

## XII. PHYSICAL OPTICS OF INVERTEBRATE EYES\*

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#### A. INTERFERENCE FILTERS IN THE CORNEAS OF DIPTERA

Many Dipteran compound eyes, especially the Tabanids (such as horseflies and deerflies), show colored reflection patterns when illuminated with white light. For instance, the female *Hybomitra lasiophthalma* compound eye, when viewed from the same direction as the illumination, shows a striped pattern consisting of five blue (B) stripes and four orange (O) stripes. There are additional thin red stripes at the boundaries between the

orange and blue. With increasing angles of illumination the blue stripes become first violet and finally red; the orange stripes become yellow, green, and finally blue; and the red stripes become orange and finally yellow. The striped pattern consists of specular reflections originating from a small locally flat part of each facet. Figure XII-1 is a photograph of such a cornea showing the reflection pattern described above.

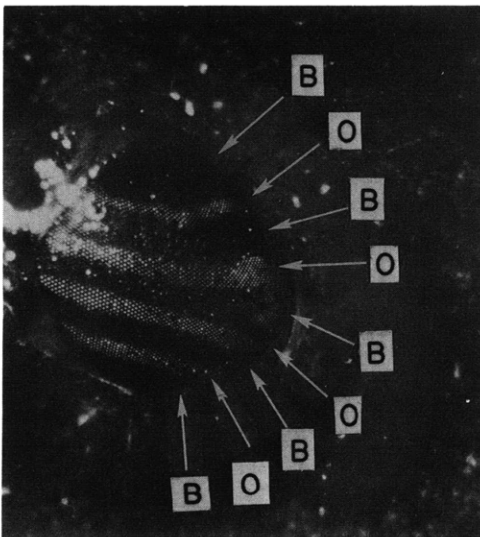


Fig. XII-1.

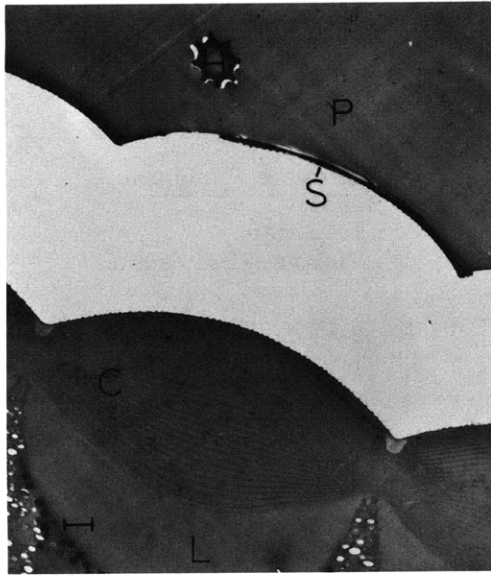
Isolated cornea of the right compound eye of a female *lasiophthalma*, showing blue stripes (B) and orange stripes (O) separated by thin red stripes.

We have studied the structure of the corneas of a number of Diptera, using the electron microscope. Figure XII-2a is an electron micrograph of a section taken normal to the corneal surface, showing the corneal structure of the wild-type *drosophila*. This is an example of a Dipteran cornea that does not show

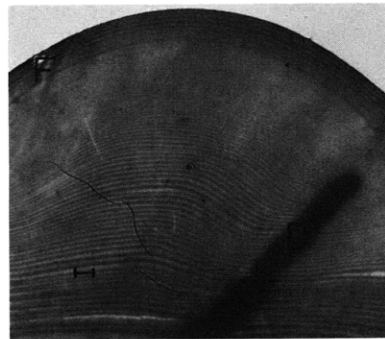
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(a)



(b)

Fig. XII-2. Electron micrographs of (a) drosophila cornea, and (b) lasiophthalma cornea of an O-facet. H, hair; P, embedding medium pulled away from corneal surface; S, subsurface nipple layer that has been pulled away from the cornea by embedding medium; C, cornea; L, crystalline cone; F, specialized layer system; D, dense region probably serving to optically isolate facets from each other. Magnification marker, 10  $\mu$ .

