



ANNUAL REVIEW OF PHYSIOLOGY



ANNUAL REVIEW OF PHYSIOLOGY

VOLUME 54, 1992

JOSEPH F. HOFFMAN, *Editor*

Yale University School of Medicine

PAUL De WEER, *Associate Editor*

University of Pennsylvania School of Medicine



ANNUAL REVIEWS INC.
Palo Alto, California, USA

COPYRIGHT © 1992 BY ANNUAL REVIEWS INC., PALO ALTO, CALIFORNIA, USA. ALL RIGHTS RESERVED. The appearance of the code at the bottom of the first page of an article in this serial indicates the copyright owner's consent that copies of the article may be made for personal or internal use, or for the personal or internal use of specific clients. This consent is given on the condition, however, that the copier pay the stated per-copy fee of \$2.00 per article through the Copyright Clearance Center, Inc. (21 Congress Street, Salem, MA 01970) for copying beyond that permitted by Sections 107 or 108 of the US Copyright Law. The per-copy fee of \$2.00 per article also applies to the copying, under the stated conditions, of articles published in any *Annual Review* serial before January 1, 1978. Individual readers, and nonprofit libraries acting for them, are permitted to make a single copy of an article without charge for use in research or teaching. This consent does not extend to other kinds of copying, such as copying for general distribution, for advertising or promotional purposes, for creating new collective works, or for resale. For such uses, written permission is required. Write to Permissions Dept., Annual Reviews Inc., 4139 El Camino Way, P.O. Box 10139, Palo Alto, CA 94303-0897 USA.

International Standard Serial Number: 0066-4278

International Standard Book Number: 0-8243-0353-7

Library of Congress Catalog Card Number: 39-15404

Annual Review and publication titles are registered trademarks of Annual Reviews Inc.

⊗ The paper used in this publication meets the minimum requirements of American National Standard for Information Sciences—Permanence of Paper for Printed Library Materials, ANZI Z39.48-1984.

Annual Reviews Inc. and the Editors of its publications assume no responsibility for the statements expressed by the contributors to this *Review*.

Typesetting by Kachina Typesetting Inc., Tempe, Arizona; John Olson, President; Janis Hoffman, Typesetting Coordinator; and by the Annual Reviews Inc. Editorial Staff

PRINTED AND BOUND IN THE UNITED STATES OF AMERICA

PREFACE

Readers of the *Annual Review of Physiology* are familiar with each volume's format that presents recurring, if not always traditional, sections that are thematic in organization. The themes in each section change yearly in response to the Editorial Committee's perception of current advances and the stage of maturation of the various areas comprising the subject matter of physiology. Because developments are rapidly occurring outside the traditional fields of physiology, the Editorial Committee also includes special topics, the purpose of which is to bring to the attention of our readers areas of related interest and usefulness. The special topics covered in this volume are Physiological Aspects of Nuclear Magnetic Resonance and Chemosensory Transduction. In addition there is an interdisciplinary theme of Signal Transduction, the specifics and generalities of which cross the customary alignments.

In order to function optimally and responsibly the Editorial Committee needs and seeks input from our colleagues and encourages the submission of suggestions to any of its members. We are aware of divergent as well as convergent aspects of the changing scene of physiological science that includes, on the one hand, cellular and molecular developments and, on the other, systems and whole animal integrations. We are also aware that much of the excitement of current work embodies the study of interrelationships among these various levels. So the pendulum of insight and understanding in constant motion across these diverse approaches will continue to yield new syntheses of physiological processes that the Committee hopes are duly recounted in our series volumes.

