Ray Path and Reflection Mechanisms in Crayfish Eyes

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In crayfish eyes image formation not due to refraction but to total internal and multilayer reflection in an orthogonal mirror system is described. Relevant optical parameters (geometry and refractive indices) in this eye are determined.

The investigation of the eyes of various crayfish species led me to a principle of image formation in crayfish eyes quite different from that of Exner [1, 2]. The superposition ray path in a crayfish eye is not formed by lenses and an equivalent distribution of refractive index but by reflections at the sides of the crystalline cones. This type of image formation was independently confirmed by M. Land in an oceanic decapod [3]. The aim of this paper is to show how a three-dimensional ray path is formed by an imaging system consisting of rectangular mirrors. Further, in this type of eye two different reflection mechanisms are functionally combined: (1) total internal reflection within the crystalline cone depending on the axial decrease of refractive index and (2) a distal multilayer reflector.

A superposition ray path in a crustacean eye can not be discussed only as a problem of the convergence of ray bundles in one plane containing all the axes of the ommatidia contributing to the image point. Such a ray path is three-dimensionally possible if it is valid for each plane containing the axis of the central ommatidium, in other words, it is possible if a ray is always reflected in that plane which is formed by the ray and the axis of the central ommatidium. (The axis of the central ommatidium connects the object point and its image.) This condition would be fullfilled if the reflecting surfaces were concentric envelopes of cones around the axis of the central ommatidium. An eye in which such an arrangement of mirror surfaces was materially realized, could of course look only into one direction and would have to scan the optical environ-

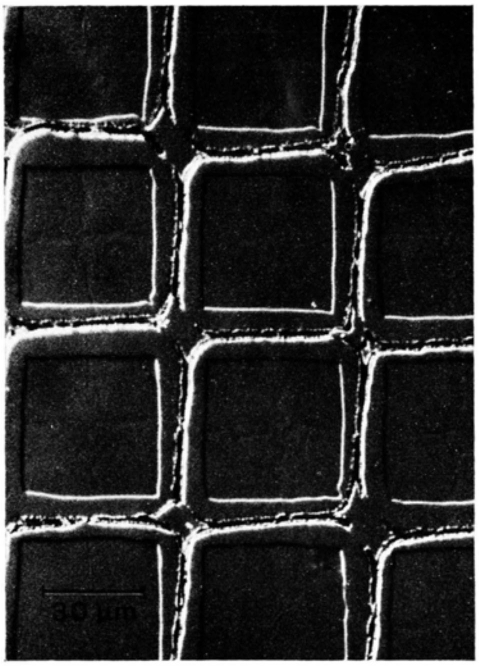

Fig. 1. Crayfish eye, tangential section through the distal part of the crystalline cones, interference contrast. The sides of the cones form angles of 90°. The distal multilayer is visible as white bands between the cones.

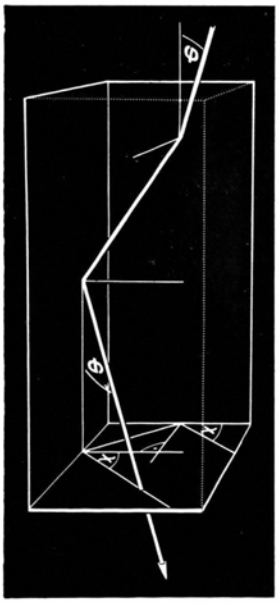

Fig. 2. Schematic drawing of a ray path in a crystalline cone. φ is the angle between the incident as well as the emergent ray and the axial direction of the cone. In a tangential plane, here the bottom plate, the projections of the ray and the perpendiculars in the reflection points are drawn. The angle χ, drawn between the hind edge and the projection of the incident ray is equal to the angle between the projection of the emergent ray and the projection of the second perpendicular of incidence.

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ment. In the crayfish eye a three-dimensional solution is possible without this handicap.

For a three-dimensional solution, the essential condition is that the sides of the crystalline cones are planes which form an angle of 90°. This is true in the crayfish eye (Fig. 1), the crystalline "cones" are regular four-sided pyramides with small top angles.

