

Mantis Shrimp Eye Structure and Function

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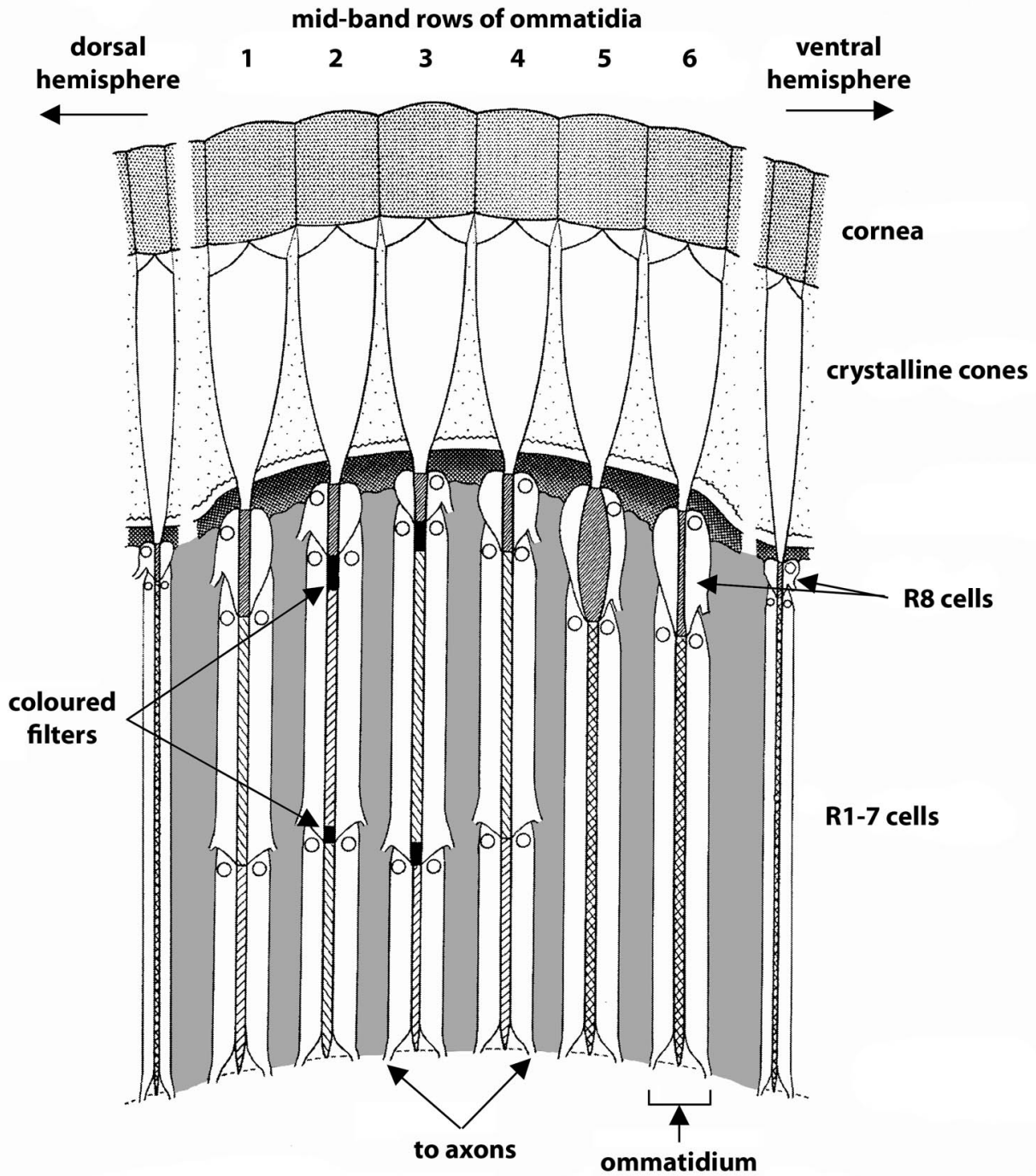
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Stomatopod crustaceans (mantis shrimps) possess an incredibly complex visual system, comprised of compound eyes that contain more types of photoreceptors than in any other known animal. The eye's optical arsenal includes monocular range finding capability, 12-channel colour vision, 2-channel linear polarization detection, and, in some species, the ability to detect and analyze circularly polarized light. Underlying this unparalleled array of functional capabilities is a structural diversification of a basic photoreceptive unit common to all compound eyes --- the ommatidium. In the following, the mantis shrimp's visual prowess is described in the context of the design variations and the distribution of its ommatidia.

