

Primitive
Motile Systems
in Cell Biology

EDITED BY

Robert D. Allen and Noburô Kamiya

PRIMITIVE MOTILE SYSTEMS IN CELL BIOLOGY

EDITED BY

Robert D. Allen

DEPARTMENT OF BIOLOGY
PRINCETON UNIVERSITY
PRINCETON, NEW JERSEY

Noburô Kamiya

FACULTY OF SCIENCE
OSAKA UNIVERSITY
OSAKA, JAPAN

The Proceedings of
A SYMPOSIUM ON THE MECHANISM OF
CYTOPLASMIC STREAMING, CELL MOVEMENT,
AND THE
SALTATORY MOTION OF SUBCELLULAR PARTICLES
Held at
Princeton University
April 2-5, 1963



1964

ACADEMIC PRESS New York and London

COPYRIGHT © 1964, BY ACADEMIC PRESS INC.

ALL RIGHTS RESERVED.

NO PART OF THIS BOOK MAY BE REPRODUCED IN ANY FORM,
BY PHOTOSTAT, MICROFILM, OR ANY OTHER MEANS, WITHOUT
WRITTEN PERMISSION FROM THE PUBLISHERS.

ACADEMIC PRESS INC.

111 Fifth Avenue, New York, New York 10003

United Kingdom Edition published by

ACADEMIC PRESS INC. (LONDON) LTD.

Berkeley Square House, London W.1

LIBRARY OF CONGRESS CATALOG CARD NUMBER: 64-15265

PRINTED IN THE UNITED STATES OF AMERICA

Symposium Participants

Numbers in parentheses indicate the pages on which the authors' contributions begin.

ABÉ, TOHRU H., *Laboratory of Biology, Hosei University, Tokyo, Japan* (221)

ALLEN, ROBERT D., *Department of Biology, Princeton University, Princeton, New Jersey and The Marine Biological Laboratory, Woods Hole, Massachusetts* (407)

ANDERSON, JOHN D., *Department of Physiology and Biophysics, University of Illinois, Urbana, Illinois* (125)

BERREND, ROBERT E., *Department of Zoology, University of Wisconsin, Madison, Wisconsin* (433)

BOUCK, G. BENJAMIN, *Biological Laboratories, Yale University, New Haven, Connecticut and Biological Laboratories, Harvard University, Cambridge, Massachusetts* (7)

BOVEE, EUGENE C., *Department of Zoology, University of California, Los Angeles, California* (189)

GOLDACRE, R. J., *Chester Beatty Research Institute, London, England* (237)

GRIFFIN, JOE L., *Department of Anatomy, Harvard Medical School, Boston, Massachusetts* (303)

GUSTAFSON, TRYGGVE, *The Wenner-Gren Institute, University of Stockholm, Sweden* (333)

HAYASHI, TOSHIO, *Biological Institute, College of General Education, Tokyo University, Komaba, Tokyo, Japan* (19)

HOFFMANN-BERLING, H., *Max-Planck-Institut für Physiologie, Heidelberg, West Germany* (365)

HONDA, S. I., *Department of Botany and Plant Biochemistry, University of California, Los Angeles, California* (485)

HONGLADAROM, T., *Department of Botany and Plant Biochemistry, University of California, Los Angeles, California* (485)

- INOUE, SHINYA, *Department of Cytology, Dartmouth Medical School, Hanover, New Hampshire* (549)
- JAHN, THEODORE L., *Department of Zoology, University of California, Los Angeles, California* (279)
- JAROSCH, ROBERT, *Biological Research Division, Austrian Nitrate Works, Linz/Donau, Austria* (599)
- KAMIYA, NOBURÔ, *Department of Biology, Faculty of Science, Osaka University, Osaka, Japan; Department of Biology, Princeton University, Princeton, New Jersey; and The Marine Biological Laboratory, Woods Hole, Massachusetts* (257)
- KITCHING, J. A., *Department of Zoology, University of Bristol, Bristol, England* (445)
- KURODA, KIYOKO, *Department of Biology, Faculty of Science, Osaka University, Osaka, Japan* (31)
- MAHLBERG, PAUL G., *Department of Biological Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania* (43)
- MARSLAND, DOUGLAS, *Department of Biology, New York University, New York* (173, 331)
- NAKAI, J., *Department of Anatomy, School of Medicine, University of Tokyo, Hongo, Tokyo, Japan* (377)
- NAKAJIMA, HIROMICHI, *Department of Biology, Faculty of Science, and Institute for Protein Research, Osaka University, Osaka, Japan and Department of Biology, Princeton University, Princeton, New Jersey* (111)
- O'NEILL, C. H., *Zoology Department, King's College, University of London, London, England* (143)
- PARPART, ARTHUR K., *Department of Biology, Princeton University, Princeton, New Jersey and The Marine Biological Laboratory, Woods Hole, Massachusetts* (471)
- REBHUN, LIONEL I., *Department of Biology, Princeton University, Princeton, New Jersey and The Marine Biological Laboratory, Woods Hole, Massachusetts* (503)
- ROBINEAUX, ROGER, *Hôpital Saint-Antoine, Paris, France* (351)