Joseph F. Hoffman
Editor

OTHER REVIEWS OF INTEREST TO PHYSIOLOGISTS

From the *Annual Review of Biochemistry*, Volume 61 (1992):

- Biochemistry of Peroxisomes*, H. van den Bosch, R. B. H. Schutgens, R. J. A. Wanders, and J. M. Tager
Vesicle-Mediated Protein Sorting, N. K. Pryer, L. J. Wuestehube, and R. Schekman
Animal Cell Cycles and Their Control, C. Norbury and P. Nurse
Protein Isoprenylation and Methylation at C-Terminal Cysteine Residues, S. Clarke
Transcription Factors: Structural Families and Principles of DNA Recognition, C. O. Pabo and R. T. Sauer
Catalytic Antibodies, S. J. Benkovic
Inositol Phosphate Biochemistry, P. W. Majerus
The Ubiquitin System for Protein Degradation, A. Herskho and A. Ciechanover
Hormone Response Elements, D. K. Granner
Control of Nonmuscle Myosins by Phosphorylation, J. L. Tan, S. Ravida, and J. A. Spudich
Neuronal Ca^{2+} /Calmodulin-Dependent Protein Kinases, P. I. Hanson and H. Schulman

From the *Annual Review of Medicine*, Volume 43 (1992):

- Glucose Transporters*, L. J. Elsas and N. Longo
The Molecular Biology of G6PD Variants and Other Red Blood Cell Enzyme Defects, E. Beutler

From the *Annual Review of Neuroscience*, Volume 15 (1992):

- Adrenergic Receptors as Models for G Protein-Coupled Receptors*, B. Kobilka
Guanylyl Cyclase-Linked Receptors, P. S. T. Yuen and D. L. Garbers
The Cerebellum and Adaptive Coordination of Movement, W. T. Thach, H. G. Goodkin, and J. G. Keating
Manipulating the Genome by Homologous Recombination in Embryonic Stem Cells, A. Zimmer
Voltage-Sensitive Dyes and Functional Activity in the Olfactory Pathway, A. R. Cinelli and J. S. Kauer
The Biosynthesis of Neuropeptides: Peptide α -Amidation, B. A. Eipper, D. A. Stoffers, and R. E. Mains

(continued) xiii

From the *Annual Review of Nutrition*, Volume 11 (1991):

Biosynthesis of Prostaglandins, W. E. M. Lands

Dietary Regulation of Cytochrome P450, K. E. Anderson and A. Kappas

Glutamine: A Key Substrate for the Splanchnic Bed, W. W. Souba

The Effects of Glyceride Structure on Absorption and Metabolism, D. M. Small

Hepatic Gluconeogenesis/Glycolysis: Regulation and Structure/Function Relationships of Substrate Cycle Enzymes, S. J. Pilkis and T. H. Claus

From the *Annual Review of Pharmacology and Toxicology*, Volume 32 (1992):

Mutagenesis of the β_2 Adrenergic Receptor: How Structure Elucidates Function,

J. Ostrowski, M. A. Kjelsberg, M. G. Caron, and R. J. Lefkowitz

Pharmacology of Protein Kinase Inhibitors, H. Hidaka and R. Kobayashi

Biochemical and Molecular Pharmacology of Kinin Receptors, S. G. Farmer
and R. M. Burch

The Central Role of Voltage-Activated and Receptor-Operated Calcium Channels in Neuronal Cells, M. Bertolino and R. R. Llinas

ANNUAL REVIEWS INC. is a nonprofit scientific publisher established to promote the advancement of the sciences. Beginning in 1932 with the *Annual Review of Biochemistry*, the Company has pursued as its principal function the publication of high quality, reasonably priced *Annual Review* volumes. The volumes are organized by Editors and Editorial Committees who invite qualified authors to contribute critical articles reviewing significant developments within each major discipline. The Editor-in-Chief invites those interested in serving as future Editorial Committee members to communicate directly with him. Annual Reviews Inc. is administered by a Board of Directors, whose members serve without compensation.

1992 Board of Directors, Annual Reviews Inc.

J. Murray Luck, Founder and Director Emeritus of Annual Reviews Inc.

Professor Emeritus of Chemistry, Stanford University

Joshua Lederberg, Chairman of Annual Reviews Inc.

University Professor, The Rockefeller University

James E. Howell, Vice Chairman of Annual Reviews Inc.

Professor of Economics, Stanford University

Winslow R. Briggs, Director, Carnegie Institution of Washington, Stanford

W. Maxwell Cowan, Howard Hughes Medical Institute, Bethesda

Sidney D. Drell, Deputy Director, Stanford Linear Accelerator Center

Sandra M. Faber, Professor of Astronomy, University of California, Santa Cruz

Eugene Garfield, President, Institute for Scientific Information

William Kaufmann, President, William Kaufmann, Inc.

