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Structure and Function of the Fused Rhabdom

Allan W. Snyder
Institute of Advanced Studies, Research School of Physical Sciences

Randolf Menzel and Simon B. Laughlin
Department of Neurobiology, Research School of Biological Sciences
Australian National University, Canberra

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Summary. This paper considers the functional significance of fused rhabdoms. Since all rhabdomeres are joined tightly together, the possibility of optical and electrical coupling between retinula cells is greatly enhanced. We study the extent and consequences of this coupling in order to understand the functional significance of fused rhabdoms. Our methods include both theory and intracellular recordings. The results are as follows:

Optical Coupling. Because rhabdomeres of different spectral types are fused into a common light guide, the absorption properties of each influence the manner in which light is transmitted along the composite rhabdom structure.

1. Each rhabdomere acts as if it were an absorption filter in front of all others, i.e. rhabdomeres function as lateral absorption filters (Fig. 4).

2. As a consequence of this filtering, the shape of the spectral sensitivity curve for each retinula cell is approximately independent of the amount of light it absorbs, i.e. independent of the rhabdomere's length and concentration of photopigment (Fig. 7). This is in direct contrast to the retinula cells of fly that have spectral sensitivity curves which become progressively flatter as more light is absorbed (Snyder and Pask, 1973). In other words, the flattening of curves by self absorption is prevented by optical coupling.

3. *Thus, one functional advantage of the fused rhabdom (due to optical coupling) is that each retinula cell can have a high absolute sensitivity while preserving its spectral identity (narrow spectral sensitivity curves). (Compare Fig. 5 to Fig. 6.)* Thus the same receptors can operate in a high sensitivity and in a colour vision system (cf. vertebrate rods and cones). *Since all spectral cell types are together in one rhabdom, the animal can have hue discrimination in a small field of view (fine grain colour vision). Thus an individual ommatidium has the potential for providing excellent spectral discrimination.*

4. If two cells have photopigments with absorption maxima close together, the maxima of their spectral sensitivity curves are moved further apart (Fig. 8).

5. In the absence of electrical coupling polarization sensitivity (PS) can depend dramatically on wavelength. The spectral composition of the rhabdom, in addition to the direction of the microvilli, profoundly influences the polarization sensitivity vs. wavelength PS(λ) curves of individual retinula cells. This is shown theoretically for the worker bee rhabdom (Fig. 10) where (a) there is a pronounced difference in PS(λ) between cells with orthogonal microvilli and (b) green retinula cells show a large PS in the green while the UV cells show a much smaller PS in the UV (Fig. 13).

6. In the absence of electrical coupling, PS(λ) measurements are a highly sensitive indicator of the rhabdom's spectral composition and thus provide a test for the validity of proposed receptor spectral types and arrangements.

Electrical Coupling. Shaw (1969a) has presented definitive evidence that electrical coupling exists between retinula cells of the *drone* bee and that it is the primary cause for the measured low PS. We conclude that there is also strong coupling between retinula cells of the *worker* bee because:

1. The PS of green retinula cells is theoretically high in the absence of electrical coupling (Fig. 13), yet our intracellular recordings show it to be negligible (Fig. 15). This result is interpreted as strong coupling between green cells with orthogonal microvilli.

2. Many of our spectral sensitivity intracellular recordings have double peaks (Figs. 14, 16, 17). Three classes of peaks were found, positioned in a manner consistent with direct coupling of cells of three different spectral types. We present compelling reasons to believe that the double peaks are *not* caused by the electrode penetrating more than one cell.

3. In dragonflies, retinula cells' PS depends on wavelength and shows both optical and electrical coupling.

4. Electrical coupling has functional advantages: (a) it removes the ambiguity between identical spectral cell types with orthogonal microvilli and (b) it decreases the upper frequency components of low intensity signals by summing quantum bumps in the retina. Because axons are low pass filters, this increases the transmission efficiency to the lamina. The advantages of the possible dynamic relationships between electrical coupling and light intensity are discussed in the text.

Structure and Function of the Fused Rhabdom. We conclude that the accurate alignment of pigment molecules, the arrangement of densely packed parallel microvilli within a rhabdomere and the symmetrical orientation of microvilli within a fused rhabdom are adaptations to maximise absolute sensitivity. PS is only a *secondary* consequence (a by-product) of these factors and is destroyed by electrical coupling. The crustacean laminated type of rhabdom, the 'ninth' cell of the bee, and certain tiered rhabdoms, are adaptations for the *specific* purpose of detecting polarized light.

In summary, the fused rhabdom cannot be considered as a loose collection of photoreceptors, sharing the same dioptric apparatus. It must be viewed as an integrated unit. The evolution of the fused rhabdom is a significant advance in the evolution of arthropod visual systems. It allows high absolute sensitivity to be combined with color vision and acuity.

A. Introduction

In the majority of invertebrate and vertebrate photoreceptors the photosensitive pigment is arranged within the receptor cell in a column of higher refractive index than the surrounding medium. This column of photopigment functions as a light guide, or more precisely as a dielectric waveguide (Snyder, 1973b), so that light is confined within the photoreceptor where it is absorbed by the photopigment and transduced to receptor potential. Thus the physical properties of the photoreceptor: its diameter, length, refractive indices, arrangement and orientation of photopigment, have a profound effect upon the sensitivity of the receptor (for examples see Snyder, 1973a, b; Snyder and Pask, 1973). In the vast