Thirteenth edition

MEDICAL PHYSIOLOGY

Edited by

VERNON B. MOUNTCASTLE

Volume two

The circulation, 837
The kidney and body fluids, 1047
Physiology of the digestive system, 1143
Metabolism, 1235
Respiration, 1359
Endocrine glands, 1599

VOLUME TWO

MEDICAL PHYSIOLOGY

Edited by

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with 2133 illustrations

Thirteenth edition

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PREFACE

The general principles on which this textbook is organized are those described in the preface to its twelfth edition. An extensive revision of that book has been made for the present edition. Completely new sections appear on endocrinology, renal physiology and the regulation of the internal milieu, gastrointestinal physiology, and the autonomic nervous system. Chapters on new subjects appear in several other sections as well. This edition thus contains twenty-eight chapters that are wholly new. The elimination and combination of others has reduced to seventy-three the eighty chapters of the twelfth edition, printed in approximately the same space. Each of the remaining forty-five chapters has been substantially revised and in many cases rewritten to take into account advances in the relevant fields of physiology since 1968.

This edition has been written by thirty-eight authors, of whom seventeen have joined this endeavor for the first time. Each is busily engaged in the work of research and teaching in physiology; each has taken time from that dedicated life to summarize here the state of knowledge in his particular field of interest. Whatever value the result of our common effort may possess is wholly due to their depth of understanding and skill in exposition and their devotion to the task. For this I am greatly indebted to each.

For them and for myself I wish to thank those authors and publishers who have allowed us to reproduce illustrations previously published elsewhere.

Vernon B. Mountcastle

PREFACE
TO TWELFTH EDITION

The twelfth edition of *Medical Physiology* presents a cross section of knowledge of the physiologic sciences, as viewed by a group of thirty-one individuals, twenty-three of whom are actively engaged in physiologic research and teaching. Each section of the book provides statements of the central core of information in a particular field of physiology, reflecting, by virtue of the daily occupations of its authors, the questioning and explorative attitude of the investigator and indeed some of the excitement of the search. These statements vary along a continuum from those with a high probability for continuing certainty to those that are speculative but, it is hoped, of heuristic value. An attempt has been made to maintain a balanced point of view. I hope this book will convey to the student who reads it the fact that physiology is a living and changing science, continuously perfecting its basic propositions and laws in the light of new discoveries that permit new conceptual advances. The student should retain for himself a questioning attitude toward all, for commonly the most important advances are made when young investigators doubt those statements others have come to regard as absolutely true. This is not a book that sets forth in stately order a series of facts which, if learned, will be considered adequate for success in a course in physiology. Many such "facts" are likely to be obsolete before the student of physiology reaches the research laboratory, or the student of medicine the bedside. Nor is it a book that provides ready-made correlations and integrations of the various fields of physiology necessary for a comprehensive understanding of bodily function. Those integrations are an essential part of scholarly endeavor not readily gained from books alone. It is my hope, however, that study of this book, combined with laboratory experience and scholarly reflection, will provide the student with a method and an attitude that will serve him long after the concepts presented here are replaced by new and more cogent ones.

The title *Medical Physiology* has been retained, for one of the purposes of this edition, in common with earlier ones, is "to present that part of physiology which is of special concern to the medical student, the practitioner of medicine, and the medical scientist in terms of the experimental inquiries that have led to our present state of knowledge." The scope of the book was and is still broader, however, and attempts to present mammalian physiology as an independent biologic discipline as well as a basic medical science. Mammalian physiology has its base in cellular physiology and biophysics, and it is from this point of view that many of the subjects treated here are approached. Above all, mammalian physiology must deal with problems of the interactions between large populations of cells, organs, and organ systems and, finally, the integrated function of an entire animal. Physiology thus must bridge the distance from cellular biology on the one hand to systems analysis and control theory on the other: each is important and any one is incomplete without the others. This approach to the problems of internal

homeostasis, of reaction to the environment, and of action upon the environment is evidenced in several sections of this book.

