Principles of Animal Physiology

SECOND EDITION

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Preface to Second Edition

Any author is pleased when a book succeeds well enough to enable a second edition to be published. My goals in writing this new edition remain the same as those described in the preface to the first edition. I have made some changes in the general organization of the text, but all the subject matter has been retained and much has been rewritten, expanded, or brought up to date (within the limits of my writing speed and publication times). The theme of regulation continues to run through this edition and is hopefully better reflected in more examples and diagrams of feedback systems and controls.

So many professors, researchers, and students have aided in the preparation of this new edition by their suggestions and comments that space does not permit me to acknowledge them all by name. However, I wish to thank all of them most sincerely for their time and trouble—without this type of input it would be impossible to produce any output.

Of course, any shortcomings or errors are entirely my own. I hope that the readers of this second edition will be as kind as those of the first and will send me their comments and criticisms.

Finally, I would like to thank the Macmillan people who have all been so helpful and patient, especially the biology editor, Woodrow Chapman, and the production supervisor, Mrs. Elaine Wetterau.

J.A.W.

Preface to First Edition

This textbook was begun, as it seems many textbooks are, because of a felt need for a better source of material for the students taking a course. Although several excellent texts are available in the areas of cellular biology, general physiology, and biochemistry, it seemed to me that students at the introductory level needed a text combining discussion of the important aspects of these three areas with a consideration of higher levels of animal structure and function—plus some consideration of the comparative aspects of physiology. To meet this need, this book is entitled *Principles of Animal Physiology*—an indication that important ideas from all areas of physiology are presented and that the approach is a broader one than is usually found in textbooks. I tend to think of physiology as a unit, not as a series of discrete areas, and I have tried here to examine animal functioning at all levels from the molecular to the whole organism.

Any textbook requires a central theme, and in this book I have taken regulation as a major concept. In addition, I have felt it important to incorporate the similarities and differences of structure and function found in various animals—in one sense, an incorporation of data from comparative physiology.

I did not hesitate to think in terms of a lengthy book. Most available texts, in my opinion, suffer from the major defect of shortness. To present adequately the basic terms, definitions, and concepts of physiology is a lengthy undertaking. Writing a short book also necessitates a degree of selectivity that amounts to mind reading on the part of the author as to what is going to be taught in physiology courses in many colleges and universities. Such a treatment can only drastically reduce the usefulness of a text. Nevertheless, I too have omitted some topics or given them only sketchy treatment. However, I have tried to include sufficient references to the literature so that the interested student can proceed on his own.

This book is written primarily for the interested student—not one who is necessarily majoring in physiology, but one who finds some fascination in the subject matter of physiology. My philosophy is that if a text is written in such a manner, it will also be good for any student taking a physiology course.

The main purpose of this book is to describe how physiological systems work, and such descriptions are presented primarily in physical-chemical terms. Since physiology is an experimental science, I have tried to include as much as possible on the instrumentation, methods, and approaches used in the study of different levels of animal functioning. As many data as possible are given so that the student may have some opportunity to see the sources of physiological hypotheses and theories. Naturally, space places a limit on such material but, again, references are provided that discuss methods and data not completely covered in the text itself.

The book is divided into four parts, beginning with the most basic levels of structure or function in animals and progressing to the most complex. Part I is

concerned with molecules and cell organization and with the chemical and physical principles upon which biochemical reactions and energy exchanges are based. The first chapter contains a brief consideration of systems analysis, feedback regulation, adaptation, and regulation. These are extremely useful concepts to the physiologist, and they are used in all later chapters of the book. I have outlined the nature of biochemical evolution in Chapter 5. Evolution at any level is one of the most important of biological theories and especially deserves recognition in a physiology book that includes elements of comparative physiology. In Chapter 5, I have also included a listing of the names, and a rough indication of the relationships, of living animals. I find that many students taking physiology courses have either forgotten or have never been acquainted with animal names and relations. It is hoped that this listing can be used by the student to identify and relate the organisms discussed in later chapters of the book.

Part II contains the basic cellular mechanisms upon which much regulatory ability, adaptation, and responsiveness to environment are based, including a discussion of specialized cells, especially nerve and muscle cells, which exhibit such mechanisms to a high degree.

