methods of measuring ion fluxes (T. I. Shaw and R. E. Taylor) and optical methods for following Ca^{2+} fluxes (A. L. Hodgkin). Recent measurements of ^{22}Na flux in voltage clamped axons at a variety of potentials have shown that the transference number for Na (as early current) is very close to unity. Some of the difficulties in using perfused axons for active transport studies were discussed. It was noted that the use of dextran in the interior of the axon seems to stabilize the membrane against what appears to be some sort of an irreversible uncoupling of the Na pump. If aequorin, a compound that emits light in the presence of Ca^{2+}, is injected into squid axons, it is possible to follow changes in $[Ca]_i$ (and therefore Ca entry) by measuring light emission from the fiber. An early Ca^{2+} entry that is synchronous with Na entry has been observed as well as a late entry seen in TTX-treated fibers. This latter process is especially interesting as it may be related to transmitter release phenomena which ordinarily are observed only in nerve terminals.

L. J. MULLINS

Department of Biophysics,
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Note

1. The organizers of the conference were D. E. Goldman, chairman, K. S. Cole, and L. J. Mullins. There were about 30 participants, but no formal lectures. The conference was held 5 to 9 April at Ann Jordon Farm, Alexander City, Alabama, a conference center of the University of Alabama. Participants were welcomed by Dr. R. Hill, vice president for health affairs of the University of Alabama in Birmingham and were entertained for dinner by President J. F. Volker. The local arrangements were handled by Dr. W. Rehm, Chairman, Department of Physiology and Biophysics University of Alabama, Birmingham. Financial support for the conference was provided by the Grass Foundation, Quincy, Massachusetts, International Business Machines Co., and the University of Alabama at Birmingham. Support for the expenses of NIH personnel was provided by the National Institute of Neurological Diseases and Stroke, Bethesda, Maryland. The organizing committee is grateful to the University of Alabama in Birmingham for providing for the needs of the conference and to the agencies whose financial support made the meeting possible.

Membrane Structure

The theme and perspective for the Conference on Membrane Structure and Its Biological Applications, which was sponsored by the New York Academy of Sciences and held 2 to 4 June 1971, was set by the first two presentations, given respectively by G. Vanderkooi and J. Singer. Vanderkooi presented de-

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tailed molecular structural models for the disk membrane of the rod outer-segment and for the membrane formed by cytochrome oxidase. Singer followed this up with a general treatment of membrane structure in which he emphasized the thermodynamic or energetic determinants of structure. The general picture given by both of these workers was very similar, namely, that the lipid in membranes exists as lamellar bilayer, just as Danielli and Davson proposed in the 1930's, but that the proteins are globular and penetrate deeply into the bilayer lipid. The terminology of intrinsic and extrinsic membrane proteins was introduced by Vanderkooi; this terminology proved very useful in the ensuing discussions of the conference, as it served to differentiate between those proteins that are an integral part of the membrane continuum (intrinsic) and those that are attached to the surface in miscellaneous ways (extrinsic).

One of the reasons for the success of this conference was the organization of the discussion periods. Most sessions consisted of three or four major papers, followed by a few programmed discussants who gave prepared remarks or a brief paper, which in turn was followed by an extended period of open questions and discussion from the floor. In this way, a partial consensus of opinion was actually gained during the course of the meeting. Such a consensus was an especially useful development for this particular meeting since the field of membrane structure has not been noted for unanimity of opinion or even for discussion of conflicting opinions.

After the papers on membrane models were presented, a long series of papers, which covered several sessions (but with no concurrent sessions running), dealt with the experimental aspects of membrane structure. While most of these consisted of experimental methods and results, the underlying thought was, "How do the data obtained by this technique contribute to our knowledge of membrane structure, and how do the results fit the various models which have been proposed for membranes?"

As a result of the numerous discussions, a higher level of agreement on the essentials of membrane structure was achieved than we have seen heretofore. The point which won universal acceptance, on the basis of several kinds of experimental data, was that the lipids in membrane exist predominantly as lamellar bilayer. It was agreed that any

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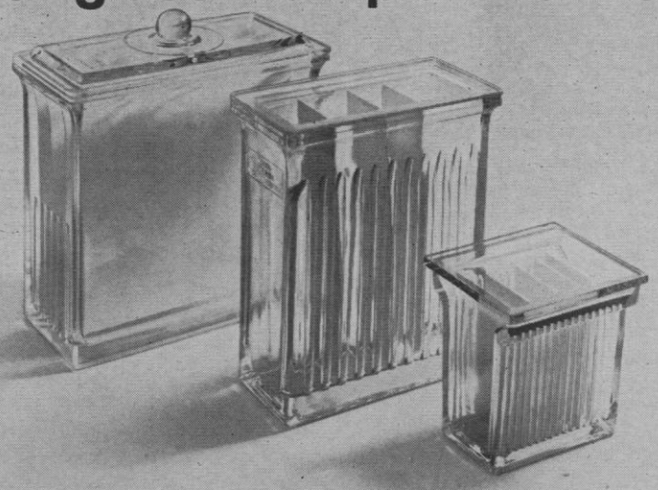