Of the eighty chapters composing this book, twenty-nine are wholly new in this edition; forty-five from the last edition have been extensively revised either by their original authors or by new ones. Six have been allowed to stand substantially as previously written, for these seemed to comprise as balanced and modern a survey as any presently possible. The names and affiliations of my colleagues in this effort have been listed. They have taken time from busy lives to survey their fields of interest; for this I am greatly indebted to each. If this book possesses any worth it is in large part due to their continuing devotion to the task of its preparation.

For them and for myself I wish to thank those authors and publishers who have allowed us to reproduce illustrations previously published elsewhere.

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WILLIAM R. MILNOR

The heart and blood vessels form a transportation system that delivers to all cells of the body the materials needed for their proper function and carries away the waste products of their metabolism. By bringing oxygen and nutritive materials to the cells and relieving them of carbon dioxide and other metabolites, the circulation provides a means of communication between the cells and the external environment. In the higher reaches of the evolutionary scale the circulation acquires additional functions, e.g., the dissemination of *hormones,* which are important to many cells of the body but manufactured only by specialized tissues or organs, and the distribution of fats and carbohydrates from storage depots to regions where they are utilized. A number of mechanisms for the defense of the organism are also transported by the vascular system and can be delivered by way of the bloodstream to regions of injury or invasion. These include leukocytes, certain proteins concerned with immunity (immune antibodies), and materials involved in blood coagulation, which not only guard the integrity of the vascular system but also provide in damaged areas a framework of fibrin on which new tissue can be built. Circulation also contributes to the control of body temperature by carrying heat generated by the processes of metabolism to areas where it can be dissipated.

The bloodstream communicates with the cells it supplies only indirectly, through the mediation of an *extracellular fluid* in which all cells are bathed. Substances that leave the vascular system through the walls of its smallest branches, the capillaries, enter the extracellular fluid and then penetrate the cell membrane to reach the interior of the cell. The composition of this pervasive extravascular and extracellular fluid, which Claude Bernard[1] termed the *milieu interieur,* is kept constant by a host of regulatory mechanisms, enabling the organism as a whole to adapt to a wide range of external conditions. This concept of a constant internal environment, communicating on the one hand with the circulating blood and on the other with the cells, is fundamental in modern physiology.

The cardiovascular system includes the heart, arteries, capillaries, and veins, all differing in function as well as structure. The heart provides the motive force to pump blood through the system, the arteries carry blood away from the heart to the tissues of the body, and the veins return blood to the heart again—a circular motion that escaped recognition for centuries. The arteries are a branching system of vessels that subdivide in a more or less orderly fashion into increasingly numerous branches of diminishing caliber and eventually lead into the capillaries. Capillaries are thin-walled vessels a few thousandths of a millimeter in diameter, extending from the smallest terminal branches of the arterial tree to the equally small branches that form the beginning of the venous system. They anastomose freely with their neighbors in a diffuse network quite different from the relatively systematic branching of the arterial and venous vessels. The capillary channels are in close contact with the cells they serve, although extracellular fluid always intervenes between the capillary wall and the cell membrane, and substances are delivered to or removed from the immediate environment of the cell by passage through the capillary wall. Blood travels from these capillary beds into the veins, which form a branching system like that of the arteries in reverse, joining together in fewer vessels of increasing diameter as they approach the heart.

The circulating blood traverses two such systems in succession: the *systemic circulation,* which supplies the tissues of the body, and the *pulmonary circulation,* which carries blood through the lungs. Blood is pumped into the systemic circulation by the left ventricle, returns to the right atrium, is pumped into the pulmonary circulation by the right ventricle, then flows back from the lungs to

the left side of the heart where it begins its journey again. This continuous circulation of the blood out to the most distal parts of the body and back to the heart was first clearly described by William Harvey (1578-1657).[5] Fragments of evidence pointing to the circular motion of the blood had been encountered by earlier observers, but this evidence was ignored or misinterpreted because it conflicted with theories that had been accepted dogmatically since the writings of Galen in the second century. Harvey's careful experiments and observations, recorded in 1628, refuted this uncritical acceptance of ancient authority and established firmly the principle "that blood is pushed by the beat of the left ventricle and distributed through the arteries to the whole body, and back through the veins to the vena cava, and then returned to the right auricle, just as it is sent to the lungs through the pulmonary artery from the right ventricle and returned from the lungs through the pulmonary vein to the left ventricle. . . ."[5]