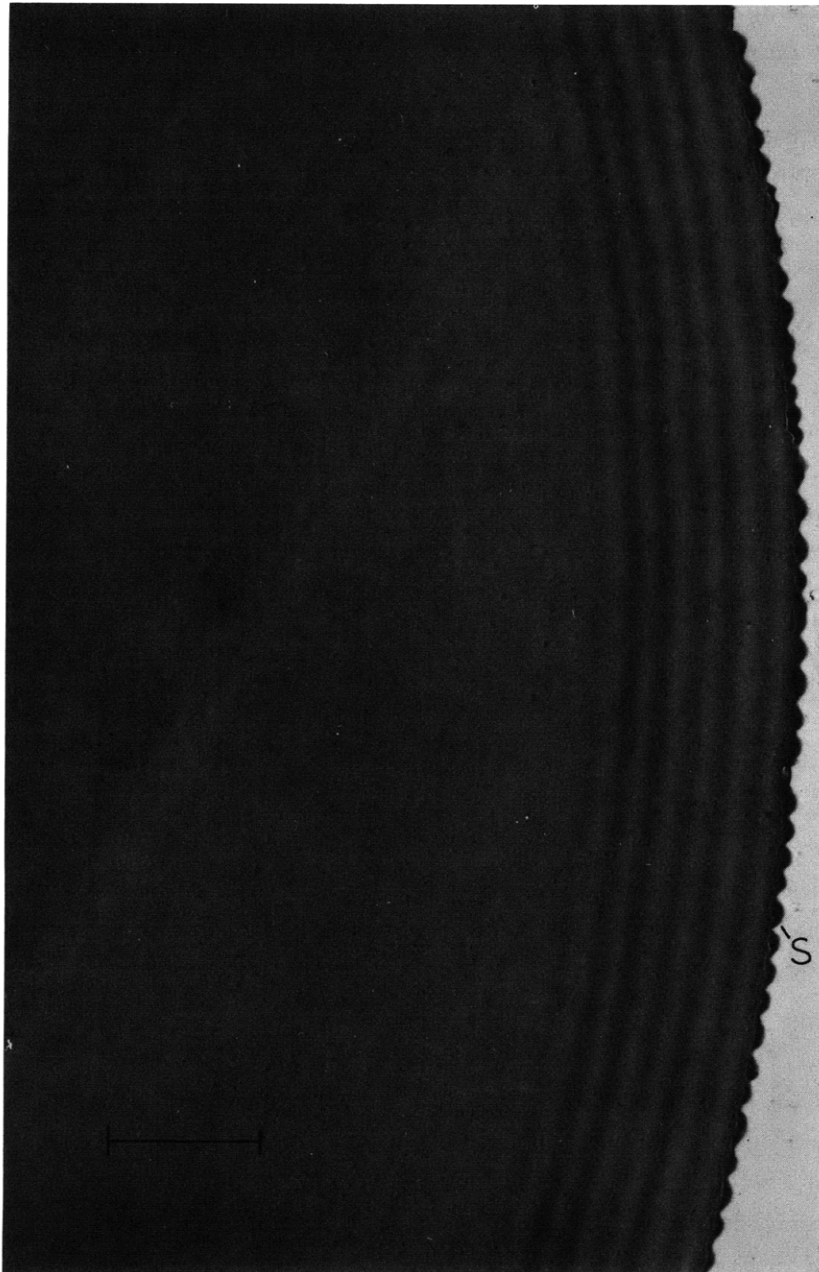


Fig. XII-3. Electron micrograph of lasiophthalma O-facet. S, subsurface nipple layer. Magnification marker, 1  $\mu$ .

## (XII. PHYSICAL OPTICS OF INVERTEBRATE EYES)

colored reflections. The cornea (C) contains fine layers that cannot be resolved by using optical microscopy. At the air-corneal interface is a layer of subsurface nipples<sup>1</sup> (S) which in this photograph has been pulled away from the cornea by the embedding medium (P).

Compare this with Fig. XII-2b which is a similar micrograph, but of an orange facet of the female Hybomitra lasiophthalma. This cornea also contains layering similar to that in drosophila, but in addition contains a specialized system of alternating dense and rare layers (F) located just beneath the front corneal surface.

This specialized system of layers (F of Fig. XII-2a) is shown at higher magnification in Fig. XII-3. In this O-facet there are six dense layers approximately 84 m $\mu$  thick, and six rare layers approximately 110 m $\mu$  thick. It should be noted that there is a seventh dense layer that is not nearly as dense as the other six.

The B-facets located in the top and bottom blue stripes contain only three dense layers and three rare layers, whereas the B-facets in the remaining blue stripes contain six dense layers and six rare layers. The dense layers are approximately 60 m $\mu$  thick, and the rare layers approximately 100 m $\mu$  thick. The results we present here for number and thickness of layers are preliminary.

We suspect that these specialized rare layers are composed, for the most part, of water, since in death the colors gradually disappear but can be restored by placing the animal in a moisture chamber or simply by depositing liquid on the cornea. The liquid need not necessarily be water, but the time required to restore the colors to full brilliance is greater for liquids of higher molecular weight.

The reflection coefficient of such systems of layers, assumed to be planar, with refractive indices of 1.33 for each rare layer and 1.75 for each dense layer, was calculated as a function of incident angle, wavelength, and polarization. The calculations show these systems to be interference filters composed of quarter-wavelength layers. The behavior of reflection coefficients as a function of incident angle and wavelength is supported by the calculations.

