BINARY MEMBRANES: A REINTERPRETATION OF MEMBRANE AND MYELIN STRUCTURE

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Summary: Membrane structure is reinterpreted in terms of a binary membrane consisting of a double layer of lipoprotein globules. In sectioned and stained mitochondrial preparations the binary membrane appears as a five-layered structure--three dark lines separated by two unstained regions. Electron micrographs published in the literature suggest that other biomembranes may exhibit this binary structure.

As a result of fragmentation studies on mitochondrial cristae we have proposed that the membrane is made up of a double layer of lipoprotein globules (1). We feel this double layer should be called a binary membrane. A similar model has been proposed for the yeast plasma membrane by Frey-Wyssling and Mühlethaler (2) on the basis of freeze etch studies. Sections of mitochondrial cristae in fixed and stained preparations show a five-layered structure, composed of three dark lines with two unstained regions between the lines, which would be consistent with a double layer membrane (3,4). This five-layered structure is seen in fig. 1, both as observed in the original electron micrograph and as depicted diagrammatically. Close examination of other membranes and of electron micrographs appearing in the literature suggest that other biomembranes are binary rather than unit membranes. The five-layer structure can be seen in the following membranes in the figures listed: (see list).

We feel that five-layer structure in membranes occurs frequently enough that it must be considered as a serious alternative to the unit membrane in some cellular structures.

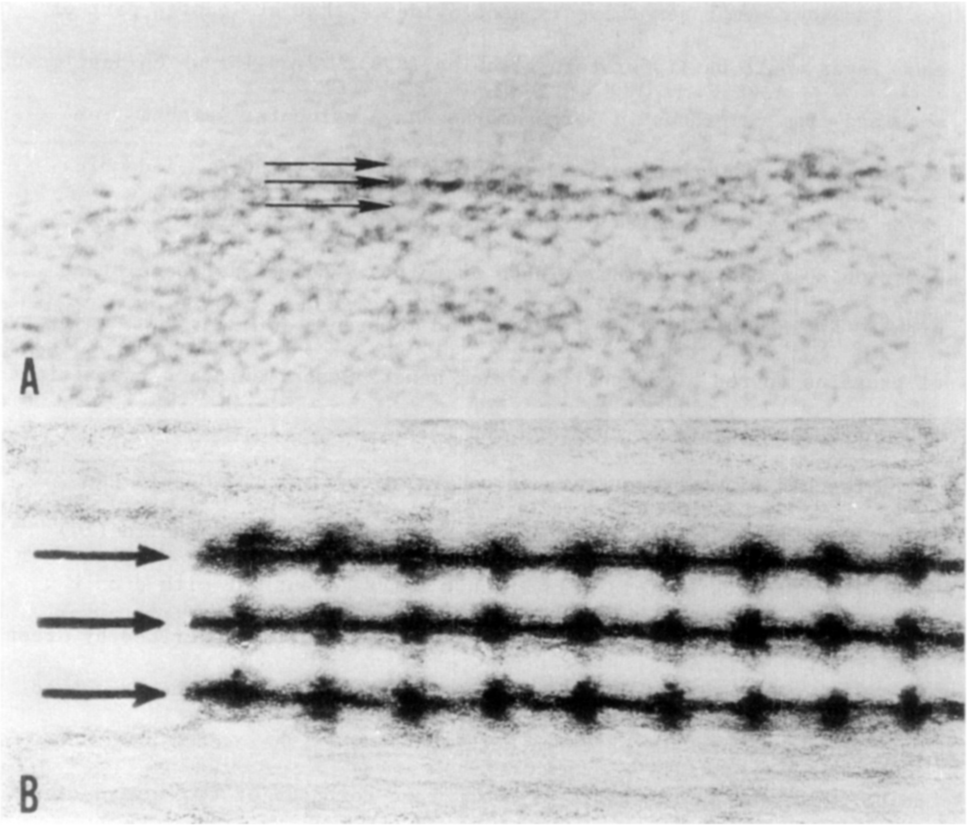

Figure 1. A. Section of beef heart mitochondria fixed in osmium tetroxide and post stained in $KMnO_4$. Arrows mark the three dark lines of the binary membrane. The membrane thickness as measured from one exterior stained line to the other exterior line is 90 Å. X 710,000.

B. Enlarged diagram of a binary membrane. Arrows mark the three darkly staining lines. Two unstained globular regions are between the lines.

Since the schwann cell membrane appears to be binary while the myelin derived from it (5) has a unit structure, there must be some kind of transition in membrane structure. It appears that one of binary layers is lost during myelin formation. Napolitano and Scallen (6) have found that the incorporation of digitonin during fixation results in the preservation of an additional layer between the major period in peripheral myelin. Perhaps this additional layer or double minor period (7) represents one of the original binary layers.

In other membranes there is good evidence that at least a part of each layer would be lipoprotein globules (8,9). Proteins which have been obtained from membranes in large amounts have molecular weights from 20,000 to 70,000 with spherical diameters of 30 Å to 50 Å. A double layer of protein molecules of this size would be required to make a membrane 80 Å to 100 Å wide. These protein sizes are also consistent with 50 Å globules observed in sectioned membranes (10,11). The majority of proteins in red blood cell membrane have 2 S sedimentation coefficients and molecular weights of about 50,000 (12).