The vascular system properly includes not only the arteries, capillaries, and veins of the systemic and pulmonary circulations but another network called *lymphatic vessels* (Chapter 40). These begin in extracellular spaces as small, thin-walled vessels resembling the blood capillaries in size and permeability but closed at one end. The "lymph capillaries" lead into larger lymphatics, which converge into progressively wider channels until they drain into large veins near the heart. The fluid *lymph* contained in these channels carries solutes that diffuse into it from the extracellular fluid and returns them to the circulating blood. Many of the larger lymph channels are supplied with valves that direct the flow toward the veins and pass through one or more *lymph glands.*

The heart. In some biologic forms the heart—or at least the organ that moves blood—is a simple muscular tube. The evolutionary development of this uncomplicated structure into a heart with four chambers, valves, and independent outflows to the pulmonary and systemic circulation is retraced in the growth of the mammalian embryo. The sequence of development, which explains many features of the structure and function of the human heart, has been carefully summarized by Patten.[7]

As we ascend the evolutionary scale, this tube gradually becomes divided into specialized regions, so that the blood first enters a relatively thin-walled muscular sac (atrium) and then passes through a valve into a thick-walled muscular chamber (ventricle) that propels the blood onward by its contractions. Septa appear in the atrium and ventricle, and in birds and mammals these partitions become complete, producing in effect two conjoined pumps, each with two chambers. The right atrium and ventricle receive blood from the systemic veins and send blood to the lungs, while the left atrium and ventricle receive blood from the pulmonic veins and eject it into the systemic arteries. This complete separation into "right heart" and "left heart" ensures that blood leaving the lungs, which is relatively rich in oxygen and poor in carbon dioxide, does not mix with blood returning from the body tissues through the systemic veins. The progress of blood through the heart is controlled at the entrance and exit of each ventricle by one-way valves that prevent retrograde flow from the outflow vessels (pulmonary artery or aorta) to the ventricles and from the ventricles to the atria. Atrial and ventricular contractions follow an orderly sequence determined by the pacemaker of the heart and by the conduction paths through myocardium and specialized tissues (Chapter 33). The strength of these contractions and the volume of blood ejected by the ventricles are controlled by the autonomic nervous system, by substances carried in the blood, and by physicochemical characteristics of the myocardial fibers and their contractile proteins (Chapter 35).

Arteries. As the arterial tree divides into successive branches, the individual vessels change gradually in physical dimensions and in the structure of their arterial wall, with important functional consequences. The data in Table 32-1, which represent estimates for a hypothetical dog weighing 13 kg, give some idea of the number and dimensions of arteries and other segments of the circulatory system. The values given are rough approximations based on a number of reasonable but unproved assumptions, and the classification into segments is somewhat arbitrary.[13, 19]

Except for the major branches leaving the aortic arch and the bifurcation of the main pulmonary artery into right and left trunks, the total cross section of the arterial bed increases with each branching toward the periphery. In the simplest form of branching, where a single vessel divides in two, the ratio of the total cross section of the two branches beyond the bifurcation to that of the parent vessel usually ranges from 1.2 to 1.7. Sub-

