Nonconventional Interactions between Photoreceptor Axons in the Butterfly Lamina Ganglionaris

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Butterflies have nine photoreceptors within each ommatidium which have been named from their positional orientation across the rhabdom. Within all ommatidia examined, there are four morphologically discrete receptor types: 1. Two dorsal-ventrally aligned cells – the vertical receptors; 2. two anterior-posteriorly aligned cells – the horizontal receptors; 3. four diagonally aligned cells – the diagonal receptors; 4. one basally occuring bilobed cell – the basal receptor. The nine retinula cell axons pass through the basement membrane and enter an optic cartridge of the lamina ganglionaris as a single bundle. The organization of these axons within their cartridge has been investigated in the nymphalid-type butterfly *Agraulis vanillae.* Prior to entry into the optic cartridge, the axonal bundle undergoes a 90° positional rotation. Retinula axons become grouped into three regions: a dorsal triad and a ventral triad of three axons, one horizontal and two diagonal retinula cells each; a central group composed of two vertical retinula cells, the basal cell, and 4–5 lamina monopolar cells. Retinula axons of the triads appear to be coupled by bulbous cytoplasmic projections. Two types of coupling appear to occur: 1. Within each triad, the horizontal retinula cell axon is coupled to both diagonal axons. 2. The horizontal retinula cell axon of one triad is coupled to the horizontal cell of the adjacent triad. Because of the 90° repositioning of the ommatidial axon bundle, specific cell types from one ommatidium appear to be linked to retinula cells of ommatidia immediately above or below them. These nonconventional receptor cell interactions are described and a possible function in receptor coupling suggested.

Insect compound eyes are composed of many ommatidia generally arranged in hexagonal arrays. In the nymphalid-type butterfly, *Agraulis vanillae,* the nine photoreceptors within each ommatidium are defined by their ultrastructure and positional orientation across the rhabdom [1]. There are two dorsal-ventrally aligned cells (vertical retinula cells), two anterior-posteriorly aligned receptors (horizontal retinula cells), four diagonally arranged cells (diagonal retinula cells), and one bilobed basally occuring cell (basal retinula cell). The nine photoreceptor axons from each ommatidium pass through the basement membrane and into the lamina ganglionaris as a discrete bundle. Each group of nine receptor axons combine with 4–5 lamina monopolar neurons to form an optic cartridge [2]. The four photoreceptor

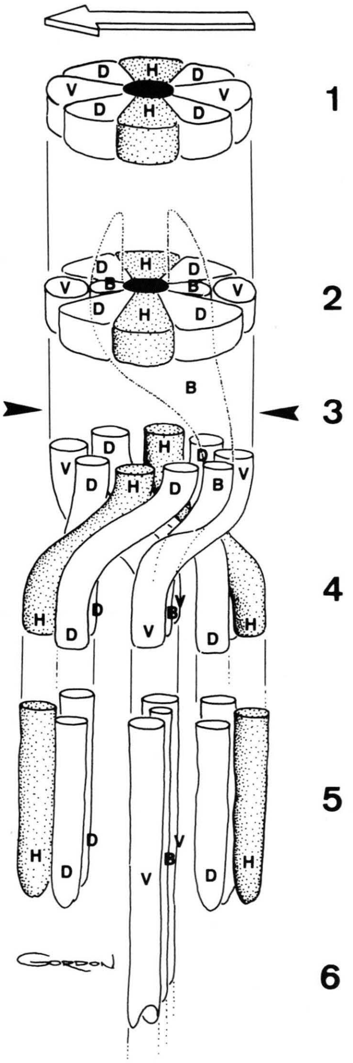

Fig. 1. A schematic representation of photoreceptor axons showing their 90° repositioning prior to entry into their lamina optic cartridge, and their final orientation within the structure of the cartridge. Dorsal is indicated to the left (large white arrow at top) to emphasize the dorsal-ventral rearrangement of the horizontally aligned retinula cells. Lamina monopolar cells have been left out to facilitate visualization of the receptor axonal component of the cartridge. V, vertical retinula cells; H, horizontal retinula cells; D, diagonal retinula cells; B, basal retinula cell. Levels: 1, section through distal region of an ommatidium; 2, section through basal region of an ommatidium; 3, basement membrane; 4, level equal to the very top of the lamina ganglionaris optic cartridge; 5, the basal portion of the lamina optic cartridge; 6, the external chiasma.