We define an incident ray by the angle φ with the direction of the axis of an ommatidium, and the angle χ between the ray's projection on the tangential plane of the ommatidium and a basal edge of the pyramid. After two reflections, the emergent ray has the same angle χ as the incident ray (Fig. 2). For any angle χ the ray seems to be reflected (apart from a small parallel displacement) by a plane, the virtual mirror plane, which is perpendicular to the plane formed by the ray and the axis of the central ommatidium. The optical structure of a crayfish eye can be described in this way by a concentric family of virtual reflecting envelopes of cones around each direction in space [2]. The families pertaining to the different directions in space intersect each other freely because they are virtual.

A necessary condition for imaging is that a ray leaves a crystalline cone after a limited number of reflections, two in the general case $\chi \neq 0$, or one in the case $\chi = 0$. (The second reflection may take place either in the same cone or in one of the neighbouring cones.) If only distal mirrors existed, a considerable part of the rays with small φ would reach the retina directly or after one instead of two reflections and thus spoil the image formation.

For most rays the former condition is fullfilled if in the proximal part of the crystalline cone the

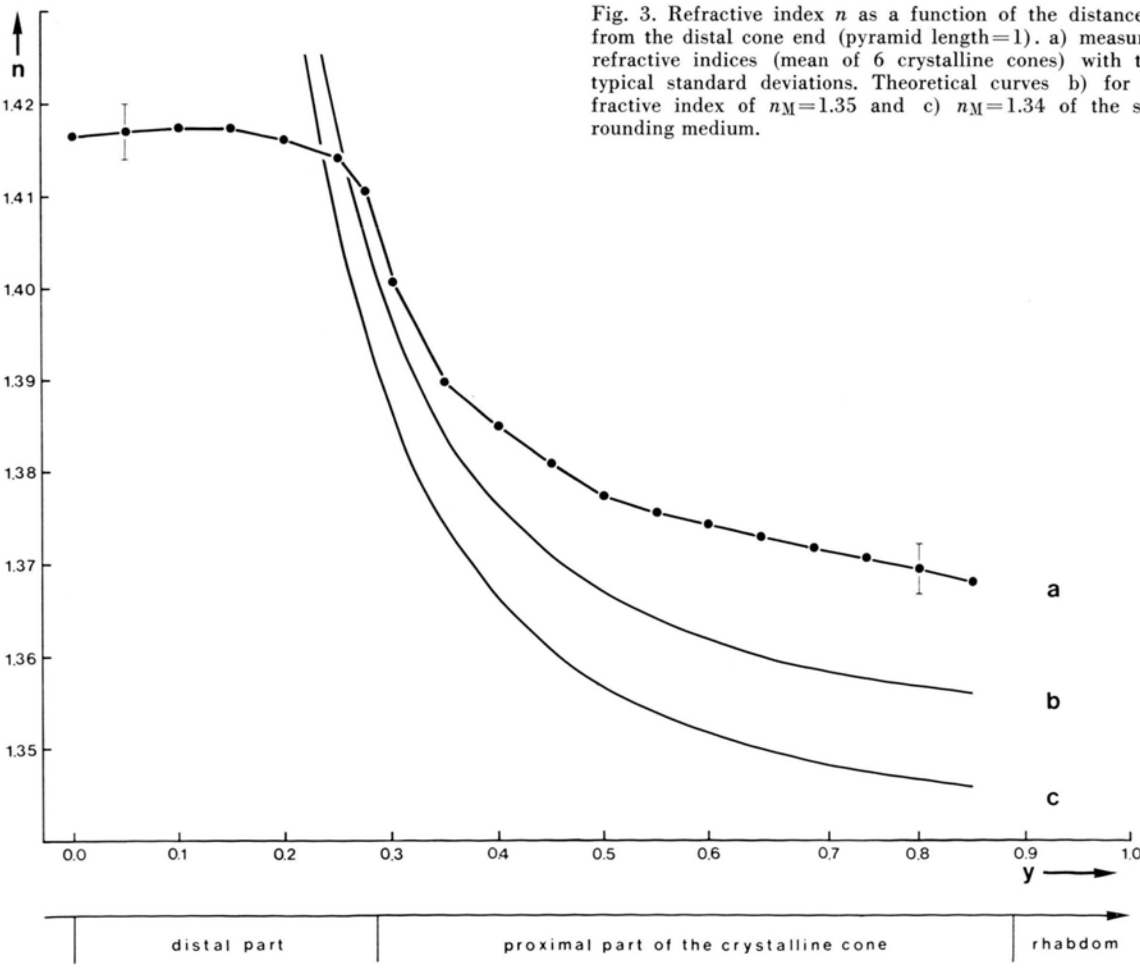

Fig. 3. Refractive index n as a function of the distance y from the distal cone end (pyramid length = 1). a) measured refractive indices (mean of 6 crystalline cones) with two typical standard deviations. Theoretical curves b) for refractive index of $n_M = 1.35$ and c) $n_M = 1.34$ of the surrounding medium.