ROTH, L. E., *Committee on Cell Biology and Department of Biochemistry and Biophysics, Iowa State University, Ames, Iowa* (527)

SHAFFER, B. M., *Department of Zoology, Cambridge University, Cambridge, England* (387)

STEWART, PETER A., *Department of Physiology, Emory University, Atlanta, Georgia and Biology Department, Brookhaven National Laboratory, Upton, New York* (69)

THOMPSON, C. M., *Zoology Department, King's College, University of London, London, England* (143)

WILDMAN, S. G., *Department of Botany and Plant Biochemistry, University of California, Los Angeles, California* (485)

WOHLFARTH-BOTTERMANN, K. E., *Zentral-Laboratorium für angewandte Übermikroskopie am Zoologischen Institut der Universität Bonn, Bonn, Germany* (79)

WOLPERT, L., *Zoology Department, King's College, University of London, London, England* (143)

Discussants

BISHOP, DAVID W., *Carnegie Institution of Washington, Baltimore, Maryland*

BURGERS, J. M., *Institute for Fluid Dynamics and Applied Mathematics, University of Maryland, College Park, Maryland*

DE BRUYN, PETER P. H., *Department of Anatomy, University of Chicago, Chicago, Illinois*

HAYES, WALLACE, *Department of Aeronautical Engineering, Princeton University, Princeton, New Jersey*

JAFFEE, LIONEL, *Department of Botany, University of Pennsylvania, Philadelphia, Pennsylvania*

KAUZMANN, WALTER, *Department of Chemistry, Princeton University, Princeton, New Jersey*

LING, GILBERT, *Pennsylvania Hospital, Philadelphia, Pennsylvania*

NOLAND, LOWELL, *Department of Zoology, University of Wisconsin, Madison, Wisconsin*

SZENT-GYÖRGYI, ANDREW G., *Dartmouth Medical School, Hanover, New Hampshire*

TAYLOR, EDWIN, *Committee on Biophysics, University of Chicago, Chicago, Illinois*

THIMANN, KENNETH V., *Department of Biology, Harvard University, Cambridge, Massachusetts*

Observers

CLARK, ELOISE E., *Department of Zoology, Columbia University, New York, New York*

COUILLARD, PIERRE, *Département des Sciences Biologiques, Université de Montréal, Montréal, Canada*

COWDEN, RONALD R., *Department of Pathology, Medical Center, University of Florida, Gainesville, Florida*

DEVILLERS, CHARLES, *Willard Gibbs Laboratories, Yale University, New Haven, Connecticut*

DOUGHERTY, WILLIAM, *Department of Biology, Princeton University, Princeton, New Jersey*

FREUDENTHAL, H., *American Museum of Natural History, New York, New York*

GREEN, PAUL, *Division of Biological Sciences, University of Pennsylvania, Philadelphia, Pennsylvania*

GUTES, E. S., *Department of Biology, Brown University, Providence, Rhode Island*

HACKETT, RAYMOND, *Department of Pathology, Medical Center, University of Florida, Gainesville, Florida*

HANSON, EARL, *Shanklin Laboratories of Biology, Wesleyan University, Middletown, Connecticut*

HAYASHI, TERU, *Laboratory of Biophysics, Pupin Hall, Columbia University, New York, New York*

HAYES, MRS. HELEN L., *Biology Branch, Office of Naval Research, Washington, D. C.*

HIRSHFIELD, HENRY, *Department of Biology, Washington Square College, New York University, New York, New York*

JACKSON, WILLIAM, *Department of Biology, Dartmouth College, Hanover, New Hampshire*