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types from each ommatidium take up specific positions within the cartridge. This is accomplished by a 90° rotation of the axon bundle as it progresses through the zona fenestrata and the cell body layer prior to its entry into the cartridge proper (Fig. 1). This is accompanied by a separation of the receptor axons into discrete groups within the cartridge [3]. In this manner, the two horizontal retinula cell axons become aligned dorsal-ventrally across the cartridge, while the two vertical retinula cell axons are ar-

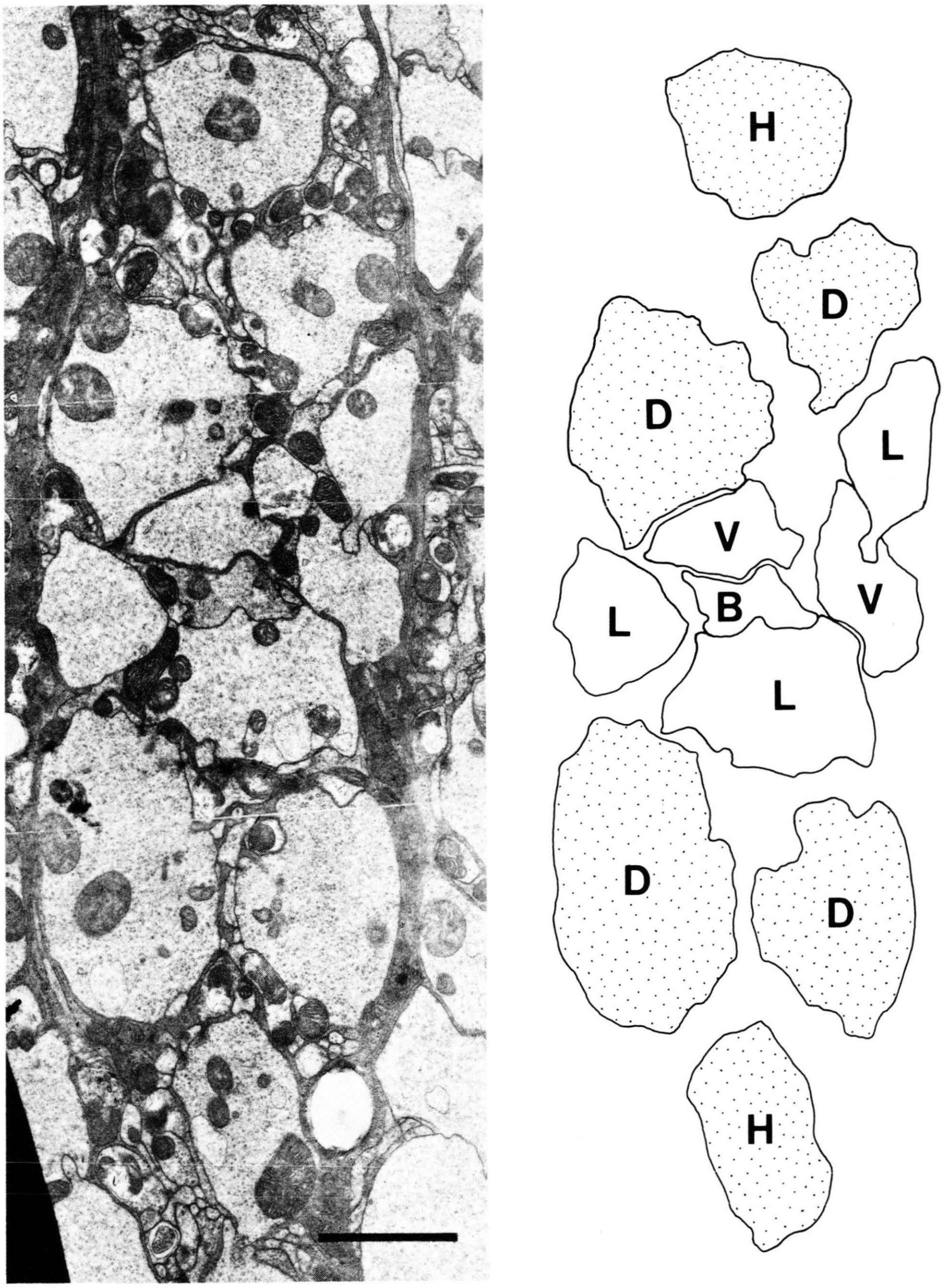

Fig. 2. Cross section through the distal region of an optic cartridge. Left: Electron micrograph illustrating the positioning of the retinula cell axons. Right: Diagramatic map of the section to left. Each triad of this cartridge (stippled cells) lies very near to a triad from an adjacent ommatidium. Dorsal is up. Scale bar; 2 μm.