It should be noted parenthetically that the reflection patterns observed in Dipteran eyes with colors actually contain two components. Superimposed upon the colored reflection pattern described above is another pattern<sup>2</sup> generated by the subsurface nipples (S in Fig. XII-3).

Work now in progress includes detailed comparison of measurements with the mathematical model, and physiological studies to determine the biological function of this interference filter system.

The authors are indebted to Professor Laverne Pechuman of Cornell University for furnishing us with Tabanids, and to Leon Garretson for technical assistance with the electron microscopy.

G. D. Bernard, W. H. Miller

## (XII. PHYSICAL OPTICS OF INVERTEBRATE EYES)

### References

1. C. G. Bernhard, W. H. Miller, and A. R. Møller, "The Insect Corneal Nipple Array," *Acta Physiol. Scand. (Suppl. 243)* 63, 14, 20 (1964).
2. W. H. Miller, G. D. Bernard, and J. L. Allen, *J. Opt. Soc. Am.* 57, 576 (1967).

### B. SUPERPOSITION OPTICS – A NEW THEORY

A new theory is advanced on the functioning of the superposition type of compound eye commonly found in nocturnal insects and some other invertebrates. Unlike Exner's "superposition theory" or the diffraction image theory of Burtt and Catton, this theory explicitly takes into account the long crystalline tracts connecting the distal dioptrics (cornea and crystalline cone) to the sensory cells in the rhabdom and assumes that these tracts are the principal light paths through the eye as pointed out by de Bruin and Crisp. A simple model of the cornea and cone is used to determine the excitation of the electromagnetic field in the crystalline tract. Dielectric waveguide theory is then applied to find the resulting fields communicated to the rhabdom (sensory) region using dimensions found in the Tobacco Hornworm Moth (Manduca sexta).

The analysis indicates that while the tract is not capable of transmitting an "image" in the usual sense, there is usable information in the cross-section distribution of energy (the "mode" patterns) in the rhabdom. For illumination by a single spot of light, the information present is a vernier indication of the plane of and the magnitude of the incident angle with respect to the axis of the ommatidial cornea and cone. It is also observed that the rhabdomeres are of about the right number and placement to analyze such information. Thus, we speculate that the outputs of the several rhabdomeres are processed in two ways: (i) the outputs are added to give a measure of the total incident intensity to contribute to a "mosaic" image formation with other ommatidia, and (ii) the multiple outputs are compared with one another to give indication of small changes in the angular distribution of background light by analysis of the mode patterns in the crystalline tract.

#### 1. Background

The so-called superposition type of compound eye found in most nocturnal insects and many other invertebrates consists of a large number of individual eyelets (ommatidia) whose morphology is essentially as indicated in Fig. XII-4. (The dimensions quoted throughout this report are from our examination of the Tobacco Hornworm Moth, Manduca sexta. The dimensions seem to be qualitatively typical of most superposition eyes on medium-to-large moths.) The ommatidia are arranged on an approximately spherical surface. The sphere diameter and ommatidial diameter are such that the axes

(XII. PHYSICAL OPTICS OF INVERTEBRATE EYES)

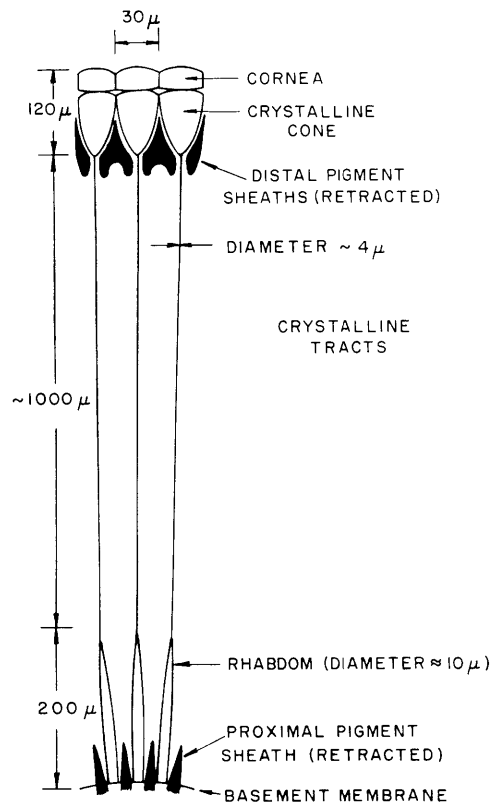


Fig. XII-4.

Ommatidia of superposition eye. Dimensions are from studies of the Tobacco Hornworm Moth. ( $\mu = 10^{-6}$  m.)

of adjacent ommatidia differ in direction by approximately  $1^\circ$  (the interommatidial angle). The optical path consists of the cornea, crystalline cone, crystalline tract and the rhabdom (sensory-cell region).

