Primitive Motile Systems in Cell Biology

EDITED BY

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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.

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R. D. Allen
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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

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