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Polarization Sensitivity

A Phenomenon Independent of Stimulus Intensity or State of Adaptation in Retinular Cells of the Crabs *Carcinus* and *Callinectes*

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Summary. Polarization sensitivity of photoreceptors of the crabs *Carcinus* and *Callinectes* were measured with intracellular microelectrodes in the dark adapted condition with stimuli of very low intensity and under conditions of selective polarized adaptation. A mean polarization sensitivity ratio of 4.5 to one ($n = 25$) was obtained. The values ranged from 3.2 to one to 9 to one. The value obtained in any given cell was independent of either (a) the intensity of the stimuli employed in its determination, or (b) any conditions of selective adaptation present during the experiment.

The results of these experiments are discussed in reference to two hypothetical explanations for the discrepancy between microspectrophotometric measurements of rhabdomeric dichroism and electrophysiological determinations of polarization sensitivity in crustacean photoreceptors. They do not support the hypothesis of Muller (1971, 1973) that the high polarization sensitivity measured in such photoreceptors is due to a passive interaction between the retinular cells which serves to enhance polarization sensitivity imparted by the dichroism of the rhabdom. They do support the hypothesis of Shaw (1966, 1969) and Snyder (1973) which suggest that the dichroic ratio of the rhabdomere and the polarization sensitivity ratio of the cell are similar *in situ*.

Introduction

One of the many interesting features of retinular cells, the primary photoreceptor found in the compound eye of arthropods, is their ability to discriminate the orientation of plane polarized light. These cells are organized into units (ommatidia) which share a common dioptric apparatus, a common photoreceptor organelle or rhabdom (diptera and some hemiptera excluded), and send separate axons to the central nervous system. The fused rhabdom is a composite of rhabdomeres, which are in turn tubular modifications (microvilli) of the constituent retinular cells. In spite of this fused rhabdom, the retinular cells maintain some degree of functional independence in their spectral sensitivity (Gribakin, 1969; Mote and Goldsmith, 1971; Bulter, 1971), axial migration of screening

pigments (Ludolph, Pagnanelli and Mote, 1973), and polarized light sensitivity (Muller, 1971, 1973).

The ability of a retinular cell to discriminate the orientation of plane polarized light has been shown to be related to the microvillar structure of the rhabdomere (Waterman *et al.*, 1969; Hays and Goldsmith, 1969). In this work the absorption of plane polarized light was microspectrophotometrically determined in portions of isolated rhabdoms of the crayfish *Orconectes* and the brachyuran crab *Libinia*. Absorption of light whose e-vector was parallel to the microvillar axis was found to be twice the absorption measured when the e-vector was orthogonal to that axis yielding a dichroic ratio of 2. This is consistent with the model that the chromophores are randomly oriented with respect to the microvillar axis (either fixed or free to rotate) and that the fine structure of the rhabdomere allows it to function as an analyzer of polarized light.

The ommatidium of decapod crustaceans is ideally suited to function as an analyzer of polarized light because of the geometrical relation of the cells within it. These cells fall into two classes based upon the orientation of their microvilli. The cells of one class share a common microvillar axis which is orthogonal to that shared by the cells of the other class (Eguchi and Waterman, 1968).

Electrophysiological measurements of polarization sensitivity (PS) in such photoreceptors have confirmed the geometrical relation of the cell classes but have also resulted in a paradoxical situation (Shaw, 1966, 1969; Waterman and Fernandez, 1970; Muller, 1971, 1973; Mote, 1972). The PS ratios measured intracellularly in several species of crustacea are commonly 4, and can be as high as 12. Shaw (1966) concluded that such ratios would be obtained if the chromophore orientation were preferentially aligned along the microvillar axis. This is in accord with conclusions based on theoretical analysis of the optical properties of fused rhabdoms presented by Snyder (1973).

Muller (1971, 1973) has proposed an alternative explanation to the discrepancy. His hypothesis supposes a dichroic ratio of near 2 in the rhabdom and explains the apparent enhancement to a larger PS ratio by a passive interaction *between* photoreceptors sharing a common rhabdom. The essence of this argument is that strongly excited cells will generate more light induced current and hence create a larger negative voltage (measured as the e.r.g. with an extracellular electrode) across extracellular current paths than do weakly excited cells. This voltage effectively reduces the total depolarization measured across the membrane of the weakly stimulated cell and increases the difference between the two classes.

Such a hypothesis can be tested if the responsiveness of the two groups of cells can be independently varied. Independent changes in the