Table 32-1. Changes that take place with branching of mesenteric artery of dog*

	Total number	Radius (cm)	Total cross-sectional area (cm^2)	Length (cm)	Mean velocity (cm/sec)	Pressure fall (mm Hg)	Volumes (% of total)
1. Mesenteric artery	1	0.15	0.07	6.0	16.80	0.8	2.6
Main branches	15	0.05	0.12	4.5	10.10	3.2	3.4
End branches	45	0.03	0.13	3.91	9.30	7.4	3.2
2. Short and long intestinal branches	1,899	0.0068	0.20	1.42	5.80	23.5	1.7
Last branches	26,640	0.0025	0.57	0.11	2.10	7.2	0.4
Branches to villi	328,500	0.00155	2.48	0.15	0.48	5.4	2.3
Arteries of villi	1,051,000	0.00122	4.18	0.20	0.28	8.1	5.3
3. Capillaries of villi	47,300,000	0.00040	23.78	0.04	0.05	2.4	5.9
						58.0	24.8
4. Veins at base of villi	2,102,400	0.00132	11.59	0.10	0.10	1.03	7.2
5. Veins before entering submucosa	131,400	0.00375	5.80	0.10	0.20	0.29	3.6
Last branches of submucosa	18,000	0.0064	2.32	0.15	0.51	0.37	2.2
Last branches of short intestinal veins	28,800	0.0032	0.93	1.1	1.30	2.50	6.4
Long and short intestinal veins	1,899	0.0138	0.84	1.42	1.40	1.40	7.4
6. Last branches of mesenteric vein	45	0.075	0.79	3.91	1.50	0.22	19.2
Branches of mesenteric vein	15	0.12	0.67	4.5	1.70	0.07	18.7
Mesenteric vein	1	0.3	0.28	6.0	4.2	0.05	10.5
						5.93	75.2

*After Mall; modified from Schleier.[19]

divisions do not occur with perfect geometric regularity, of course, and multiple branching at some sites yields a more rapid increase in total cross section, while at others a single small lateral branch may issue from a much larger parent vessel. The net effect is a rapid increase of total cross section in the periphery of the arterial bed, so that total cross-sectional area increases more than 100-fold between aorta and terminal systemic arterioles and is still greater in the systemic capillary bed (Table 32-1). Since the same average volume of blood passes through each cross section of the circulation per unit time, this overall widening of the bed results in a decrease in the velocity of blood flow as it moves through the arterial tree. Blood moves through the ascending aorta at an average velocity of about 20 cm/sec but slows with progressive branching of the arterial tree until its velocity in the capillaries is probably less than 0.2 cm/sec. Beyond the capillaries the process is reversed, and the flow of blood accelerates as the total cross-sectional area of the veins decreases.

The branching pattern and changing dimensions of the arteries are major factors in determining the resistance to flow in different parts of the bed. The concept of vascular resistance is described in detail in Chapter 36, but in general terms it expresses the principle that the flow produced by a constant driving force is a function of the radius and length of the vessel and of the physical properties of blood. The smaller the radius and the greater the length, the higher the resistance to flow. The total resistance of a vascular bed depends on the number of parallel channels as well as on the dimensions of the individual vessels.

One manifestation of resistance to flow is the constant drop in pressure within the vascular tree from arteries to veins, which can be represented by the "pressure profile" shown in Fig. 32-1. As this diagram shows, the major part of the total fall in pressure from aorta to inferior vena cava occurs in the vessels smaller than 0.5 mm in diameter. The pressure drop across the capillary bed itself is difficult to measure exactly but is probably in the neighborhood of 20 mm Hg in the systemic capillaries—slightly greater than the drop in the venules but much less than that in the smallest arteries and arterioles, where almost half the total resistance to flow occurs.

