

is to a large extent offset by the lower accuracy of the polarisation data, but nevertheless careful analyses of polarisations have shown anomalies that are not yet understood.

An example of this is provided by the work of Boschitz (*Phys. Rev. Lett.*, **17**, 97; 1966), who analysed a series of differential cross sections and polarisations. He was able to obtain good overall fits to the polarisation data but the optimum values of the parameters of the spin-orbit term in the optical potential showed marked variations from one nucleus to another and as a function of proton energy. So far there is no convincing explanation of this behaviour.

From these examples it will be seen that the processes that must be considered explicitly are of several types. The polarisation and the dependence on the nuclear asymmetry can easily be incorporated in the optical model. The others require quite sophisticated calculations before the effects due to the general optical potential and the special process can be disentangled. The calculations with both processes included give directly the elastic cross section and there is no effective optical model potential as an intermediate stage. It is thus not possible to think of a general optical potential in which the effects of coupling to excited states, two-step reactions, core-polarisation exchange processes and so on are included by appropriate analytical terms in a general expression of the optical potential. In this sense the optical potential ceases to be a concept able to give a detailed physical account of all the data; it has been superseded in some regions by more sophisticated calculations that give an accurate account of the data that cannot be obtained in any other way.

One has thus arrived at a third concept of the optical potential as one that includes as many effects as possible in the parameterisation of its parameters as functions of Z and A but which has to be used in a more sophisticated formalism if certain other effects are to be treated adequately. Thus some of the simplicity of the model has been lost, but further insight into more complicated phenomena has been attained.

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Correction

In the News and Views article "Vegetational change in an aboriginal environment" (*Nature*, **249**, 11; 1974), the date in line 7 of the first paragraph should be 5,500 radiocarbon years.

Biogenesis of surface membranes

from R. Colin Hughes

ACCORDING to the membrane flow theory, membrane biogenesis involves the physical transfer of membranes from one subcellular compartment to another. The endoplasmic reticulum is the precursor of Golgi membrane which is in turn processed into plasma membrane. Surface membrane proteins and glycoproteins, therefore, are considered as a special class of secreted substances.

The basic assumption of the theory, that membrane proteins are synthesised on the rough endoplasmic reticulum, must obviously be re-interpreted, however, since Lodish (*Proc. natn. Acad. Sci. U.S.A.*, **70**, 1526-1530; 1973) and Lowe and Hallinan (*Biochem. J.*, **136**, 825-828; 1973) have described synthesis of some membrane proteins on free polysomes. The converse proposal that soluble cytoplasmic proteins are made only on free polysomes is similarly an oversimplification. At least one soluble enzyme, serine dehydrase, is synthesised on membrane-bound ribosomes and a similar role seems likely in non-secretory tissues such as brain or muscle. So far as membrane proteins are concerned, it is possible that integral membrane components are made in a way different to extrinsically bound proteins. Synthesis of glyceraldehyde-3-phosphate dehydrogenase on cytoplasmic polysomes is expected, for example, yet this protein forms stable interactions with high affinity for a limited number of sites on the cytoplasmic face of the erythrocyte membrane (Kant and Steck, *J. biol. Chem.*, **248**, 8457-8464; 1973). The enzyme seems therefore to be a specific membrane component, made on free polysomes.

An indication that integral proteins, by contrast, may follow an intracellular route analogous to the secretory process comes from an extensive radioautographic study by Leblond and his colleagues (*J. Cell Biol.*, **60**, 258-284; 1974). This suggests a final step in surface membrane biogenesis in which fusion takes place between the cell surface membrane and Golgi vesicles, the membranes of which carry proteins and glycoproteins destined ultimately for the surface membrane. The chief difficulty in accepting completely this proposal, is that the membrane composition of highly purified rat liver Golgi membranes, as described recently by Palade *et al.* (*J. Cell Biol.*, **59**, 45-72; 73-88; 1973) is clearly different to the homologous plasma membrane. The role of the Golgi vesicles therefore, may be to ferry a few proteins from intracellular smooth membranes to the cell surface as follows: fusion

of the vesicles with the cell surface membrane, lateral diffusion of selected proteins into the area of plasma membrane surrounding the fusion site and finally re-entry of the Golgi vesicular membrane into the cell by endocytosis. In this case, the membranes of Golgi vesicles before fusion would contain a relatively small proportion of plasma membrane components superimposed on a background of purely Golgi membrane proteins and after fusion only Golgi specific proteins.

The membrane flow theory also predicts that at earlier stages of membrane biogenesis, the proteins and glycoproteins are restricted to membrane-bounded intracellular vesicles. Presumably, the membrane precursors made on membrane-bound ribosomes are either discharged into the lumen of the endoplasmic reticulum to be inserted into smooth membranes elsewhere or remain inserted directly into membranes at their sites of biosynthesis. Hirano *et al.* (*Proc. natn. Acad. Sci. U.S.A.*, **69**, 2945-2949; 1973) found earlier that the membranes of rough microsomal vesicles are asymmetrically substituted with carbohydrate groups, capable of reacting with certain lectins coupled with ferritin. The membrane facing inwards carried carbohydrate whereas the cytoplasmic face did not. Since the intraluminal face of the endoplasmic reticulum is equivalent to the external face of the plasma membrane, at which carbohydrates are also localised, this finding is interpreted as a flow of membrane with retention of configuration from intracellular biosynthetic sites to the cell surface. It does not, of course, prove that this is the case. Kreibach *et al.* (*Fed. Proc.*, **32**, 2133-2138; 1973; *J. Cell Biol.*, **60**, 616-627; 1974) now confirm these observations by testing the accessibility of rat liver microsomal proteins to lactoperoxidase labelling. The glycoproteins are labelled only when the closed microsomal vesicles are made permeable by treatment with low concentrations of detergents. Two classes of glycoproteins are labelled; one class is released by mild detergent treatment whereas the other requires higher detergent concentrations and disassembly of the microsomal membranes. It is not clear, however, whether these last components are stable membrane constituents or precursors of glycoproteins.

The glycoproteins detected by Hirano *et al.* and Kreibach *et al.* are not known to be precursors of surface membrane glycoproteins and could equally well be glycoproteins destined for secretion. The next step is application of the techniques for the selective solubilisation of microsomal glycoprotein precursors to defining the kinetics of flow of these substances.