Z. vergl. Physiologie 68, 154—174 (1970)

E-Vector and Wavelength Discrimination by Retinular Cells of the Crayfish *Procambarus**

TALBOT H. WATERMAN and HECTOR R. FERNÁNDEZ
Department of Biology, Yale University, New Haven, Connecticut, U.S.A.

Received March 6, 1970

Summary. 1. Receptor potentials have been recorded intracellularly from single retinular cells in the anterior and dorsal quadrants of the compound eye of the crayfish *Procambarus* (Fig. 1) stimulated with equal quantum flashes of linearly polarized monochromatic light. Comparisons between two orthogonal stimulus *e*-vectors respectively parallel and perpendicular to the microvilli of each receptor cell's rhabdomere were made sequentially in about one minute's running time at 20 nm intervals between 400 and 740 nm (Fig. 2).

2. Of the 91 cells studied 17 responded maximally in the violet (av. $\lambda_{max} =$ 440 nm) whereas the other 74 cells were most responsive in the yellow-orange (av. $\lambda_{max} = 594$ nm) (Table 1). For the latter group the λ_{max} of individual cells ranged widely from 538 to 634 nm (Fig. 4). Violet sensitive cells were found only in the anterior quadrant of the eye.

3. For 29 cells spectral sensitivity curves were plotted from the spectral efficiency curves using response-energy functions determined at λ_{max} or spectral efficiency curves taken at two or more stimulus energy levels (Figs. 5B, 6B, 7). When the sensitivity curves are normalized the vertical and horizontal *e*-vector responses are closely similar indicating that dichroism of the visual pigment is undoubtedly responsible for the observed differential sensitivity (Figs. 5C, 6C).

4. For 51 yellow-orange cells where *e*-vector comparisons can be made more than half (57%) were more responsive to vertical *e*-vector (Table 2) corresponding very closely with the estimated percentage of retinular cells with microvilli parallel to the body's dorso-ventral axis (57.2%). In contrast five of the seven violet cells available for this comparison gave stronger responses to horizontal *e*-vector suggesting they may predominantly be the one asymmetrical cell in each ommatidium. Nevertheless both color discriminating types were found to be present in both *e*-vector channels.

5. For the 29 cells for which spectral sensitivity curves can be plotted the average sensitivity ratio for the two polarization planes is 3.1 with a range from 1.2 to 11.9 at λ_{max}. Since dichroic absorption ratios directly measured in crayfish have previously been shown to be about 2, the origin of greater spectral sensitivity ratios in individual retinular cells most likely must depend on other functions than photon absorption by a single rhabdomere.

---

* These experiments were carried out in the Laboratory of Professor Tsuneo Tomita, Department of Physiology, Keio University School of Medicine. A preliminary report on this work was made at the December, 1969 meeting of the American Society of Zoologists.

Introduction

Despite widespread study at many levels (Bernhard, 1966) our understanding of arthropod vision remains fragmented and incomplete even for repeatedly investigated forms like crayfish. For instance we still cannot say much about the way in which various stimulus parameters like *e*-vector orientation and wavelength are channeled and ultimately utilized in regulating behavioral output. Intracellular recordings in insects demonstrated some time ago that individual retinular cells of compound eyes are sensitive to changes in *e*-vector orientation of a linearly polarized stimulus (Kuwabara and Naka, 1959; Burkhardt and Wendler, 1960; Autrum and von Zwehl, 1962; Giulio, 1963). More recently in the green crab *Carcinus* this technique disclosed two types of retinular cells with their major *e*-vector sensitivities at right angles (Shaw, 1966, 1969b).

Another series of studies proves directly that these two orthogonal visual input channels in decapod crustaceans are correlated with rhabdom fine structure as well as dichroism of the visual pigment and are in fact present in each ommatidium (Waterman and Horch, 1966; Eguchi and Waterman, 1968; Hays and Goldsmith, 1969; Waterman, Fernández and Goldsmith, 1969). Differential *e*-vector sensitivity within a single ommatidium has also been reported in the insects *Calliphora* (Langer, 1965, 1966; Langer and Thorell, 1966a, b) and *Locusta* (Shaw, 1967).

With relation to wavelength discrimination we know in general that at least two categories of receptor cells tuned to different frequencies of electromagnetic radiation are required. More specifically, selective adaptation of the electroretinogram (ERG) in a number of crustaceans (detailed below), optomotor responses in *Carcinus* (Horridge, 1967) and intracellular recordings from single retinular cells in *Procambarus* (Nosaki, 1969) have demonstrated two categories of receptor elements in the species concerned, one maximally sensitive to yellow-orange wavelengths, the other to blue-violet (or in one case to near UV).

So far there is no direct evidence in crustaceans whether the two or more types of wavelength discriminating units occur within a single ommatidium or in different ommatidia. Nor are the relations known between the wavelength discriminating cells and the two orthogonal *e*-vector channels. Consequently the present experiments were designed to examine these relationships for their relevance to further understanding the mechanism of polarized light perception and its relation to the broader problem of information processing in visual pathways like the crustacean eyestalk.

This report specifically describes the intracellularly recorded response of upwards of 90 retinular cells of *Procambarus* when both wavelength