuromuscular Transmission	111 117 121
Section III. MOTOR FUNCTIONS OF THE NERVOUS SYSTEM	ſ
Chapter 5	
SPINAL REFLEXES AND SYNAPTIC TRANSMISSION	130
By Harry D. Patton	
Properties of the Synapse.  Analysis of Synaptic Function	130 131
Chapter 6	
Chapter 6  REFLEX REGULATION OF MOVEMENT AND POSTURE	167
By Harry D. Patton	107
Clinical Significance of Reflexes	194
Chinical Significance of Reflexes.	194
Chapter 7	
TRANSECTION OF THE HUMAN SPINAL CORD: THE NATURE OF HIGHER CONTROL	400
By Theodore C. Ruch	
Consequences of Spinal Transection	
Chapter 8	
PONTOBULBAR CONTROL OF POSTURE AND ORIENTATION IN SPACE	206
By Theodore C. Ruch	
Reticular Formation and the Stretch Reflex	210
Chapter 9	
THE AUTONOMIC NERVOUS SYSTEM	220
By Harry D. Patton	
Chapter 10	
HIGHER CONTROL OF AUTONOMIC OUTFLOWS: THE HYPOTHALAMUS	234
By Harry D. Patton	~

CONTENTS	xiii
Chapter 11	
THE CEREBRAL CORTEX: ITS STRUCTURE AND MOTOR FUNCTIONS	249
By Theodore C. Ruch	
Structure  Motor Function  Clinical Physiology of the Motor Systems	250 250 277
Chapter 12	
BASAL GANGLIA AND CEREBELLUM	277
By Theodore C. Ruch	
Motor Functions of the Basal Ganglia	277 285
Section IV. SENSORY FUNCTIONS OF THE NERVOUS SYSTEM	
Chapter 13	
SOMATIC SENSATION	300
By Theodore C. Ruch	
Sense Organ Discharge	303 310
Chapter 14	
NEURAL BASIS OF SOMATIC SENSATION	323
By Theodore C. Ruch	
Peripheral Nerve and Spinal Roots	323
Sensory Pathways of the Spinal Cord	330
Sensory Systems of the Brain Stem  Thalamus and Cerebral Cortex	335 337
Chapter 15	
PATHOPHYSIOLOGY OF PAIN	350
By Theodore C. Ruch	
Deep Pain	354 358
Chapter 16	
TASTE, OLFACTION AND VISCERAL SENSATION	369
By Harry D. Patton	
Taste Olfaction Visceral Sensation	369 374

Chapter 17	
AUDITION AND THE AUDITORY PATHWAY	386
By A. L. Towe AND Theodore C. Ruch	
Audition The Auditory Pathway	386 403
Chapter 18	
THE EYE AS AN OPTICAL INSTRUMENT.	409
By Frank W. Weymouth	
Formation of an Image.  Accommodation.  Optical Defects and Abnormalities.  Optical Effects of Other Factors.  Chief Instruments for Eye Examination.	409 414 417 421 423
Chapter 19	
VISION	426
By Theodore C. Ruch	
Photochemical Basis of Vision  Neural Basis of Retinal Function  Visual Acuity and Detail Vision  Color Vision	429 433 439 443
Chapter 20	
BINOCULAR VISION AND CENTRAL VISUAL PATHWAYS	450
By Theodore C. Ruch	
Visual Fields and Binocular Vision	452 454
Section V. CEREBRAL CORTEX IN GENERAL; NEUROPHYSIOLOGY OF BEHAVIOR	
Chapter 21	
ASSOCIATION AREAS AND THE CEREBRAL CORTEX IN GENERAL	464
By A. L. Towe AND Theodore C. Ruch	
Electrical Activity.  Association Areas.  Agnosia, Appasia, Aphasia	464 473

CONTENTS	XV

Chapter 22	
NEUROPHYSIOLOGY OF EMOTION AND MOTIVATION	483
By Theodore C. Ruch	
Outward Expression of Emotion.  Inner Aspects of Emotion.  Excitement.	484 493 497
Section VI. PROPERTIES AND CONSTITUENTS OF BLOOD	
Chapter 23	
GENERAL PROPERTIES OF BLOOD: THE FORMED ELEMENTS	502
By Helen Payling Wright	
General Properties of Blood	502 510 520 525
Chapter 24	
PHYSICAL CHEMISTRY OF BLOOD	529
By David I. Hitchcock	
Chemical Composition of Blood Osmotic Equilibrium Membrane Equilibrium Blood Gas Equilibria Acid-base Equilibrium Proteins of Blood	530 532 534 536 538 546
Chapter 25	
COAGULATION OF BLOOD.	552
By Rosemary Biggs	
Fibrinogen, Thrombin and Fibrin  Prothrombin and the Conversion of Prothrombin to Thrombin  Blood Thromboplastin  Calcium and Blood Coagulation  Surface Contact and Coagulation  Theory of Coagulation and Tests for Clotting Function  Natural Inhibitors of Coagulation  Miscellaneous Coagulants and Anticoagulants  Excessive Coagulation  Blood Coagulation and Hemostasis	553 554 559 562 562 563 564 565 566 567

#### CONTENTS

# Section VII. CIRCULATION OF BLOOD AND LYMPH

Chapter 26	
MECHANICAL EVENTS OF THE CARDIAC CYCLE	570
By Allen M. Scher	
Events of the Cardiac Cycle	575 579
Chapter 27	
ELECTRICAL CORRELATES OF THE CARDIAC CYCLE	587
By Allen M. Scher	
Excitation of the Heart	594 620
Chapter 28	
NUTRITION OF THE HEART	625
Cardiac Circulation	625 633
Chapter 29	
HEMODYNAMICS AND THE PHYSICS OF THE CIRCULATION	643
By Alan C. Burton	
Chapter 30	
THE PRESSURE GRADIENT AND PULSE IN THE VASCULAR SYSTEM	667
By Donald H. Barron	
Establishment of Pressure Gradient Arterial Pressure Arterial Pulse Venous Pressure Venous Pulse	667 674 680 684 689
Chapter 31	
VASOMOTOR REGULATION	691
By Donald H. Barron	
Regulation by the Nervous System	694 703

CONTENTS	xvii
Chapter 32	
CONTROL OF CARDIAC OUTPUT	708
By Robert F. Rushmer	
Control of Heart Rate.  Control of Stroke Volume  Coordinated Cardiovascular Response.  Methods for Measuring Cardiac Performance in Man	709 710 716 719
Chapter 33	
CIRCULATION THROUGH SPECIAL REGIONS	724
Blood Flow through the Lungs Blood Flow through the Liver Blood Flow through the Spleen Blood Flow through the Kidney Blood Flow to the Skin Blood Supply to the Skeletal Muscles  Circulation through the Brain  By John L. Patterson, Jr.  Chapter 34  THE CAPILLARIES AND LYMPHATICS  Circulation through the Capillaries The Lymphatics	726 729 731 732 734 736 738 741
Section VIII. RESPIRATION	
Chapter 35	
ANATOMY AND PHYSICS OF RESPIRATION	772
By Loren D. Carlson	112
Mechanical Function  Work of Breathing  Mixture of Gases in the Lungs  Artificial Respiration	774 780 784 786
Chapter 36	
GAS EXCHANGE AND TRANSPORTATION	789
By Loren D. Carlson	
Properties of Gases and Liquids.  Properties of Respired Air	789 791