Part III on homeostasis carries regulation one step further—to the level of organized systems. The many differences that may be found among animals in the structures and functional abilities used in homeostasis are emphasized, although, as stressed in the first two parts of the book, cellular organization and functioning have many similarities in all animals.

Part IV includes elements of sensory physiology and a brief discussion of animal behavior based on selected examples. It is hoped that these examples will give an indication of how the cellular and organismal activities of the whole animal are coordinated and integrated to produce successful responses to the environment.

Each chapter has its own reference and reading list, usually a lengthy one. Although textbooks are not the place for presenting long lists of shorter research papers, monographs and reviews by workers in various specialized fields are an aid in a bibliography that includes discussions of the research and its results. Therefore, research papers of proven significance or with important methodological details are given in the reference lists. Citations are inserted in the text in a way that creates a minimum of disruption. The citations were chosen to provide both a chronological map of physiological discoveries and also a listing of researchers associated with particular fields of study. Recognizing that some readers will not have all important sources of physiological information available to them, I have tried to provide two or more references to a given subject when possible, hoping that at least one will be available to the interested reader.

The book certainly has shortcomings, but I hope it will be of value to students, the people for whom it is written. I have not designated it as suitable for any particular level of student. Anyone with a background containing some chemistry, a little physics and mathematics, and some biology can easily learn to appreciate the physiological data. Graduate students may find it useful both for the material covered and for the references to the literature; however, it is a textbook and not an advanced treatise.

No author could be an expert in all the areas covered by this book. I have tried to present those ideas which appear most generally accepted by workers in a given area. At the same time I have not hesitated to present less well-accepted hypotheses, to give my own opinions or interpretations where necessary, and to go out on a limb when extrapolating present knowledge (or lack of it) to future work in physiology. It is hoped that the reader of this book will arrive at the conclusion that comparatively little is settled in physiology and that much remains to be done.

I gratefully acknowledge the many people who have read and criticized all or part of the manuscript. These include Professors G. S. Araki, K. S. Guthe, W. N. Holmes, T. C. Jegla, L. E. Moore, L. M. Passano, and J. Thomas. Of course, all

errors both of omission and commission are my responsibility.

I also wish to thank John and Mary Richardson for their invaluable help in the preparation of the illustrations and in the preparation of the manuscript. Nearly all of the illustrations are either new or completely redrawn and corrected. Originally I had planned to use many more electron micrographs, but it appeared that in too many cases such micrographs would be of value only to people expert in their interpretation. Therefore, many morphological details are illustrated by line drawings rather than original halftones.

Last, but certainly not least, I wish to express my sincere gratitude to Mr. William D. Eastman, Executive Editor at The Macmillan Company, for his enthusiasm, his help, and especially for his patience when deadlines arrived but manuscript did not.

J.A.W.

Brief Contents

Detailed Contents

Part III Homeostasis: Regulation of the Internal Environment

Part I Some Basic Properties of Living Systems

Following a brief introduction to the history and nature of physiology, Chapter 1 discusses regulation, control, and adaptation as basic properties of all living systems. Feedback regulation and systems analysis are introduced because they provide one conceptual framework upon which physiological regulation may be placed. The idea of regulation in animals was conceived long before the development of cybernetics. However, cybernetics provides a language and the mathematics for describing rigorously any regulatory system. Chapter 1 also contains a listing of the major animal groups.

Certain classes of molecules are also basic to all living systems, and these are described in Chapter 2. Some emphasis is placed on that unique and ubiquitous molecule, water. The nature and general functions of the major classes of biological molecules are described, but much of the discussion centers on macromolecules, especially the proteins. Macromolecules are of importance because they can provide the information required by living systems for synthesis, growth, development, regulation, and adaptation. All the activities and structures discussed in later chapters depend upon the molecules described here.

The organization of molecules into cellular organelles and cell structure generally is the topic of Chapter 3. Instrumentation and methods are given consideration because at the cellular and molecular levels of biological organization instrumentation is required to analyze dimensional realms far beneath those normally perceived by human senses. Most of the discussion