Fracture of membranes through central non-polar regions in the freeze etch procedure as described by Branton (13) and Staehelin (14) is consistent with a lipid bilayer unit membrane but not with a unit membrane composed of a single layer of lipoproteins as described by Green and Perdue (8). If the central septum of the binary membrane is a good fracture plane then the patterns obtained by the freeze etch procedure can be explained on the basis of a membrane composed of two layers of lipoprotein globules. In some membranes the globules would be close packed to give smooth surfaces on the fracture planes, e.g., plasma membranes (13), whereas in chloroplasts uneven globules give a rough surface (15).

There are two possible reasons why five-layered structure is not always observed in sectioned membranes. In some procedures the staining of one layer may not be complete. As an alternative, conformational changes in membranes (16,17) may represent a shift from binary to unit structure. For example, apparent differences in membrane thickness between the coupled and uncoupled state of chloroplasts (18) or mitochondria (19) could be related to a shift from binary to unit membrane structure. Certainly the binary structure offers mechanical advantages for membrane conformational change since a shift or structure change in one layer can induce tension in the second layer.

Pictures which show Binary Membrane Structure

Schwann cell membrane enclosing axon	fig. 6, J. Finean, Circulation 26, 1151 (1963).
Schwann cell inner mesaxon around axon at fusion point	fig. 1, J. Finean, Circulation 26, 1151 (1963)
Bacillus cereus plasma membrane and spore membrane	fig. 17, C. F. Robinow, Circulation 26, 1092 (1963).
Bacillus subtilis plasma membrane	fig. 15 & 16, C. F. Robinow, Circulation 26, 1092 (1963).
Bacillus mycoides mesosomes	fig. 8,10,12, C. F. Robinow, Circulation 26, 1092 (1963).
Bacillus mycoides plasma membrane	fig. 7, C. F. Robinow, Circulation 26, 1092 (1963).
intestinal microvilli (frog)	fig. 13, P. W. Brandt, Circulation 26, 1075 (1963).
mitochondrial cristae	fig. 7 & 8, H. Fernandez Moran, Circulation 26, 1039 (1963).
intestinal microvilli	fig. 6, S. Ito, Fed. Proc. 28, 12 (1969).
axon membrane	fig. 41b, J. D. Robertson, in Cellular Membranes in Development, Ed. M. Locke, Academic Press, New York, 1964, p. 1.
mitochondrial cristae	fig. 10 & 11, F. S. Sjostrand in The Membranes, Ed. A. J. Dalton and F. Haguenau, Academic Press, New York, 1968, p. 151.
plasma membrane (& mitochondria)	fig. 2, above the arrow, F. S. Sjostrand in The Membranes, Ed. A. J. Dalton and F. Haguenau, Academic Press, New York, 1968, p. 151.
plasma membrane	fig. 181, D. W. Fawcett, The Cell, Saunders, Philadelphia, 1966, p. 341.
liver cell endoplasmic reticulum	Fig. 5, P. Gaylarde and I. Sarkany, Science 161, 1157 (1968).

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REFERENCES

1. F. L. Crane, J. W. Stiles, K. S. Prezbindowski, F. J. Ruzicka, and F. F. Sun, in Regulatory Functions of Biological Membranes, Ed. J. Järnefelt, Elsevier, Amsterdam, p. 21 (1968).
2. A. Frey-Wyssling and K. Muhlethaler, Ultrastructural Plant Cytology, Elsevier, Amsterdam, p. 150 (1965).
3. K. S. Prezbindowski, Ph.D. Thesis, Purdue University (1968).

4. K. S. Prezbindowski, F. J. Ruzicka, F. F. Sun, and F. L. Crane, Biochim. Biophys. Res. Commun. 31, 164 (1968).
5. J. D. Robertson, in Cellular Membranes in Development, Ed. M. Locke, Academic Press, New York, p. 1 (1964).
6. L. M. Napolitano and T. J. Scallen, Anat. Rec. 163, 1 (1969).
7. J. P. Revel and D. W. Hamilton, Anat. Rec. 163, 7 (1969).
8. D. E. Green and J. F. Perdue, Ann. N. Y. Acad. Sci. 137, 667 (1966).
9. E. D. Korn, Science 153, 1491 (1966).
10. F. S. Sjostrand, in The Membranes, Ed. A. J. Dalton and F. Haguenau, Academic Press, New York, p. 151 (1968).
11. E. D. P. DeRobertis, W. W. Nowinski, and F. A. Saez, Cell Biology Saunders, Philadelphia, p. 113 (1965).
12. S. A. Rosenberg and G. Guidotti, J. Biol. Chem. 243, 1985 (1968).
13. D. Branton, Proc. Nat. Acad. Sci. 55, 1048 (1966).
14. L. A. Staehelin, J. Ultrastruct. Res. 22, 326 (1968).
15. D. H. Northcote, Brit. Med. Bull. 24, 107 (1968).
16. C. R. Hackenbrock, J. Cell Biol. 30, 269 (1966).
17. J. T. Penniston, R. A. Harris, J. Asai, and D. E. Green, Proc. Nat. Acad. Sci. 59, 624 (1968).
18. S. Izawa and N. E. Good, Plant Physiol. 41, 544 (1966).
19. D. E. Green, J. Asai, R. A. Harris, and John T. Penniston, Arch. Biochem. Biophys. 125, 684 (1968).