ranged anterior-posteriorly. The four diagnoal receptor cell axons separate into pairs arranged between the horizontal and vertical receptor axons. The basal cell axon remains in a central position. This arrangement results in a dorsal-ventrally elongated cartridge that is morphologically divided into a dorsal (horizontal cell/diagonal cell/diagonal cell) triad, a centrally located (vertical cell/basal cell/vertical cell) complex that has 4–5 monopolar interneurons associated with it, and a ventral (horizontal cell/diagonal cell/diagonal cell) triad (Fig. 2). This physical segregation produces two functional regions within each cartridge: 1) The central complex is composed of those retinal and lamina elements that terminate in the medulla externa cartridges, while the cell axons of the triads terminate at the base of each lamina cartridge. 2) The triads of each cartridge are oriented dorsal-ventrally, bringing the horizontal axon component from one ommatidium into close proximity to a horizontal receptor cell axon from the nearest dorsal or ventral ommatidium. The cells of the central complex form a *through channel* whereas

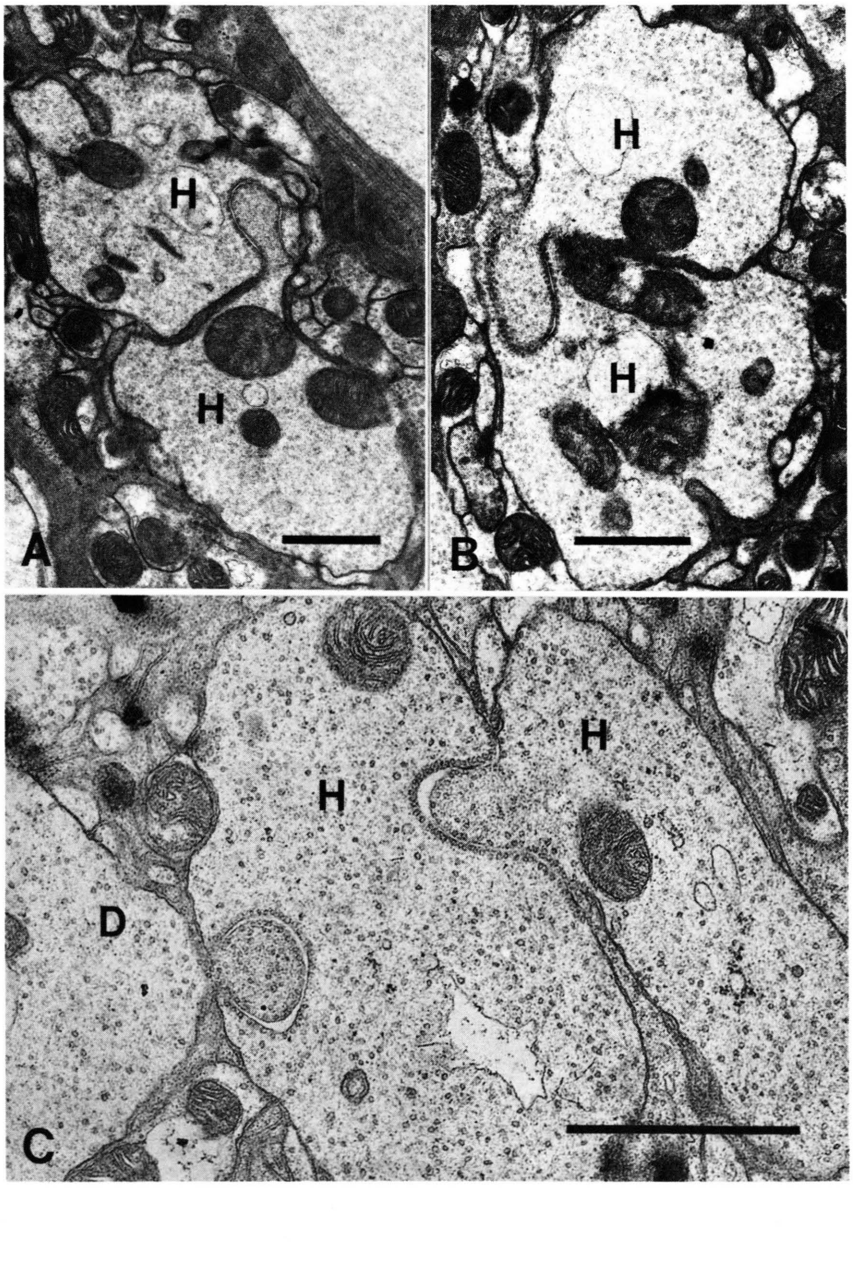

Fig. 3. Sections through the distal region of optic cartridges showing photoreceptor axonal projections. A. and B. Horizontal cell/horizontal cell interactions between two adjacent cartridges. C. Two projections (one from a diagonal retinula cell [D], one from the horizontal retinula cell [H] of an adjacent cartridge) contacting a horizontal cell axon. Scale bars; 1 μm.

the cells of the triads form a *terminal channel.* It is among the cells of the triads that nonconventional cell-to-cell interactions occur.

The receptor axons of the horizontal and diagonal cells are synaptically coupled. This coupling takes the form of fingerlike projections 0.2–0.7 µm in diameter that invaginate the adjacent receptor axons (Fig. 3). These projections are derived from both the horizontal and diagonal cells, and appear slightly bulbous in shape. Neither the membrane of the protruding cell nor the invaginated membrane demonstrate typical synaptic specializations. Within a triad, each diagonal cell is coupled to the horizontal cell, but the origin of the projection is not always constant; within the same section, in different cartridges, diagonal cell axons both supply projections to the horizontal cells as well as receive projections from them. Projections from one diagonal cell to another have not been observed. In addition to diagonal cell/horizontal cell coupling within a triad, the horizontal components are coupled between adjacent