The Photoreceptor Cells

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1. Introduction

Insect photoreceptor cells are usually slender, cylindrical, and aggregated into various species-specific combinations beneath the corneal lens of a compound eye, ocellus, or larval stemmata. Individual cells are so sensitive to light that some are able to signal catches of a single photon (e.g., Lillywhite, 1977). This exquisite sensitivity is founded on the presence of an incompletely characterized glycoprotein (rhodopsin). Rhodopsin is the functional molecule of the photoreceptor cell, and is the major constituent of the plasma membrane of the rhabdomeric microvilli. This photopigment-containing organelle (rhabdomere) is found in the distal region of the cell (Section 5). In its more proximal reaches, the cell becomes a functional neuron with an axon (Section 7) conveying graded depolarizations to chemical and electrical synapses (Section 8).

Because of the dichotomy of structure and function in these two parts of the photoreceptor cell, it is now suspected or becoming apparent that each requires a different ionic microenvironment. To that end, crucial partitions are present (effected by membrane specializations) which form a complex barrier system between the retina and the first optic neuropil (Section 7). This is a story that is just beginning to unfold.

Because of all of this beautifully adapted ultrastructure, photoreceptor cells have the miraculous ability to transduce light energy from the environment into electrical energy meaningful to the central nervous system (CNS). Thus, the visual system reconstructs such elements of the photic environment as wavelength (UV to red), electric vector, light intensity shifts, and other temporal...
and spatial features. If the resulting retinal mosaic is coarse and unfocused by vertebrate standards, other attributes of the image are sufficient to make vision a key factor in the survival of this preeminent group of animals.

An important part of our total understanding of insect vision comes from the knowledge of the photoreceptor cell’s ultrastructure and its intermembranal relationship with its glial neighbors. (A detailed account of these glial cells can be found in Chapter 12 of this volume.)

Our goal in the present chapter is to explore the fine structural features of insect photoreceptor cells and briefly to relate these, where possible, to function. For the purpose of our discussion, the photoreceptor cell will be divided into three parts: receptor (soma), axon, and synaptic terminal. We will concentrate on the photoreceptor cells of the compound eye of Diptera and there is a ready rationale for this specialization. Diptera possess the best understood of all insect eyes and it is the one that we are the most familiar with. Further, the fly eye is a functional composite or hybrid of an apposition eye and a superposition eye. The best optical features of both types of eye are present in the fly; thus, its “neural superposition” eye (Kirschfeld, 1967) operates efficiently during the fly’s diurnal and nocturnal forays and enhances both sensitivity and acuity.

2. **Historical Record**

The compound eyes of many insects are among their most obvious external features. It is not clear when man first intuitively understood that the two multifaceted hemispheres on the insect head were eyes. Late in the 17th century, van Leeuwenhoek had observed the corneal lens of a beetle under his glass lenses and found “that each lenslet forms a reduced inverted image located in the eye close to the cornea” (cited in Bernhard, 1966). With the help of better glass lenses, insect eyes were soon being dissected and sketched. In 1737-1738, Swammerdam (see Bernhard, 1966) provided useful depictions of the excised honeybee eye. But it was not until the 19th century that two landmark concepts of insect optics were developed, the issues and implications of which are still being studied. In 1826, Johannes Müller put forth the mosaic theory of insect vision which was modified and expanded for clear-zone eyes by Exner in 1891.

From visual function the torch was passed to structure and in 1909 the great neuroanatomist, Ramón y Cajal, published a histological treatise on the comparative anatomy of the retinas, one of which was the optic neuropil of the housefly. Using the technique of his contemporary and scientific adversary (Camillo Golgi), Ramón y Cajal clearly visualized photoreceptor cells, many kinds of visual interneurons and their accompanying glial cells. The neuronal inventory in insect eyes was further expanded upon by Ramón y Cajal and Sanchez (1915). During the same period (1910-1913), von Frisch began to obtain evidence that honeybees possessed color vision, and by 1927 Kühn had found that bees could distinguish the UV from other spectral areas. However, it was not until 1949 that von Frisch showed that honeybee vision encompassed polarization sensitivity. For a far greater wealth of historical detail on insect