The essentials of the rhabdom cross section of the night moth *Erebus*<sup>1</sup> are indicated schematically in Fig. XII-5. The rhabdom typically consists of 7 or 8 individual sensory cells called "rhabdomeres." A portion of the cross section of each rhabdomere is composed of closely packed microtubules with axes mutually perpendicular to the ommatidial axes to the adjacent cell wall.<sup>1-4</sup> Each cell has a single synaptic connection. We assume this structure to be typical of superposition rhabdoms.

The earliest theory on the functioning of the superposition eye, and the one from which the name is taken, is due to Exner.<sup>5</sup> He stated that the cornea-cone combination functions as a lens cylinder with length equal to twice its focal length, thereby producing an upright image with the paraxial ray emerging from the lens at the negative of the incident angle. An array of such lens cylinders on the surface of a sphere would focus an image by superposition at the half-radius of the sphere, as indicated schematically in Fig. XII-6. The pigment migration would control the intensity of the image by limiting the number of lens cylinders contributing to any image.

More recently, Burt and Catton<sup>6</sup> have suggested that the superposition eye makes use of the higher order diffraction images one would expect if the eye is modeled as a series of regularly spaced pinholes separated by many wavelengths. If the intervening crystalline tracts and pigment sheaths are ignored and curvature neglected, such an array would produce alternating light and dark spots at several distances behind the array from a single incident plane wave.

Both of the foregoing theories ignore the presence of the crystalline tract. De Bruin and Crisp<sup>7</sup> have pointed out, however, that since the tract index of refractions is higher than that of the surrounding media, the light should tend to be trapped in and guided by the tracts. It would seem questionable, then, to neglect their presence in formulating

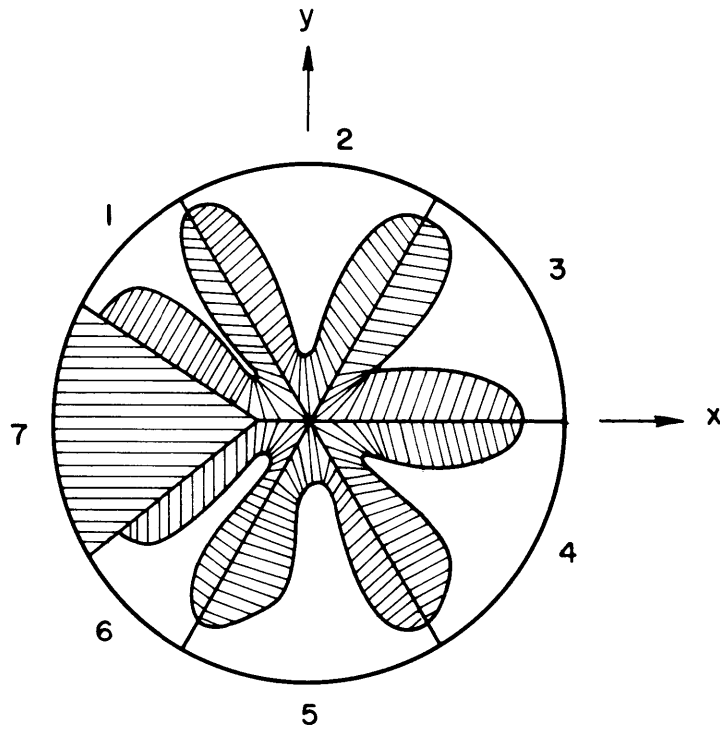


Fig. XII-5. Illustration of *Erebus* rhabdom structure (after Fernandes-Moran).

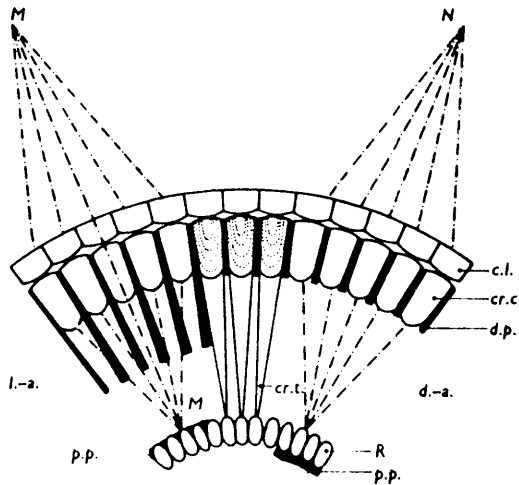


Fig. XII-6

Diagram of the light rays in the superposition eye. The position of the distal pigment d.p. and the proximal pigment p.p. is shown in the light-adapted state (l.-a.), and the dark-adapted state (d.-a.). In the three central ommatidia the crystalline tracts (cr. t.) are drawn. M and N are two light sources, and R is the rhabdom.