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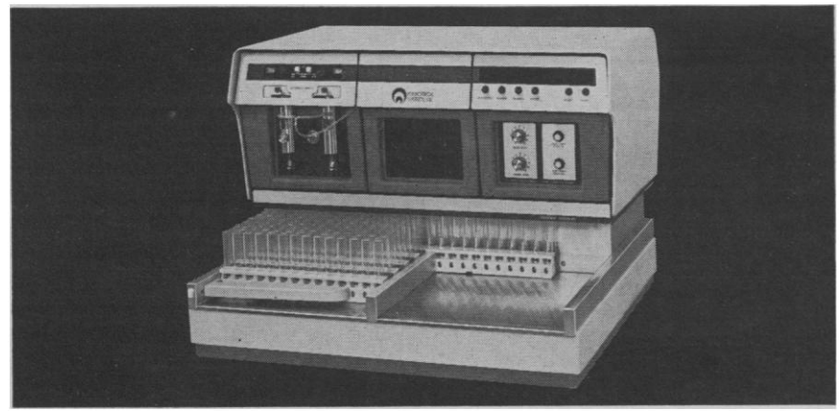

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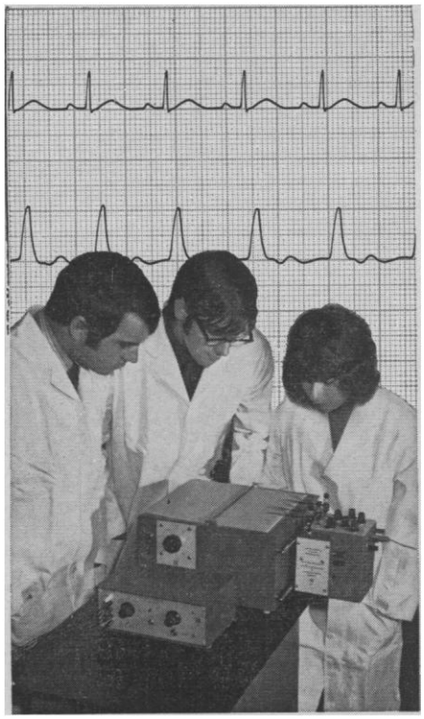

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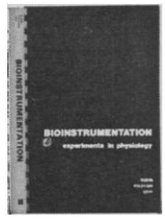

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model that does not assign this structure to bulk lipid can be rejected. The second point on which there seemed to be general agreement, although with a somewhat weaker experimental foundation than for the first point, was that membrane proteins are globular, just as the majority of soluble proteins are, rather than extended fibrous structures which were proposed in the old unit membrane model. Further, there seemed to be general consent to the idea that the globular proteins that are intrinsic to the membrane do penetrate into the lipid bilayer, and that they do not simply bind electrostatically to the bilayer surface.

As far as general membrane models are concerned, the conferees were loath to accept the concept that a single membrane model could be constructed that will account for the basic structure of all membranes. It was pointed out by D. E. Green, however, and seconded by others, that the state of membranology may be likened to the concepts concerning nucleic acids before Watson and Crick. Confusion reigned until it was shown that the principle of the double helix could organize a wealth of data into a sensible picture. Likewise, there ought to be some fundamental similarities of membrane structure, which, once they are discovered, will simplify the whole membrane field.

In spite of the reluctance of the group to adopt a particular membrane model—possibly a reflection of the anxiety to avoid replacing the dogma of the unit membrane with a new progress-inhibiting dogma—a model was tentatively adopted for the structure of one particular membrane, the retinal rod outer-segment disk membrane. M. H. F. Wilkins reported that a careful analysis of his x-ray diffraction data on the retinal rods, interpreted with the assistance of molecular model building, now appears to indicate that the globular proteins are in fact about half submerged in the lipid bilayer, as proposed in 1970 by G. Vanderkooi and M. Sundaralingam. In his summarizing talk at the end of the conference, O. Hechter stated that the general opinion seemed to him to be that this retinal rod membrane model is "probably correct."