triads in such a way that a horizontal retinula cell from one ommatidium is linked to a horizontal cell from the ommatidium immediately dorsal or ventral to it. Adjacent triads thus form a group of six linked receptor axons (two horizontal cells and four diagonal cells) derived from two dorsal-ventrally adjacent ommatidia. This coupling occurs only within the first 5–10 µm of the external plexiform zone, but results in a potential linking of all ommatidia into a dorsal-ventral network composed of: 1) direct coupling of horizontal cells, and 2) indirect coupling of diagonal cells through horizontal components.

Retinula cell specializations similar to these have been described only for the dipteran “neural superposition eye” of *Musca domestica* [4]. Within the fly optic cartridge, the six short receptor axons R1–R6 are linked by extensive projections throughout the external plexiform zone. It is very tempting to speculate on a physiological function for these receptor axonal projections.

Evidence for electric coupling between receptor cells has been accumulating. Electrical coupling has been physiologically demonstrated or very strongly suggested in the drone honey bee [5], the locust [5, 6], and the ant [7] eye. Morphologically, gap junctions have been found coupling R1–R6 in the distal third of the fly cartridge [8, 9]. While there seems to be some question about the precise location and nature of these junctions in the diptera, their presence is not disputed. Recent work with the *Papilio* butterfly by Horridge *et al.* [10] and by Matič [11] also supports coupling between receptor types. As many as eight or more different spectral sensitivities have been recorded from *units* in the papilio retina [10]. Four primary photoreceptors have been described based on their peak absorptions of 380 nm, 450 nm, 550 nm, and 610 nm. Additionally, complex waveforms have been described that are positive-going in some portions of the spectrum and negative-going in others, often in a manner similar to the H1, H2, and H3 horizontal cells in the goldfish neural retina [12]. Based upon the accumulating physiological and morphological evidence, it would seem likely that the observed responses of the photoreceptor *units* result from neural coupling within the lamina optic cartridges. While the receptor axonal projections between the horizontal retinula cells and the diagonal retinula cells of the butterfly seem to offer a means through which this coupling could occur, conclusive evidence that these structures are involved still remains to be found.

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