is shown in Fig. 2. Note that Fig. 2 is rotated 90° relative to Fig. 1 so that the beam stop is along the equator. The two-dimensional array is hexagonal with $a = 620$ Å and the light direction is coincident with the (11) direction of the two-dimensional arrays. The orientation of the two-dimensional array of microvilli relative to the light direction is shown in Fig. 3.

It is known from electron microscopy[7,8] that the adjacent microvilli arrays of different retinula cells are approximately perpendicular to each other but it is not known to what extent this kind of packing is followed throughout the whole retina. If the X-ray specimen of squid retina contained only two orientations (which are perpendicular to each other) then the recording of the off-meridional reflections would be sensitive to the direction of the incident X-ray beam. But no such sensitivity has been recorded. The pinhole-collimated X-ray patterns indicate that the (11) direction is a rotation axis. Thus, although adjacent arrays may be perpendicular to each other[7,8], this kind of packing is not maintained over the whole retina.

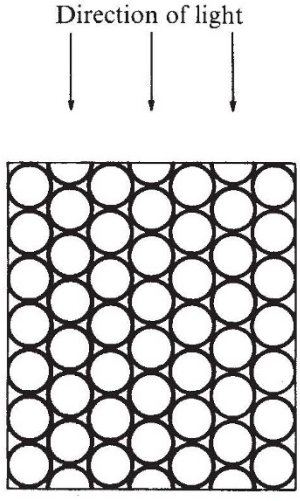
A model for a single microvillus is a long thin cylinder where the wall is made up of a single membrane of width m. It is assumed that $m \sim 75$ Å—that is, the microvillus membrane has the same thickness as the disk membrane[1-4]—and that the outer surfaces of the cylinders are separated by a fluid layer about 5 Å wide. The single membrane is centred at a distance r from the axis of the cylinder and $r = 1/2\ (620 - m - 5)$ Å, that is, $r = 270$ Å. The Fourier transform of the membrane with respect to its centre is denoted by $M(R)$ where R is the reciprocal space coordinate. The Fourier transform of the two-dimensional array of microvilli is denoted by $T(R)$; and using X-ray diffraction theory appropriate to concentric membrane layers[11], $T(R)$ can be written

$$T(R) \sim 2\pi r J_0(2\pi r R) M(R) \Phi(R)$$

where J_0 is the zero-order Bessel function and Φ is the interference function for the two-dimensional array.

A test of the correctness of the above model can be made by comparing the calculated and observed intensities for the (10), (11) and (20) reflections. In the squid retina the two-dimensional arrays of microvilli are effectively rotated about the (11) direction. To refer intensities to an unrotated array the following corrections are made. The off-meridional reflections (01),(10) and (12),(21) are increased four to five times, while the off-meridional reflections (02),(20) and (13),(31) are increased eight to ten times. The X-ray intensities for the first three reflections of the unrotated array have the following variation: $I(10) \gg I(20) > I(11)$. To calculate intensities from our model it is necessary to first estimate values of $M(R)$, the Fourier transform of the microvillus membrane. For the first two or three reflections which correspond to very small angles of diffraction, $M(R)$, can be approximated[11] by a membrane of constant density so that $M(R)$ is proportional to $(1/R)\sin(\pi m R)$ and where $m \sim 75$ Å. The $J_0(2\pi r R)$ variation is sensitive to the choice of r and we use $r = 270$ Å. By combining the $M(R)$ and $J_0(2\pi r R)$ variations, our model provides an intensity variation for the first three reflections, which is the same as recorded experimentally. Thus, the observed intensities of the first few reflections in the pinhole-collimated X-ray patterns are in agreement with the microvillus membrane having a thickness of about 75 Å and with the concentric membrane having a radius of about 270 Å.

Fig. 3 A drawing of a section through the two-dimensional hexagonal array of microvilli. The section contains the light direction and is perpendicular to the long axes of the microvilli cylinders.



In summary, it has been possible to record X-ray diffraction from the photoreceptor structures of squid retina. So far, these X-ray patterns refer to fixed eyes. X-ray analysis of the pinhole-collimated patterns has provided information on the dimensions of the microvilli and on the molecular organisation of the microvilli in the distal segments of squid retina. Information on the internal structure of the microvillus membrane has not been obtained but this information may be forthcoming in future work provided that more reflections can be recorded in pinhole-collimated X-ray patterns.

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1 Gras, W. J., and Worthington, C. R., *Proc. natn. Acad. Sci. U.S.A.*, **63**, 233–238 (1969).
2 Blaurock, A. E., and Wilkins, M. H. F., *Nature*, **223**, 906–909 (1969).
3 Corless, J. M., *Nature*, **237**, 229–231 (1972).
4 Worthington, C. R., *A. Rev. Biophys. Bioengng*, **3**, 53–80 (1974).
5 Eakin, R. M., in *Handbook of Sensory Physiology*, **VII/1**, *Photochemistry of Vision*, 625–684 (Springer, Berlin, 1972).
6 Moody, M. F., *Biol. Rev. Camb. phil. Soc.*, **39**, 43–86 (1964).
7 Zonana, H. V., *Johns Hopkins Hosp. Bull.*, **109**, 185–205 (1961).
8 Cohen, A. I., *J. comp. Neurol.*, **147**, 351–378 (1973).
9 Yamamoto, T., Tasaki, K., Sugawara, Y., and Tonosaki, M. D., *J. Cell Biol.*, **25**, 345–359 (1965).
10 Elliott, G. F., and Worthington, C. R., *J. Ultrastruct. Res.*, **9**, 166–170 (1963).
11 Worthington, C. R., in *Biophysics and Physiology of Excitable Membranes*, 1–46 (Van Nostrand-Reinhold, New Jersey, 1971).

Corrigendum

In the article "Intact 3′ end of 16S rRNA is not required for specific mRNA binding" by J. V. Ravetch and K. S. Jakes (*Nature*, **262**, 150; 1976) the sentence at the beginning of paragraph 4 should read "The colicin-treated ribosomes used in the experiment shown in Fig. 1 were lowered in their ability to carry out f2 RNA-directed protein synthesis by 75%" and not as printed.

Errata

IN the article "Constraints on the nature of the ancient lunar magnetic field" by J. N. Goswami (*Nature*, **261**, 675; 1976) two lines were omitted from the end of page 676. The sentence 'One of these . . . Fe–FeS . . . ' should continue ' . . . melt a few hundred kilometres below the lunar surface, initiating such local fields[12] on the Moon, is yet to be verified.'

The title of the article by M. S. N. Carpenter and L. Civetta (*Nature*, **262**, 276; 1976) should read "Hercynian high pressure/low temperature metamorphism in the Ile de Groix Blueschists" and not as printed.