refractive index decreases axially according to the function

$$n_y = n_M \left[1 + \left(\frac{\sin \delta}{y + \cos \delta - 1} \right)^2 \right]^{\frac{1}{2}} ;$$

whereby n_y is the refractive index depending on y, and y is the distance from the distal end of the crystalline cone divided by the length of the pyramid. n_M is the refractive index of the surrounding medium and δ is the angle between the opposite sides of the crystalline cone (better crystalline pyramid).

This function is derived on the assumption that rays within the crystalline cone propagate linearly. This approximation is possible because a ray tracing based on the refractive indices of that function for the proximal part of the crystalline cone leads again to essentially the same function.

Fig. 3 shows this function calculated for a pyramid angle $\delta = 4.5°$ for two values of the external refractive index and the measured distribution of refractive index within the cone (mean of 6 crystalline cones). Because the measurements were made with glutaraldehyde fixed material the refractive indices are somewhat high. The shape of the measured curve is in the proximal part quite similar to a theoretical one, whereas in the distal part it remains constant. On the border between the proximal and the distal part the theoretical curves take values which can not be realized in the crystalline cone. Therefore, if rays with $\varphi > \arccos n_M/n_{\text{distal}}$ (for $\chi = 0$) should contribute to the image a second reflection mechanism is necessary in the distal part which is not based on total internal reflection.

This mechanism is a multilayer reflector parallel to the sides of the crystalline cones which is composed of three to four layers of crystals. Although there are only few layers, the reflectance is high because of the great angles of incidence on the layer. If the layers are isolated together with crystalline cones they show interference colours as also observed by Land [3]. The interference colours depend on the angle and the direction of polarisation of the incident light. The latter results from the high negative uniaxial double refraction of the crystals. The optic axis is parallel to the ommatidium axis. Fig. 4 is a polarisation microscope image showing the radially arranged distal birefringent multilayers and the retina. Fig. 5 is an electron microscope picture of a thick section through a distal pigment cell showing three rows of the multilayer crystals. A detailed treatment of this imaging system will be given elsewhere.

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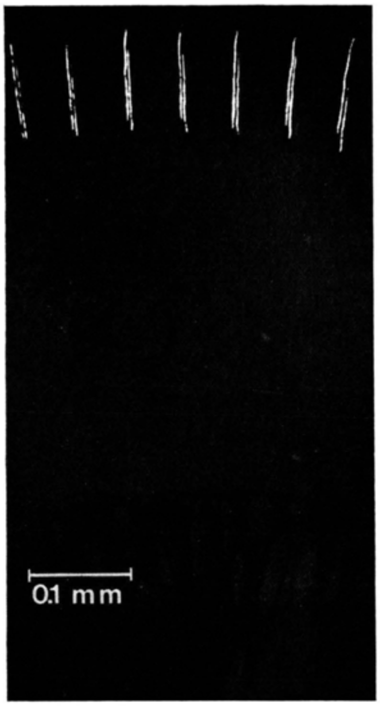

Fig. 4. Polarisation microscope image of a radial section through a crayfish eye showing the distal birefringent multilayers and the retina.

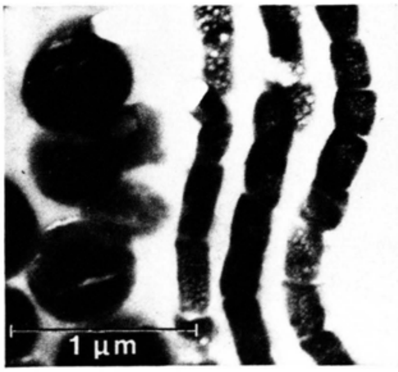

Fig. 5. Electron microscope image of a thick section from a distal pigment cell showing three layers of crystals bordered by some pigment granules.

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[2] K. Vogt, Z. Naturforsch. **30 c**, 691 [1975].
[3] M. Land, Nature **263**, 764–765 [1976].