[From J. W. Kuiper, *Symp. Soc. Exptl. Biol.*, Vol. 16 (1962), pp. 58-71, Fig. 9. Reproduced with the permission of The Company of Biologists Limited, Cambridge, England.]

## (XII. PHYSICAL OPTICS OF INVERTEBRATE EYES)

any theory of the functioning of such eyes. We have therefore been led to an examination of the capacity of such tracts for transmitting optical information, and the results of this examination have suggested a new explanation for the functioning of the superposition eye.

### 2. Synopsis of the Theory

We seek an explanation for the operation of the superposition ommatidium which is consistent with its structure, as we understand it at present, and the basic principles of electromagnetic theory. We have evolved such an explanation which we shall summarize briefly.

It has long been known<sup>8</sup> that electromagnetic fields could be guided by dielectric rods and that the allowed field solutions far from the source of the excitation consisted of a finite series of "modes," each with a characteristic field distribution in cross section and a characteristic phase velocity, dependent upon the wavelength of the excitation. Such mode patterns have indeed been observed and studied in fine glass rods,<sup>9-11</sup> and even in vertebrate light receptors,<sup>12, 13</sup> in which they have been studied as a possible color discrimination mechanism. The number of allowed modes depends upon the rod diameter in wavelengths and the difference in index of refraction between the rod and its surround. For the 4- $\mu$  ( $\sim 10\lambda$ ) radius of interest here, more than 20 modes are possible.

The "low-order" modes vary only slowly across or around the rod, whereas the high-order modes have rapid spatial variation. For rods with radii small as compared with a wavelength, only the lowest order mode can propagate; for large radii more modes can propagate. Thus, one might casually assume that a multiplicity of available modes would make it possible to convey an "image" down such a rod, at least to a degree of detail limited by the highest allowed mode. In rods that are long with respect to their width, but whose width is only moderately large with respect to wavelength, however, the different modes propagate with sufficiently different velocity so that the "picture" would become quite jumbled as it traversed the wave guide.

Hence, no "image" in the usual sense of the word is transferred by the tract from the cone to the rhabdom.

On the other hand, the complexity of the rhabdom structure of Fig. XII-5 is suggestive of a greater sensory capability than that required to only give a single response proportional to the total light intensity in the ommatidium, as held by Muller's "mosaic theory."<sup>14</sup> The complexity could be associated with polarization and/or color discrimination. The lack of a uniform orientation of the microtubules in each rhabdomere of such moths (as contrasted with their uniform orientation in bees and Diptera) seems to rule out the possibility that the different rhabdomeres are specialized on a polarization basis. It then seems unlikely that the insect would require 7 discriminators solely for



## (XII. PHYSICAL OPTICS OF INVERTEBRATE EYES)

any color discrimination it might possess.

Consequently, it appears necessary to look further for an explanation for the multiplicity of rhabdomeres. The peripheral arrangement of six of them (numbers 1-6 in Fig. XII-5) strongly suggests that they may be arranged to analyze the distribution of the light intensity across the cross section of the rhabdom. Since the crystalline tract makes a smooth transition into the rhabdom, such an analysis would be tantamount to analyzing the distribution of light in the tract. The fact that the rhabdomeres are "optically fused"<sup>15</sup> (i. e. , the microtubules of adjacent rhabdomeres are separated only by a membrane that is thin compared with a wavelength of light) in no way precludes such analysis by the rhabdomeres, as long as they have independent neural responses.

To determine whether there could be useful information in the outputs of rhabdomeres, which are localized in different regions of the light path, we have carried out a rigorous analysis of a simplified electromagnetic model of an ommatidium. The principal simplification was to neglect the dependence of all quantities on one of the two cross-section dimensions. This makes the mathematics much more tractable, while yielding, at least, qualitative results. The details of the analysis are being incorporated in an internal memorandum.

From the results of the analysis, we are led to offer the following theory of operation, which we choose to call the "waveguide mode theory of the superposition eye." The principal tenets of the theory follow.

1. Although the tract can support many modes, only a very few are strongly excited, at least for incident angles up to the interommatidial angle of  $1^\circ$ . This is a consequence of the large Airy disc produced by the cornea and cone, because of the long focal length.<sup>16</sup> In red light, the disc is of such a diameter as to almost fill the tract, while in blue light it has almost half the tract diameter. The center of the disc moves with the angle that the light source makes with the ommatidial axis. When the light is on-axis, the disc is centered on the tract, and only the modes with even symmetry are excited. The intensity distribution of the lowest order even mode is shown in Fig. XII-7a. As the disc is moved off center in some plane (e. g., the plane containing the ommatidial axis and the x-axis of Fig. XII-7b), combinations of modes producing a field having an odd symmetry in that plane will be excited. The strength of excitation of the odd distribution will increase in proportion to the angular displacement of the source, while the even-mode excitation decreases.