- JACOBS, WILLIAM P., *Department of Biology, Princeton University, Princeton, New Jersey*
- LEE, JOHN, *American Museum of Natural History, New York, New York*
- RHEA, ROBERT PERRY, *Rockefeller Institute, New York, New York*
- ROSENBERG, MURRAY, *Rockefeller Institute, New York, New York*
- RUSTAD, RONALD, *Institute for Molecular Biophysics, Florida State University, Tallahassee, Florida*
- SATO, HIDEMI, *Department of Cytology, Dartmouth Medical School, Hanover, New Hampshire*
- SCOTT, THOMAS, *Department of Biology, Princeton University, Princeton, New Jersey*
- TASAKI, ICHIJI, *Laboratory of Neurobiology, National Institutes of Mental Health, Bethesda, Maryland*
- TAYLOR, A. CECIL, *Rockefeller Institute, New York, New York*
- VISHNIAC, ROMAN, *New York, New York*
- YANAGITA, T. M., *Department of Zoology, Ochanomizu University, Tokyo, Japan*
- ZIMMERMAN, ARTHUR M., *Department of Pharmacology, Downstate Medical College, Brooklyn, New York*

Preface

This book is intended for scientists and students of the biological, biophysical, and medical sciences who are interested in the movements in and of living cells. In it are collected thirty papers presented at the *Symposium on the Mechanism of Cytoplasmic Streaming, Cell Movement, and the Saltatory Motion of Subcellular Particles*, held at Princeton University in April, 1963, together with the edited discussions.

At this Symposium nearly a hundred scientists, representing such disciplines as cell biology, plant physiology, protozoology, developmental biology, biophysics, physical chemistry, biochemistry, rheology, physics, engineering, and medicine, gathered to consider one of life's most elusive problems: How does movement occur at the cell level and below? Until quite recently, nearly all of these phenomena of movement, which we classify as "primitive motile systems," were so poorly understood that theories about them were almost as numerous as facts.

Within the past decade, however, research on motility has begun to bear fruit, due largely to the introduction of improved methods. Each contribution to the volume represents a sample of the best work being done in each area of the field. Each paper contains not only enough background material and bibliographic references to serve as an effective guide to the literature, but is followed by an edited version of the symposium discussion. The discussion should be a most valuable part of the volume for students and for new workers entering the field, for it points the way to the uncertainties and disagreements in each area of study.

"Free Discussion" sections contain remarks and comments by invited discussants, which by themselves would be worth publishing irrespective of the papers. For example, there are pertinent comments by Andrew G. Szent-Györgyi and G. Ling regarding the molecular mechanism of contraction and its control system, a discussion of wave motion by W. D. Hayes, a description of how mathematical models may be useful to biologists studying motility phenomena by J. M. Burgers, and a "running battle" among proponents of the various theories of ameboid movement.

It is over two decades since a similar volume was published in the motility field. The scope of the meeting and the resulting volume is so broad that its influence should doubtless be felt in many fields.

The editors would like to express their appreciation to a number of individuals who contributed to the success of the conference and speedy publication of its proceedings; to the other members of the organizing

committee, Drs. Eugene Bovee, Douglas Marsland, and Lionel Rebhun; to the conference assistants, Mrs. Eleanor Benson Carver, Mrs. Prudence Jones Hall, Mr. Christopher D. Watters, and Mr. Konrad Bachmann; to Mrs. Olive Loria, stenotypist, and to Mrs. Mildred Nunziato and Mrs. Sarah Hayashi who assisted in the preparation of the discussions. We are also grateful to Drs. Lionel I. Rebhun, Walter Kauzmann, and Peter Stewart for performing important editorial tasks.

The conference was supported by a generous research grant [Nonr(G) 00023-63] from the Biology Division of the Office of Naval Research, United States Navy.

January, 1964

R. D. ALLEN
N. KAMIYA

Introduction

One might properly ask what "primitive motile systems" are and why they are of interest. If it had not been for the invention of the microscope, the study of motility might well have remained restricted to the study of muscular contraction. However, early microscopists saw and described the marvelous diversity of movements among protozoans and other lower organisms, and it was not long before hypotheses were advanced to explain the movements of these creatures. Each succeeding generation of biologists has seen the gliding of cells, protoplasmic streaming, pseudopodial movement, the beating of cilia and flagella, mitotic movements of chromosomes, saltatory motions of various cytoplasmic particles, contractions of myonemes and other structures, and various other "nonmuscular" movements. Despite two centuries or more of study with ever-improving methods of study, however, the basic problem as to the mechanism of these various movements has remained unsolved.