Daniel E. Koshland, Jr., Professor of Biochemistry, University of California, Berkeley

Donald A. B. Lindberg, Director Emeritus, National Library of Medicine

Gardner Lindzey, Director, Center for Advanced Study in the Behavioral Sciences, Stanford

Charles Yanofsky, Professor of Biological Sciences, Stanford University

Richard N. Zare, Professor of Physical Chemistry, Stanford University

Harriet A. Zuckerman, Professor of Sociology, Columbia University

Management of Annual Reviews Inc.

William Kaufmann, Editor-in-Chief and President

John S. McNeil, Publisher and Secretary-Treasurer

Mickey G. Hamilton, Promotion Manager

Donald S. Svedeman, Business Manager

Richard L. Burke, Electronic Communications Manager

ANNUAL REVIEWS OF

Anthropology

Astronomy and Astrophysics

Biochemistry

Biophysics and Biomolecular Structure

Cell Biology

Computer Science

Earth and Planetary Sciences

Ecology and Systematics

Energy and the Environment

Entomology

Fluid Mechanics

Genetics

Immunology

Materials Science

Medicine

Microbiology

Neuroscience

Nuclear and Particle Science

Nutrition

Pharmacology and Toxicology

Physical Chemistry

Physiology

Phytopathology

Plant Physiology and

Plant Molecular Biology

Psychology

Public Health

Sociology

SPECIAL PUBLICATIONS

Excitement and Fascination
of Science, Vols. 1, 2,
and 3

Intelligence and Affectivity,
by Jean Piaget

For the convenience of readers, a detachable order form/envelope is bound into the back of this volume.



François Muret



CONTENTS

PERSPECTIVES

- Methods in Kidney Physiology: Past, Present, and Future,
Francois Morel 1

RENAL AND ELECTROLYTE PHYSIOLOGY

- Erich Windhager, Section Editor*
Receptors of Atrial Natriuretic Factor, *Thomas Maack* 11
Renal Epithelial Chloride Channels, *W. Brian Reeves and*
Thomas E. Andreoli 29
Epithelial Na Channels: Function and Diversity,
Lawrence G. Palmer 51
Parathyroid Hormone Receptors in Control of Proximal Tubule
Function, *Roman Muff, Jan A. Fischer, Jurg Biber,*
and Heini Murer 67
Renal Potassium Channels and Their Regulation, *Wenhui Wang,*
Henry Sackin, and Gerhard Giebisch 81
Water Channels in Cell Membranes, *Alan Verkman* 97

See also

- Methods in Kidney Physiology 1
Growth Factor Signaling Pathways 195
Hepatic Transport Mechanisms 415
Inositol Trisphosphate Receptors 469
K⁺ Channel Structure and Function 537
NMR in Physiology 733
NMR of Proteins 749
NMR of Cells 775
Localized In Vivo NMR 799
MRI in Physiology 827
Glucose Transporter Family 911

CELLULAR AND MOLECULAR PHYSIOLOGY

Paul DeWeer, Section Editor

Charge Movement and the Nature of Signal Transduction in Skeletal Muscle Excitation-Contraction Coupling, <i>Eduardo Ríos, Gonzalo Pizarro, and Enrico Stefani</i>	109
Mechanotransduction, <i>Andrew S. French</i>	135
Role of cGMP and Ca^{2+} in Vertebrate Photoreceptor Excitation and Adaptation, <i>U. B. Kaupp and K.-W. Koch</i>	153
Signal Transduction and Protein Phosphorylation in the Regulation of Cellular Metabolism by Insulin, <i>John C. Lawrence, Jr.</i>	177
Transmembrane Receptors and Intracellular Pathways That Control Cell Proliferation, <i>Jacques Pouyssegur and Klaus Seuwen</i>	195

