X-ray scattering by partially disordered membrane systems

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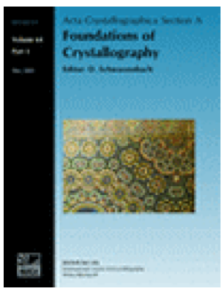
DOI: 10.1107/S0567739478001540

Issue



Acta Crystallographica Section A

Volume 34, Issue 5, (/doi/10.1111/aya.1978.34.issue-5/issuetoc) pages 751 753, September 1978

Additional Information

How to Cite

Baianu, I. C. (1978), X-ray scattering by partially disordered membrane systems. Acta Cryst. A, 34: 751 753. doi: 10.1107/S0567739478001540

- Abstract
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Acta Cryst. (1978). A 34, 751–753

Acta Cryst. (1978). A34, 751–753

X-ray Scattering by Partially Disordered Membrane Systems

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(*Received* 1 *February* 1978; *accepted* 6 *April* 1978)

A method of analysing the X-ray diagrams of imperfect membrane lattices with degrees of stacking disorder between 2 and 6% is presented. The method is, however, generally applicable to partially disordered lattices of centrosymmetric membranes. This can also be extended to the case of asymmetric membranes occurring in one orientation only, or in pairs, back-to-back. The procedure allows the determination of the statistical quantities characteristic of the partially disordered lattices and the separation of the diffuse scattering component. As a direct consequence, the refinement of membrane electron density projections becomes feasible and an example is presented for erythrocyte membrane lattices. A one-dimensional model of the refined electron density profile of the erythrocyte membrane is used to calculate numerically the X-ray scattering for a partially disordered lattice of N membrane units. A residual of 15% is obtained with this model and the difference between the observed and calculated values can be minimized further with the proposed refinement procedure.

Introduction

The analysis of X-ray diffraction patterns of membrane lattices has been previously carried out for well orientated membrane systems (Finean & Burge, 1963; Moody, 1963; Worthington & Blaurock, 1968; Caspar & Kirschner, 1971; Levine & Wilkins, 1971; Worthington & Liu, 1973). The degrees of disorder of these systems were less than 2% in the directions of layering of membrane lamellae and, apart from the Lorentz correction and the limited resolution obtainable, the correction of experimental X-ray intensities did not pose further problems. Subsequent model calculations by Weick (1974) and Moody (1975) allowed the estimation of the extent of membrane asymmetry from the corrected intensity profile of membrane dispersions and thus extended the analysis of X-ray data to the case of systems with no positional correlations among the membrane lamellae. Most membrane preparations give lamellar diffraction patterns characteristic of imperfect lattices with degrees of disorder higher than 2% and it therefore becomes important to employ methods developed for the analysis of X-ray data from partially disordered lattices.

An attempt is made here to apply selectively the general calculations. introduced previously for paracrystals, to the interpretation of X-ray diagrams of erythrocyte membrane lattices with degrees of stacking disorder between 2 and 6% (Baianu, 1974, 1978). The approach can be generalized to other membrane systems by taking into account the membrane asymmetry (Moody, 1975).

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One-dimensional models

The total scattering intensity for a paracrystal can be written as

$$I_{\text{tot}} = I_B + I_C, \tag{1}$$

where I_B is the Babinet component and I_C is the crystalline term (Hosemann & Bagchi, 1962; Blundell, 1970). For a lattice made of N stacked lamellae of widths X_j with uniform density in their plane and electron density profiles $R(x_j)$, the two intensity components are

$$I_B(s_1) = 2/(2\pi s_1)^2 \times \mathrm{Re}\{1/\bar{X}[J - P_x G_x F_z/(1 - F_x F_z)]\} \tag{2}$$

$$I_C(s_1) = 2/(2\pi s_1)^2 \times \mathrm{Re}\{P_x G_x F_z[1 - (F_x F_z)^N]/N\bar{X}(1 - F_x F_z)^2\} \tag{3}$$

with the notation:

$$F_x = \int_0^\infty f H(x) \exp(-2\pi i s_1 x)\, \mathrm{d}x,$$

$$P_x = \int_0^\infty f^* H(x) \exp(-2\pi i s_1 x)\, \mathrm{d}x,$$

$$F_z = \int_0^\infty h(z) \exp(-2\pi i s_1 z)\, \mathrm{d}z,$$

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