One might think that a good molecular model for myelin would have emerged from this conference, but it did not. This situation exists in spite of extensive electron microscopy and high quality (for membranes) x-ray diffraction data now available on the

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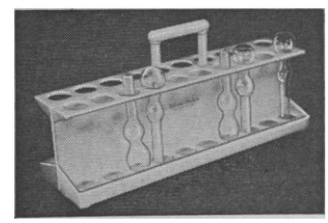

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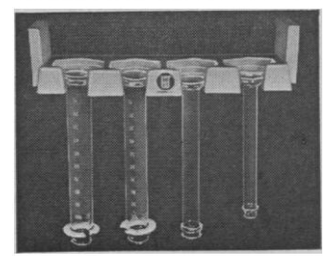

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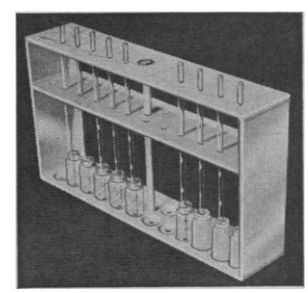

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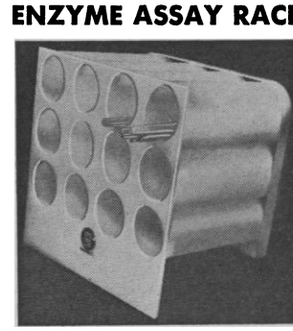

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myelin system. In one of the lively discussion sessions, C. Tanford felt compelled to point out that electron microscopy and one-dimensional x-ray analysis by themselves are incapable of solving membrane structure. These techniques are useful and provide valuable information, but the results must be interpreted in terms of a model. The x-ray and microscopy results put definite constraints on any suggested model, but do not of themselves provide sufficient information to generate a model. Thus we are back once again to model building: propose a model on the basis of as much evidence from as many different sources as possible, and judge the result on the basis of self-consistency of explanation.

At least two of the six sessions of the conference were devoted to phenomena, the rationalization of which depends heavily on our knowledge of membrane structure—facilitated transport through membranes, membrane permeases, complement fixation, and plasma lipoproteins. It was noteworthy that in attempting to visualize the kind of membrane structure that would account for facilitated transport, both W. P. Stein and S. Roseman proposed models not unlike those proposed by Singer and Vanderkooi.

A glimpse into the future of electron miscroscopy was provided by H. Fernández-Morán and the conference proceedings were summarized by O. Hechter.

The conference was organized by J. F. Danielli and D. E. Green. An international group of participants included x-ray diffractionists (F. O. L. Schmitt, M. H. F. Wilkins, C. R. Worthington, D. A. Kirschner, D. D. L. Caspar, D. F. Parsons, and M. Sundaralingam), electron microscopists (J. D. Robertson, G. Nicholson, Fred Crane, H. Fernández-Morán, W. Stoeckenius, and C. R. Hackenbrock), protein chemists (C. Tanford, J. Folch-Pi, J. A. Reynolds, J. Heller, and S. J. Singer), physical probe experts (D. W. Urry, circular dichroism; J. M. Steim, thermal analysis; D. Chapman, nuclear magnetic resonance; H. M. McConnell, electron spin resonance; and G. Colacicco, surface films), and those closely concerned with biological function (A. M. Scanu, S. Roseman, W. P. Stein, R. Kaback, S. Fleischer, and S. C. Kinsky). In all there were 40 participants on the program and about 700 in attendance.

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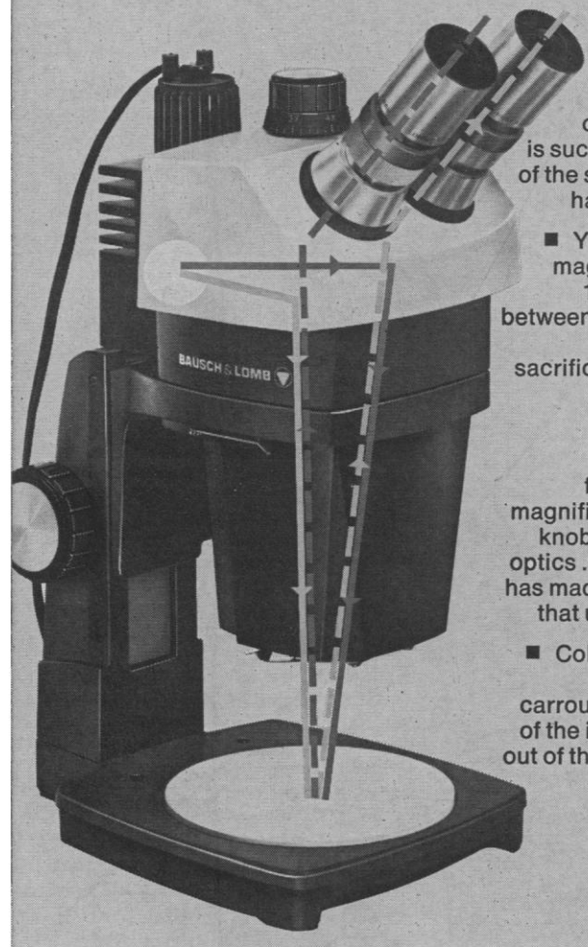

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