See also

ANF Receptors	13
Renal Epithelial Chloride Channels	29
Epithelial Na Channels	51
PTH Receptors in Kidney Function	67
Renal Potassium Channels	81
Cell Membrane Water Transport	97
Adenosine Receptors	211
The Stunned Myocardium	243
Endothelin and Ca^{2+} Dynamics	257
Cardiac Cellular Pacemaking	279
Smooth Muscle Excitation	395
Hepatic Transport Mechanisms	415
Electrical Rhythmicity in GI Muscles	439
GI Somatostatin Receptors	455
Inositol Trisphosphate Receptors	469
NMDA-Receptor-Independent LTP	489
Glutamate Receptors	507
K^{+} Channel Structure and Function	537
Taste Transduction	715
Regulation of Substrate Cycle Enzymes	885
Glucose Transporter Family	911

CARDIOVASCULAR PHYSIOLOGY

Howard E. Morgan, Section Editor

Adenosine Receptors, <i>Gary L. Stiles and Mark E. Olah</i>	211
Cardiac Actions of Angiotensin II: Role of an Intracardiac Renin-Angiotensin System, <i>Kenneth M. Baker, George W. Booz, and David E. Dostal</i>	227
Cellular Mechanisms of Myocardial Stunning, <i>Hideo Kusuoka and Eduardo Marban</i>	243
Endothelin and Calcium Dynamics in Vascular Smooth Muscle, <i>Robert F. Highsmith, Karen Blackburn, and David J. Schmidt</i>	257
Ionic Current Mechanisms Generating Vertebrate Primary Cardiac Pacemaker Activity at the Single Cell Level, <i>Donald L. Campbell, Randall L. Rasmusson, and Harold C. Strauss</i>	279
<i>See also</i>	
Signal Transduction in E-C Coupling	109
Mechanotransduction	135
Protein Phosphorylation and Insulin	177
Inositol Trisphosphate Receptors	469
K ⁺ Channel Structure and Function	537
Brain Adaptation to Anoxia	601
NMR in Physiology	733
NMR of Cells	775
Localized in Vivo NMR	799
Modeling Insulin Action	861
Glucose Transporter Family	911

RESPIRATORY PHYSIOLOGY

John A. Clements, Section Editor

Arachidonic Acid Metabolism in Airway Epithelial Cells, <i>Michael Holtzman</i>	303
Host Defense in Pulmonary Alveoli, <i>Michael P. Sherman and Tomas Ganz</i>	331
Pulmonary Alveolar Epithelial Cell Differentiation, <i>Jerome S. Brody and Mary C. Williams</i>	351
Developmental Changes in Lung Epithelial Ion Transport and Liquid Movement, <i>Richard D. Bland and Dennis W. Nielson</i>	373
<i>See also</i>	
Epithelial Na Channels	51

Cell Membrane Water Transport	97
Mechanotransduction	135
Growth Factor Signaling Pathways	195
Endothelin and Ca^{2+} Dynamics	257
Adaptation to Pressure	557
NMR in Physiology	733
NMR of Cells	775
Localized In Vivo NMR	799
MRI in Physiology	827

GASTROINTESTINAL PHYSIOLOGY

David C. Dawson, Section Editor

Contraction Coupling in Colonic Smooth Muscle, <i>E. A. Mayer, X. P. Sun, and R. F. Willenbacher</i>	395
Hepatic Transport Systems Regulating pH_i , Cell Volume, and Bile Secretion, <i>J. L. Boyer, J. Graf, and P. J. Meier</i>	415
Ionic Mechanisms of Electrical Rhythmicity in Gastrointestinal Smooth Muscles, <i>Kenton M. Sanders</i>	439
The Somatostatin Receptor in the GI Tract, <i>Miguel J. M. Lewin</i>	455

See also

Renal Epithelial Chloride Channels	29
Epithelial Na Channels	51
Renal Potassium Channels	81
Cell Membrane Water Transport	97
Growth Factor Signaling Pathways	195
Adenosine Receptors	211
Lung Ion/Liquid Movement Near Birth	373
Inositol Trisphosphate Receptors	469
Hepatic Glucose Uptake In Vivo	847
Regulation of Substrate Cycle Enzymes	885
Glucose Transporter Family	911