One point of view toward these "primitive motile systems" is that they may be slightly different manifestations of some single basic mechanism such as, for example, gel contraction. Such general viewpoints have been expressed from time to time and are very attractive from a theoretical point of view. However, before accepting any unifying theory at face value, it is desirable to classify motile systems into representative phenomenological groups, bearing in mind that the classification may be artificial, and then to test the predictions of any such unifying theory with representatives of each type of motile system. This approach has been applied only to a limited extent, with the result that unifying theories are few and rest on tenuous evidence.

The simplest kind of motion in cells is the *Brownian motion* of particles of micron dimensions, produced by the thermal agitation of neighboring molecules. These molecules are in motion in living and nonliving fluids alike, and therefore have little to do with motility, except insofar as any restrictions imposed on Brownian motion may contribute information regarding the structural properties of certain parts of the cytoplasm.

There are, however, other motions in cells that superficially resemble Brownian motion. These are the "*saltatory*" (or *jumping*) motions, which are sudden excursions of cytoplasmic particles over distances too extensive to be accounted for as Brownian motion. Such motions have been described in the plant literature as "Glitchbewegung" or "agitation." *Mitotic movements* of chromosomes are phenomenologically somewhat similar,

except that they occur within a highly organized structure, the mitotic spindle.

Cytoplasmic streaming is a broad term applied to perhaps a dozen or more different kinds of phenomena in which visible particles move in groups in such a way as to indicate that they are carried by the streaming of cytoplasmic ground substance. The distinction between cytoplasmic streaming and saltatory motion must not be overemphasized, for there are apparently transitional states between the two situations. It needs to be established in many types of "cytoplasmic streaming" whether the flow of ground substance is solely responsible for the motion of particles. Cytoplasmic streaming occurs in cells of both plants and animals, as well as in such acellular organisms as slime molds. Within the plant kingdom alone, the diversity of streaming phenomena is impressive; it is possible to list perhaps a dozen types. Of these, it is now quite well established that two of the plant systems have very dissimilar aspects. This will be brought out in Part I. Little is known about the other types of streaming in plant cells.

Ameboid movement has usually been defined as "locomotion by means of pseudopodia," but it has often been considered by textbook writers as a special case of cytoplasmic streaming in which pseudopodia form and are used in locomotion. It is brought out in Part II that there may well be fundamental differences among two or three groups of amebae as to structure, details of movement, and mechanism of pseudopod formation. It seems abundantly clear, at least, that the cytoplasmic streaming which accompanies pseudopod formation has little in common, as far as mechanism at the cellular level is concerned, with the streaming which occurs in plant cells.

According to the definition of ameboid movement above, the Foraminifera, Radiolaria, and Testacea, among the Protista, and the numerous metazoan tissue cells that move by means of pseudopodia should be included in the same phenomenological grouping as the free-living amebae. However, when the details of movement are compared, the diversity found gives cause for concern whether the same basic mechanism could apply to all types of "ameboid movement."

At first sight, it would appear that the problems of mechanism might be more easily solved with the "less primitive" (i.e., more highly organized) motile systems, such as *ciliary and flagellar movement*, and of course, muscular contraction. However, the degree of structural organization in these systems is a mixed blessing, and here also the fundamental questions of molecular mechanics are still largely unsolved, although in the case of muscular contraction most authorities have settled on one of two leading theories, both of which lack decisive evidence.

What kind of information should we seek in studies of primitive motile systems? First and foremost, the observational details of each system must be recorded in as objective a manner as possible—free from interpretation in terms of any model. This is particularly true of the more complex movements of ameboid cells, which are highly dependent upon external environmental and internal physiological conditions. The advantages of recording observations on cine film are worth considering, especially if it is possible to publish the film and make it available at cost to other investigators. Second, since movements are produced by forces, it is important to identify the forces as contractile, electrical, osmotic, or whatever, and to localize within the cell the site at which the force is applied. Third, we must find out about the nature and availability of the chemical fuel; is it always ATP? How is the fuel withheld from the motile machinery during inactivity? Finally, we must find out as much as possible about the machinery which uses the fuel. Of what units is it composed? How are the forces generated within it and controlled?

In principle, most of these questions can now be posed with the aid of existing instrumentation. In fact, some of the more favorable experimental materials have been subjected to experiments, which in effect constitute the beginnings of such approaches. The next decade promises to be a very exciting one in the study of primitive motile systems, as one by one these systems emerge from the stage of descriptive analysis to the kind of approach outlined above.