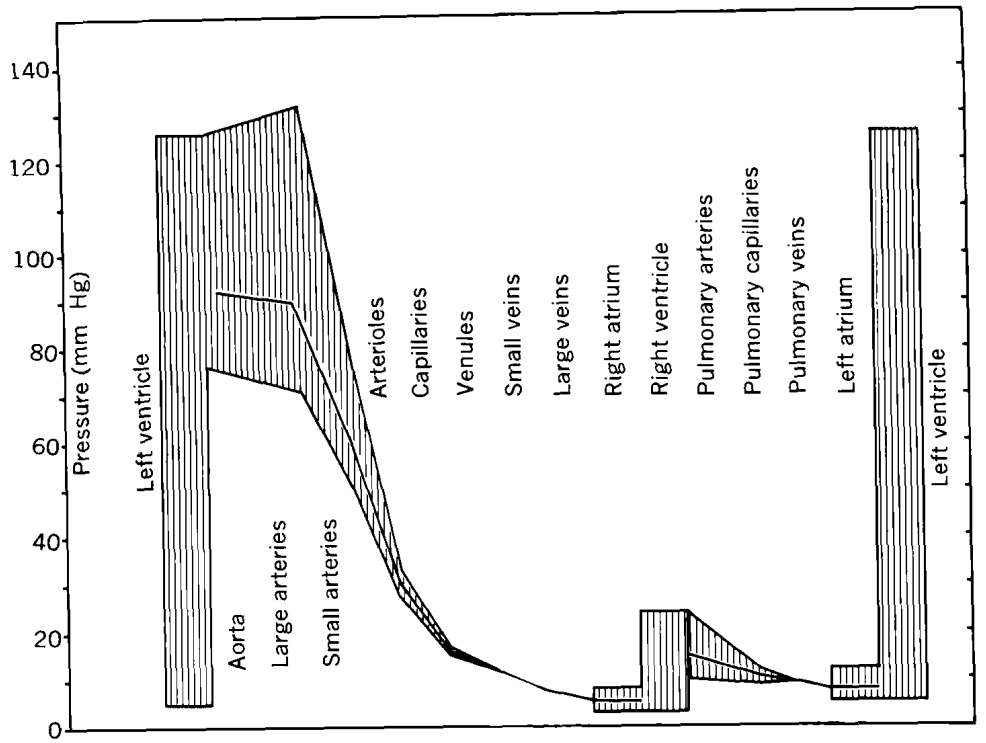

Fig. 32-1. Typical pressures in human cardiovascular system. Solid line indicates mean pressures, and shaded area indicates pulsations in systole and diastole.

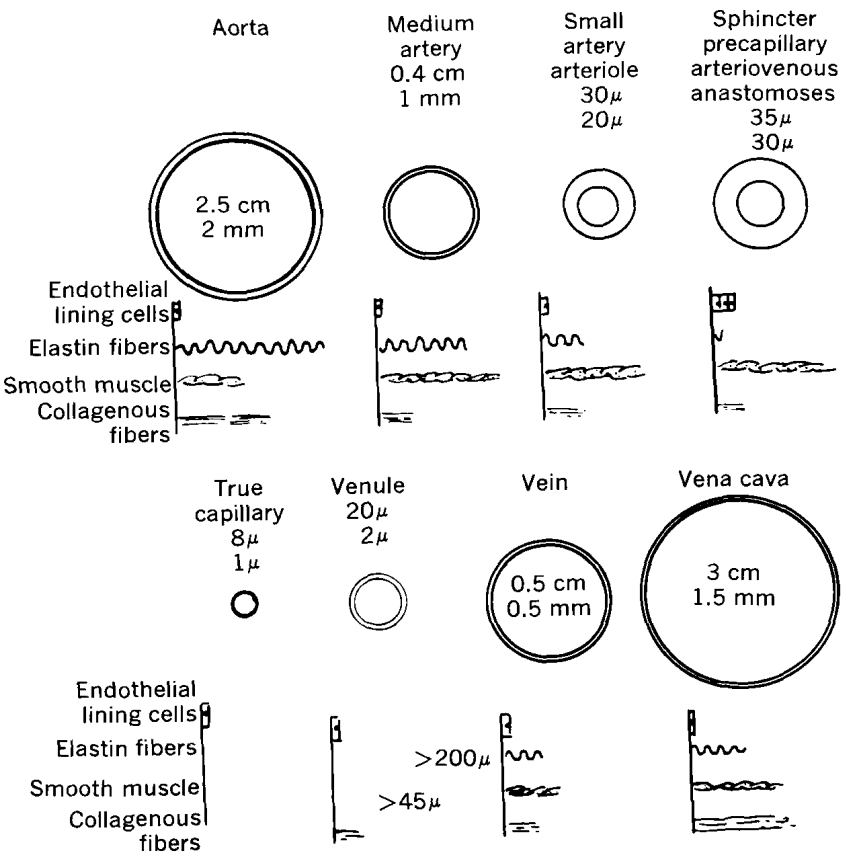

Fig. 32-2. Size, wall thickness, and admixture of four basic tissues in walls of different blood vessels. First figure below name of vessel represents diameter of lumen; figure below that indicates thickness of wall. (From Burton.[2])

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