2. Each excited-mode pattern propagates down the tract at its particular velocity, which depends on the wavelength, guide dimensions, and the indices of refraction. We assume the tract to be lossless. Since only the low-order modes are excited, which are very nearly of zero intensity near the edges of the rod, their propagation will be little influenced by small irregularities (slow changes in tract diameter, gradual bends). If the surrounding is lossless (dark-adapted eye), the modes will propagate unattenuated.

(XII. PHYSICAL OPTICS OF INVERTEBRATE EYES)

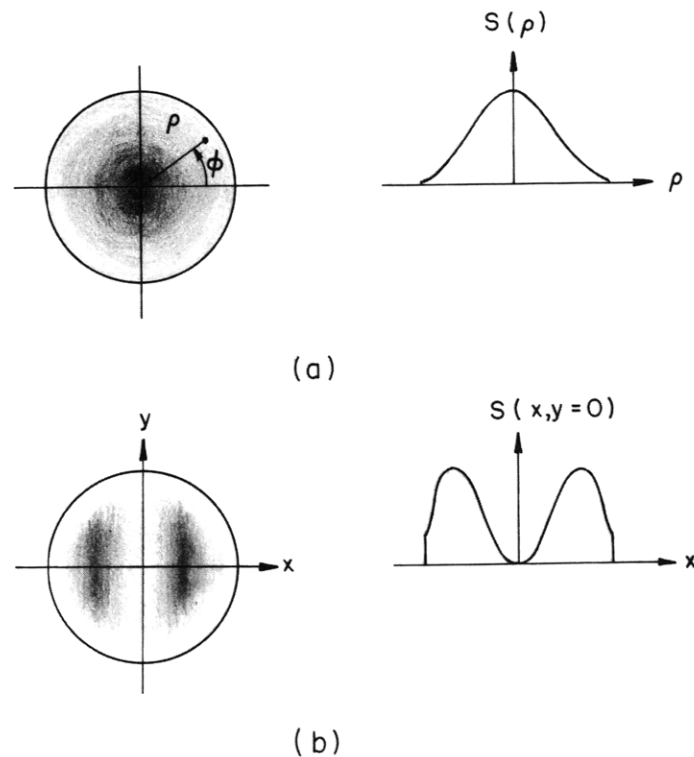


Fig. XII-7. Power density in low-order modes in cylindrical waveguide. (a) Power density distribution  $S(\rho, \phi)$  for lowest order ( $HE_{11}$ ) mode. (b) Power density in lowest order pattern having odd symmetry in transverse fields about the  $y$ -axis ( $S$  is proportional to the field squared). Superposition of  $TE_{01}$ - $HE_{21}$  (after Snitzer and Osterberg<sup>10</sup>).

It is assumed that the tract flares smoothly and slowly into the rhabdom without changing the relative mode excitation.

3. Owing to their slightly differing phase velocities and the long electrical length of the tract, the different modes that were excited at the input with a certain phase relationship will in most cases have undergone several cycles of differential phase shift by the time they reach the rhabdom. (There are some exceptions to this statement, in that some of the modes have almost identical phase velocities. This is the case for the two modes superimposed in Fig. XII-7b, for example.) The resulting phase difference will be different for different wavelengths. For polychromatic light, under the assumption that the insect responds over a bandwidth of at least 10 per cent, the "smearing" of the phase difference between modes at the input and output is complete, and there will be no average (with respect to wavelength) crosscorrelation between modes. That is, the energy contained in any cross-section area of the rhabdomere will be just the sum of the energies in each mode in that region. If we assume that the synaptic response of

(XII. PHYSICAL OPTICS OF INVERTEBRATE EYES)

the rhabdomere is a monotonic function of the field intensity therein, the  $n^{\text{th}}$  rhabdomere of Fig. XII-5 will give an output proportional to the intensity of all modes integrated over the active region of that rhabdomere; i. e. , the rhabdomeres can function as mode analyzers to determine which modes were excited at the tract input. To summarize, we find that (a) On-axis illumination will cause essentially equal excitation of all rhabdomeres, and (b) If the direction of the source is moved off axis in the plane containing the ommatidial axis and the x-axis of the figures, the energy in the even mode (Fig. XII-7a) will be reduced and that in the odd modes (Fig. XII-7b) increased from zero. We would qualitatively expect the outputs from rhabdomeres 2 and 5 of Fig. XII-5 to decrease and those of 3, 4, 1, and 6 to increase. Thus, a comparison (e. g. , ratio) of the rhabdomere outputs could establish that there had been a movement of the source in the x-direction and what the magnitude of the movement was (but not the direction of motion; i. e. , +x or -x). As we shall show, changes in angle much smaller than the interommatidial angle should be detectable if the intensity is sufficient. This statement concerns only accuracy of angular measurement. No enhancement of resolution is implied.

