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# Polarization Sensitivity of Individual Retinula Cells

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*Summary.* This paper elucidates the influence of the structure of a rhabdom on the polarization sensitivity of its retinula cells. The terminology polarization sensitivity (PS) and dichroic sensitivity ($\Delta$) needs clarification. $\Delta$ expresses the directional property of the local microvillar medium and is independent of the gross morphology of the rhabdom. The PS of a retinula cell is that found by single cell electrophysiology and depends strongly on the gross morphology of the rhabdom. Both $\Delta$ and PS are ratios of the effects of the $\boldsymbol{E}$ vector of linear polarized light parallel to, to that perpendicular to the microvilli. From the theoretical analysis and its correlation with experiments the following is concluded.

*Retinula Cells of Diptera.* 1. The longer a dipteran rhabdomere or the greater the concentration of photopigment within it, (a) the lower the PS of the retinula cell, (b) the greater the absolute sensitivity and (c) the broader or flatter the spectral sensitivity curves. Only when the absolute sensitivity of a dipteran retinula cell is low can its PS be high (Fig. 2). Thus retinula cells 1–6 of Diptera have a high absolute sensitivity but a low PS.

2. Due to waveguide effects, (a) the smaller the diameter of the rhabdom the greater the PS and (b) off-axis illumination of the rhabdomere leads to a greater PS than on axis illumination.

3. Because rhabdomeres 7 and 8 are shorter and have a smaller diameter than 1–6, they have a larger PS. Furthermore, rhabdomere 7 is distal to rhabdomere 8 and acts like a polarization filter increasing the PS of 8. Theoretically the PS of retinula cell 8 can be as large as 5. Thus retinula cells 7 and 8 have a lower absolute sensitivity but higher PS than 1–6.

4. The correlation of theory with experiment suggests that $\Delta$ is greater than 3.

*Retinula Cells with Crustacean Like Rhabdoms.* 1. The PS of each retinula cell is independent of the absolute sensitivity and identical to $\Delta$. This high theoretical PS is a consequence of the layered rhabdom with interdigitating orthogonal microvilli. Thus each retinula cell of the crustacean type rhabdom has a high absolute sensitivity as well as a high PS.

2. Since the PS $\equiv \Delta$, single cell electrophysiology provides direct information about $\Delta$ and its dependence on wavelength.

3. It is concluded that $\Delta \geqq 10$. Microspectrophotometric determination of $\Delta$ is shown to be misleading because glutaraldehyde fixation probably alters the alignment of the chromophore within the microvillar membrane.

*Retinula Cells of Fused Rhabdoms when the Microvilli Are Uniform Along Its Length* (e.g. ant and bee). 1. The PS depends acutely on the arrangement, cross sectional area, PS and spectral sensitivity of all the rhabdomeres and can vary

from a value much less than $\Delta$ to a value greater than $\Delta$. Examples are given in the text.

2. The criterion for a large PS is that the light absorbed by the entire rhabdom due to the $\boldsymbol{E}$ vector parallel to the microvilli of the measured retinula cell must equal the light absorbed by the entire rhabdom due to the $\boldsymbol{E}$ vector perpendicular to the microvilli of the measured cell. When this condition is satisfied $\mathrm{PS} \equiv \Delta$ just as in the crustacean rhabdom. This puts a constraint on the parameters and arrangement of the other retinula cells. Both the worker and drone bee fail the criterion, consistent with poor single cell PS measurements. However, an example is given of a fused rhabdom with an enormous PS which appears to satisfy the criterion.

3. It is shown that if the rhabdomeres of the UV cells are only a very small fraction of the total rhabdom's cross sectional area, as may be the case with the ant *Formica polyctena*, then the UV PS is very large but with low absolute sensitivity.

*Ninth Retinula Cell.* In the proximal portion of the ant and bee a 9'th retinula cell is formed. The 9'th cell bears the same relationship in its length to total rhabdom length as rhabdomere 8 in Diptera. Thus we predict that the 9'th cell has a greater PS but lower absolute sensitivity than cells 1–8.

*Partitioned or Tiered Rhabdoms* (e.g. damsel fly). We conclude that the functional significance of this type of rhabdom is to enhance the PS of the retinula cells at a loss of absolute sensitivity in addition to altering the spectral sensitivity of the more proximal cells due to colour filtering effects of the distal rhabdomeres.

*Functional Advantages of Fused Rhabdom Structures.* We conclude that the most significant advantage of a fused rhabdom is for hue discrimination in a small field of view (fine grain colour vision) because several spectral cell types together in a rhabdom can look at one point in space. A functional consequence of the crustacean (layered) type of rhabdom is a high PS *at low light intensities*. This offers a distinct adaptive advantage both to aquatic animals that live on the sea floor where the light intensity is greatly reduced and to animale that are active in moonlight.

## I. Introduction

Behavioral evidence has shown that invertebrates, in particular numerous arthropods and mollusks, are sensitive to the direction of the electric vector ($\boldsymbol{E}$) of linearly polarized light (see the table of Waterman, 1966).

All these animals have a light absorbing organelle known as the rhabdomere. The rhabdomere is made up of an array of microvilli (tubules) formed as outfoldings of the retinula cell membrane and is presumed to contain the visual photopigment.

The fact that absorption by a rhabdomere is sensitive to the direction of the $\boldsymbol{E}$ vector of linearly polarized light has been demonstrated electrophysiologically by intracellular retinula cell recordings (e.g. Autrum and von Zwehl, 1962; Shaw, 1969a, b; Waterman and Fernández, 1970). This directional sensitivity is related to the orientation of the microvilli (Langer, 1965; Langer and Thorell, 1966; Eguchi and Waterman, 1968). Rhabdomeres 1–6 in the fly *Calliphora* absorb maximally when the $\boldsymbol{E}$ vector is parallel to their microvilli; however, rhab-