NEUROPHYSIOLOGY

Arthur M. Brown, Section Editor

Inositol 1,4,5-Trisphosphate-Activated Calcium Channels, <i>Christopher D. Ferris and Solomon H. Snyder</i>	469
---	-----

NMDA-Receptor-Independent Long-Term Potentiation, <i>Daniel Johnston, Stephen Williams, David Jaffe, and Richard Gray</i>	489
Molecular Neurobiology of Glutamate Receptors, <i>Gregory P. Gasic and Michael Hollmann</i>	507
Structural Elements Involved in Specific K ⁺ Channel Functions, <i>Lily Yeh Jan and Yuh Nung Jan</i>	537
See also	
Signal Transduction in E-C Coupling	109
Vertebrate Photoreceptor	153
Cardiac Cellular Pacemaking	279

COMPARATIVE PHYSIOLOGY

<i>Donald C. Jackson, Section Editor</i>	
Adaptations to High Hydrostatic Pressure, <i>George N. Somero</i>	557
Anhydrobiosis, <i>John H. Crowe, Folkert A. Hoekstra, and Lois M. Crowe</i>	579
Mechanisms for Anoxic Survival in the Vertebrate Brain, <i>Peter L. Lutz</i>	601
Natural Freeze Tolerance in Ectothermic Vertebrates, <i>Kenneth B. Storey and Janet M. Storey</i>	619
See also	
Cell Membrane Water Transport	97
Mechanotransduction	135
The Stunned Myocardium	243
Glutamate Receptors	507
Hepatic Glucose Uptake In Vivo	847
Regulation of Substrate Cycle Enzymes	885

SPECIAL TOPIC: CHEMOSENSORY TRANSDUCTION

<i>Judith Van Houten, Special Topic Editor</i>	
Chemosensory Transduction in Eukaryotic Microorganisms, <i>Judith Van Houten</i>	639
Peripheral Processes in Insect Olfaction, <i>M. Stengl, H. Hatt, and H. Breer</i>	665
Behavioral Responses in Bacteria, <i>Judith P. Armitage</i>	683
Chemosensory Transduction Mechanisms in Taste, <i>Sue C. Kinnamon and Thomas A. Cummings</i>	715

See also

Signal Transduction in E-C Coupling	109
Mechanotransduction	135
Vertebrate Photoreceptor	153
Protein Phosphorylation and Insulin	177
Growth Factor Signaling Pathways	195
Adenosine Receptors	211
Inositol Trisphosphate Receptors	469
Glutamate Receptors	507

SPECIAL TOPIC: NMR

Robert J. Gillies, Special Topic Editor

Nuclear Magnetic Resonance and Its Applications to Physiological Problems, <i>R. J. Gillies</i>	733
Solving Solution Structures of Physiologically Relevant Proteins by NMR Spectroscopy, <i>Neil E. MacKenzie, Paul R. Gooley, and Lori A. Hardaway</i>	749
NMR Spectroscopy of Cells, <i>Benjamin S. Szwergold</i>	775
Application of Localized in Vivo NMR to Whole Organ Physiology in the Animal, <i>Alan P. Koretsky and Donald S. Williams</i>	799
The Utilization of Magnetic Resonance Imaging in Physiology, <i>Jeffrey R. Alger and Joseph A. Frank</i>	827

See also

Methods in Kidney Physiology	1
Epithelial Na Channels	51
Vertebrate Photoreceptor	153
Protein Phosphorylation and Insulin	177
Growth Factor Signaling Pathways	195
The Stunned Myocardium	243
Hepatic Transport Mechanisms	415
Vertebrate Freeze Tolerance	619

ENDOCRINOLOGY

Daryl K. Granner, Section Editor

Regulation of Net Hepatic Glucose Uptake In Vivo, <i>M. J. Pagliassotti and A. D. Cherrington</i>	847
Modeling of Insulin Action In Vivo, <i>Richard N. Bergman, Garry M. Steil, David C. Brodley, and Richard M. Watanabe</i>	861

xii CONTENTS (continued)