4. We then speculate that the output of the rhabdomeres might be processed as follows: (a) The outputs of all rhabdomeres<sup>15</sup> are weighted and added, or perhaps the output of the odd rhabdomere is used to form an image in the mosaic manner. Our

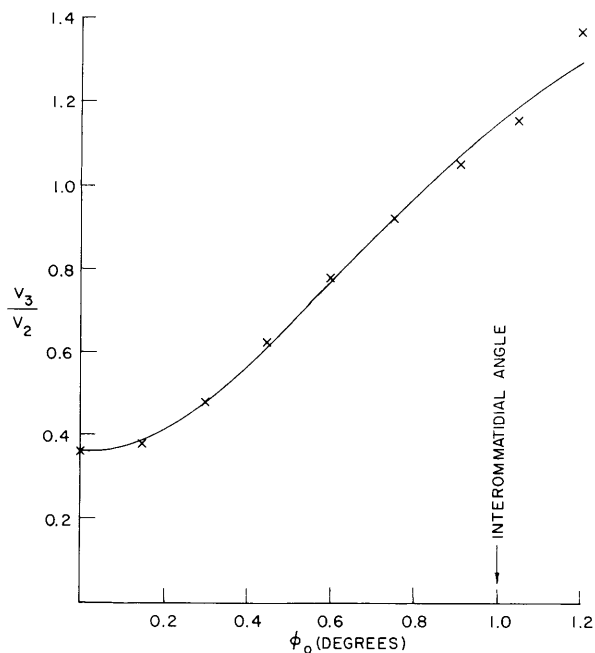


Fig. XII-8. Ratio of energy in outer rhabdomere to that in central rhabdomere vs incident angle for the assumed model.

## (XII. PHYSICAL OPTICS OF INVERTEBRATE EYES)

motivation for the latter speculation is the appearance of the odd rhabdomere, its identical location in different rhabdoms over large regions of the compound eye and the observation of Hanström<sup>17</sup> that the synaptic connection from this cell is different from those of the other rhabdomeres. (b) The remaining 6 outputs are compared (e. g., by taking ratios) to establish their relative excitations from which the direction of the "center of intensity" of the scene viewed by that ommatidium is inferred. The ratio of the output of rhabdomeres 3 and 2 in Fig. XII-5 (denoted  $v_3/v_2$ ) is of the general nature of the curve of Fig. XII-8 for source displacement through an angle  $\theta$  parallel to the x-axis of Fig. XII-5. The curve is the quantitative prediction of the two-dimensional model for a particular set of parameters. It is included here only as indicative of the form of the result. It is apparent that changes in incident angle of a fraction of an interommatidial angle cause a significant change in the ratio of the rhabdomere outputs.

### 3. Effect of Pigment Sheaths in the Light-Adapted State

With the eye in the light-adapted state, the pigment sheaths extend over a portion of the length of the crystalline tract and rhabdom, thereby resulting in a reduction of light intensity in the rhabdom compared with that entering the crystalline tract.<sup>18</sup> For this reason Kuiper<sup>15</sup> refers to the crystalline tract-pigment system as a "longitudinal pupil." We agree with this, but do not agree with his suggested explanation for the effect. Kuiper suggests that "... The refractive index of this pigment is rather high. When this pigment makes contact with the tract it reduces internal reflection and therefore the transmission of the tract ..."

We feel that the physical mechanism of the "longitudinal pupil" is the following: The crucial fact is not that the pigment granules are of high index of refraction but that they are lossy, meaning that the index of refraction of the granules is complex and that the granules support conduction currents. Each mode supported by the crystalline tract has a nonzero value of electric field at the outer radius of the tract, and decays exponentially into the surrounding medium. Therefore, the pigment granules close to the tract are immersed in the electric fields of the modes, creating conduction currents in the granules which, in turn, convert a portion of the light energy of the modes into heat energy in the pigment granules.

Höglund<sup>18</sup> shows that attenuation rates down the pigment-coated tract are of the order of 0.1 db/micron. This is a small attenuation rate; thus, we can treat the effect of the pigment as a perturbation on the dark-adapted situation, and the result is that each mode simply attenuates exponentially as it propagates down the tract and otherwise behaves exactly the same as in the dark-adapted state.

In the light-adapted state each mode attenuates at its own rate as it propagates down the pigment-coated crystalline tract, with the higher order modes attenuating at a greater rate than the lower order modes. The reason for this is that the higher order

modes have a greater field amplitude at the tract boundary and decay more slowly into the surrounding medium. Since it has been estimated<sup>18</sup> that the light-adapted eye has a sensitivity loss of at least 30 db, the high-order modes are attenuated to insignificance as compared with the low-order modes. Thus our theory predicts that the eye should transmit more information in the dark-adapted state than in the light-adapted state.