THE EDITORS

Contents

SYMPOSIUM PARTICIPANTS	v
DISCUSSANTS	viii
OBSERVERS	ix
PREFACE	xi
INTRODUCTION	xiii

Part I Cytoplasmic Streaming in Plants and Myxomycetes (Mycetozoa)

Introduction	
KENNETH V. THIMANN	3
Fine Structure in <i>Acetabularia</i> and Its Relation to Protoplasmic Streaming	
G. BENJAMIN BOUCK	7
Role of the Cortical Gel Layer in Cytoplasmic Streaming	
TOSHIO HAYASHI	19
Behavior of Naked Cytoplasmic Drops Isolated from Plant Cells	
KIYOKO KURODA	31
Rates of Organelle Movement in Streaming Cytoplasm of Plant Tissue Culture Cells	
PAUL G. MAHLBERG	43
The Organization of Movement in Slime Mold Plasmodia	
PETER A. STEWART	69
Differentiations of the Ground Cytoplasm and Their Significance for the Generation of the Motive Force of Ameboid Movement	
K. E. WOHLFARTH-BOTTERMANN	79
The Mechanochemical System behind Streaming in <i>Physarum</i>	
HIROMICHI NAKAJIMA	111
Regional Differences in Ion Concentration in Migrating Plasmodia	
JOHN D. ANDERSON	125
Free Discussion	135

Part II Cytoplasmic Streaming and Locomotion in the Free-Living Amebae

Introduction	
P. P. H. DE BRUYN	139

Studies on the Isolated Membrane and Cytoplasm of <i>Amoeba proteus</i> in Relation to Ameboid Movement L. WOLPERT, C. M. THOMPSON, AND C. H. O'NEILL	143
Pressure-Temperature Studies on Ameboid Movement and Related Phenomena: An Analysis of the Effects of Heavy Water (D ₂ O) on the Form, Movement, and Gel Structure of <i>Amoeba proteus</i> DOUGLAS MARSLAND	173
Morphological Differences among Pseudopodia of Various Small Amebae and Their Functional Significance EUGENE C. BOVEE	189
Mechanisms of Ameboid Movement Based on Dynamic Organization: Morphophysiological Study of Ameboid Movement, IV TOHRU H. ABÉ	221
On the Mechanism and Control of Ameboid Movement R. J. GOLDBERG	237
The Motive Force of Endoplasmic Streaming in the Ameba NOBURÔ KAMIYA	257
Relative Motion in <i>Amoeba proteus</i> THEODORE L. JAHN	279
The Comparative Physiology of Movement in the Giant, Multinucleate Amebae JOE L. GRIFFIN	303
Free Discussion	323

Part III Cytoplasmic Streaming, Locomotion, and Behavior of Specialized Ameboid Cells

Introduction DOUGLAS MARSLAND	331
The Role and Activities of Pseudopodia during Morphogenesis of the Sea Urchin Larva TRYGGVE GUSTAFSON	333
Movements of Cells Involved in Inflammation and Immunity ROGER ROBINEAUX	351
Relaxation of Fibroblast Cells H. HOFFMANN-BERLING	365
The Movement of Neurons in Tissue Culture J. NAKAI	377
Intracellular Movement and Locomotion of Cellular Slime-Mold Amebae B. M. SHAFFER	387
Cytoplasmic Streaming and Locomotion in Marine Foraminifera ROBERT D. ALLEN	407

Filopodial Movement in <i>Cyphoderia ampulla</i> (Ehr.) ROBERT E. BERREND	433
The Axopods of the Sun Animalcule <i>Actinophrys sol</i> (Heliozoa) J. A. KITCHING	445
Free Discussion	457

Part IV Non-Brownian and Saltatory Motion of Subcellular Particles, and Mitotic Movements

Introduction DAVID W. BISHOP	469
Echinochrome Granule Motion in the Egg of <i>Arbacia punctulata</i> ARTHUR K. PARPART	471
Characteristic Movements of Organelles in Streaming Cytoplasm of Plant Cells S. I. HONDA, T. HONGLADAROM, AND S. G. WILDMAN	485
Saltatory Particle Movements in Cells LIONEL I. REBHUN	503
Motile Systems with Continuous Filaments L. E. ROTH	527
Organization and Function of the Mitotic Spindle SHINYA INOUÉ	549
Screw-Mechanical Basis of Protoplasmic Movement ROBERT JAROSCH	599
Free Discussion	623

SUBJECT INDEX	635
---------------------	-----