Molecular Physiology of the Regulation of Hepatic Gluconeogenesis and Glycolysis, <i>S. J. Pilkis and D. K. Granner</i>	885
Mammalian Facilitative Glucose Transporter Family: Structure and Molecular Regulation, <i>Jeffrey E. Pessin and Graeme I. Bell</i>	911
<i>See also</i>	
Protein Phosphorylation and Insulin	177

INDEXES

Subject Index	931
Cumulative Index of Contributing Authors, Volumes 50-54	954
Cumulative Index of Chapter Titles, Volumes 50-54	957

METHODS IN KIDNEY PHYSIOLOGY: PAST, PRESENT, AND FUTURE

François Morel

Laboratoire de Physiologie Cellulaire, Collège de France, 75231 Paris cedex 5-France

KEY WORDS: kidney tubules, microperfusion, microtechniques

INTRODUCTION

In the letter inviting me to prepare this prefatory chapter, the Editor of Annual Review of Physiology indicated that the author is now expected to "summarize the key background material, provide a state-of-the-art view of the subject, pose the important unanswered questions (as well as approaches to possible solutions) and speculate a bit about future developments."

I entered the field of kidney physiology about forty years ago, namely, when this domain of physiology was expanding quite rapidly. Since that time, I have enjoyed observing how experimental sciences progress and why, sometimes, a break-through changes their course. In fact, the history of kidney physiology illustrates perfectly how often new steps in physiology required the development of appropriate methods so designed as to answer right questions. I hope to keep in line with the Editor's advice when devoting this prefatory chapter to the relationships between progress in methods and knowledge in the past, present, and future of kidney physiology.

PAST

Although the key role of kidneys in body fluid homeostasis has been well-recognized for a long time, and the intricate anatomical organization of

nephrons has been established, advances in renal physiology were initiated following the introduction of two specific techniques: (a) Firstly, the *in vivo* micropuncture of tubular fluid from amphibian kidneys, introduced by Richards and associates (16, 17, 22), made it possible to demonstrate the relevance of the filtration-reabsorption theory of kidney function and to analyze changes in tubular fluid composition that occur along successive nephron portions. At that time, however, micropuncture experiments, which required microanalyses with less than one microliter samples of fluid, were tedious and few physiologists performed them. (b) Secondly, the discovery by Homer Smith that inulin represents an ideal marker for measuring the glomerular filtration rate (GFR) led to the development of the renal clearance technique (18): GFR measurements with inulin made it possible to calculate accurately overall rates of tubular transport (reabsorption or secretion) for any kind of filtered molecular species simply by measuring the concentrations of inulin and of the studied species in collected urine and blood plasma samples. The clearance technique could be used to study quantitatively a great variety of questions related to kidney functions under normal, experimental, or physiopathological conditions in laboratory animals and in humans. As a consequence, use of this new approach spread rapidly and resulted in the tremendous development of kidney physiology, which occurred after World War II. It should be pointed out, nevertheless, that clearance data, although accurate, correspond only to a balance measurement between filtered load (input) and urinary excretion rate (output): the kidney itself remains a black box. In particular, clearance measurements give no information about the nephron segments where the observed net solute transport take place. This limitation could be overcome by extrapolating to the mammalian kidney the precise localizations previously established for the same solutes by micropuncture in the amphibian kidney. Our present basic knowledge of main kidney functions has been largely acquired in this way.

However, extrapolation to mammals of amphibian micropuncture data later proved to be completely inadequate to explain the mechanism of urine concentration. It is now clear that this failure originated in the fact that the amphibian kidney has no loops of Henle and is unable to produce hypertonic urine. At that time, it appeared necessary that water must be actively reabsorbed (out of late distal tubules and perhaps collecting tubules) in order to account for the formation by the mammalian kidney of urine hyperosmotic to plasma (vasopressin-dependent "facultative water reabsorption") (19). Although erroneous, this view appeared so coherent and was so widely accepted that eight years elapsed before the mechanism of urine concentration in collecting tubules by passive water abstraction along a medullary gradient of osmotic pressure, as proposed by Wirz et al as early as 1950 (24), was finally accepted and the role of Henle's loops was recognized in 1959 (20).