Similarly, the proximal pigment in the light-adapted position causes attenuation of the modes in the rhabdom. This means that only a distal portion of the rhabdom is effectively stimulated when in the light-adapted state.

#### 4. Discussion of Results and Future Work

Some experimental observations will be attempted to check the validity of the theory. The most direct experimental test of the theory is to examine the distribution of light in the tracts and rhabdom areas of fresh excised insect eyes by microscopy in a manner similar to Enoch's<sup>12</sup> experiments on vertebrates. To be able to directly observe the modes, we plan to assemble apparatus permitting observation in monochromatic, polarized, as well as white, unpolarized light. Although the existence of the modes in the waveguides is well established, such an experiment seems necessary to confirm that the effects of the cornea, cone, and surround of the dark-adapted eye have been adequately modeled.

A number of less direct experiments also suggest themselves. Two behavioral experiments that would partially check the validity of the model are the following.

1. Test the alertness of the insect to small movements under both light- and dark-adapted conditions and with various light levels. The theory predicts maximum alertness when dark-adapted, but reasonably illuminated (e. g., similar to the condition on a moonlit night, perhaps).

2. Observe the insects' behavior in monochromatic light. The mode crosscorrelations "washed out" by the assumed small but finite spectral spread would be restored and the insect might be confused by this situation.

We plan to devote most of our research in the immediate future to two efforts: (i) the experiment outlined above attempting to directly observe modes in an excised eye, and (ii) the mathematical analysis of a more realistic three-dimensional model of the ommatidium with a circular symmetry.

J. L. Allen, G. D. Bernard

#### References

1. H. Fernandes-Moran, "Fine Structure of the Light Receptors in the Compound Eyes of Insects," *Exptl. Cell Res. Suppl.* 5, 586-644 (1958).
2. Wm. H. Miller, "Morphology of the Compound Eye of Limulus," *J. Biophys. Biochem. Cytol.* 3, 421-428 (1957).

(XII. PHYSICAL OPTICS OF INVERTEBRATE EYES)

3. T. H. Goldsmith and D. E. Philpott, "The Microstructure of the Compound Eye of Insects," *J. Biophys. Biochem. Cytol.* 3, 429-440 (1957).
4. G. Yasuzumi and N. Deguchi, "Submicroscopic Structure of the Compound Eye as Revealed by the Electron Microscope," *J. Ultrastruct. Res.* 1, 259-270 (1958).
5. S. Exner, Die Physiologie der facettieren Augen von Krebsen und Insekten (Franz Deuticke, Vienna, 1891).
6. E. T. Burt and W. T. Catton, "The Resolving Power of the Compound Eye," *Symp. Soc. Exptl. Biol.* 16, 72-85 (1962).
7. G. H. P. de Bruin and D. T. Crisp, "The Influence of Pigment Migration on the Vision of Higher Crustacea," *J. Exptl. Biol.* 34, 447-463 (1957).
8. D. Hondros and P. Debye, *Ann. Physik* 32, 465 (1910).
9. E. Snitzer, "Cylindrical Dielectric Waveguide Modes," *J. Opt. Soc. Am.* 51, 491-498 (1961).
10. E. Snitzer and H. Osterberg, "Observed Dielectric Waveguide Modes in the Visible Spectrum," *J. Opt. Soc. Am.* 51, 499-505 (1961).
11. N. S. Kapany and J. J. Burke, "Fiber Optics. IX. Waveguide Effects," *J. Opt. Soc. Am.* 51, 1067-1078 (1961).
12. J. M. Enoch, "Optical Properties of the Retinal Receptors," *J. Opt. Soc. Am.* 53, 71-85 (1963).
13. A. W. Snyder, "Excitation of Surface Modes along a Semi-infinite Dielectric Cylinder," *Electronics Letters*, September 1965.
14. J. Muller, "Zur vergleichenden Physiologie des Gesichtsinnes des Menschen und Tiere" (Cnobloch, Leipzig, 1826).
15. J. W. Kuiper, "The Optics of the Compound Eye," *Society of Experimental Biology Symposium* 16, pp. 58-71, 1962.
16. J. L. Allen, Quarterly Progress Report No. 85, Research Laboratory of Electronics, M. I. T., April 15, 1967, pp. 69-70.
17. B. Hanström, *Z. Verg. Physiol.* 6, 566-597 (1927).
18. G. Höglund, "Pigment Migration and Retinular Sensitivity," in The Functional Organization of the Compound Eye, C. G. Bernhard (ed.) (Pergamon Press, London, 1966), pp. 77-101.