Figure 1 shows the eye of the scaly-tailed mantis, *Lysiosquilla scabricauda*. It consists of upper and lower (dorsal and ventral) hemispheres separated by a narrow central band. A close examination of the eye's surface reveals that each region consists of closely-spaced parallel rows of facets --- tiny ones in the hemispheres and much larger ones in the band. The hemispheres have many rows of facets but the band has only six. Looking beneath the surface reveals that each facet is the tip of an elongate structural unit, known as an **ommatidium**. All ommatidia are optically sensitive devices, but those in the band are the most complex, most functional, and most interesting.



Figure 2 depicts a cross section of the eye showing the six rows of ommatidia in the band, flanked by rows in the dorsal and ventral hemispheres.



The various ommatidia share certain general structural features. In particular, each ommatidium consists of the following three sections, from top to bottom: (i) the cornea (ii) the crystalline cone (a hexagonal converging lens), and (iii) the **rhabdom** (rod). The rhabdom is a transparent light sensor/guide consisting of 8 photoreceptor cells --- a short cell (R8) sitting atop 7 long cells (R1, R2, ..., R7) that are fused along a central axis. Each cell has numerous interdigitating, coplanar, finger-like constructs (**microvilli**) containing light-sensitive molecules. At the bottom of each rhabdom there is a conduit (**axon**) that conveys electrical signals to **neurons**. Within the framework of these general similarities, the various ommatidia have internal structural differences that give them quite different light-sensing functionalities. These will now be described.

Ommatidia in the Hemispheres

Each ommatidium in the hemispheres is long and thin, with a rhabdom consisting of a short R8 cell on top of a ring of R1-R7 cells. There are two sets of microvilli distributed over the 8 cells. One set consists of parallel planes of coplanar microvilli, while the other set is similarly distributed in planes that are perpendicular to those of the first set. The R8 cell has both sets, but the other R1-R7 cells have one set each. This may have significance, as discussed below.

When non-polarized sunlight enters the earth's atmosphere it interacts with atmospheric molecules and is scattered (preferentially in the blue end of the spectrum) in all directions. When viewed at an angle of 90° to the incident beam, the scattered light appears **linearly polarized**, meaning that the electric vector of the light wave is along a line that is perpendicular to both the incident beam and the line of sight. The sky is therefore full of linearly polarized light. Many animal species (e.g. bees, locusts) have developed an ability to use this ambient polarization to navigate even when the sun is obscured [2].

The parallel planes of coplanar microvilli is suggestive of sensitivity to linear polarization. The aligned light-sensitive molecules of the microvilli will sense linear polarization by oscillating only in response to electric vectors vibrating parallel to the molecule's vibration axis. Perpendicular planes of microvilli should therefore detect light with perpendicular planes of polarization. In the R8 cell the presence of the two sets of perpendicular planes likely has a "null" effect --- a linearly polarized wave enters the cell, splits into two perpendicular components oscillating parallel to each plane, and the two components recombine on exit to regenerate the original linearly polarized ray. As if nothing had happened. The two sets of planes thereby **destroy** linear polarization sensitivity (LPS). However, it is not clear what happens next in the R1-R7 cells. Since each of these cells has only **one** set of parallel microvillar planes, it all depends on what the receiver of the seven independent signals does with them. It could either merge them to destroy LPS or use them to advantage. Which of these actually happens is still not known.

The long axes of the ommatidia in the first few rows adjacent to the midband are skewed slightly inwards relative to the optical axes of the ommatidia in the midband, which are perpendicular to the cornea. The ommatidia in the more distant rows have axes nearly parallel to the midband axes. It has been suggested [3] that the intersections of these skewed optical axes from opposite sides of the

midband, and hence intersections of the visual fields of these ommatidia, give rise to a **monocular range-finding** and **speed-measuring** capability. Experiments have shown that stomatopods have both monocular and binocular range-finding capability, the former being short-range and the latter long-range. Most of the ommatidia in the hemispheres, however, are parallel to each other as well as to the ommatidia in the midband, and therefore sample nearly the same narrow visual fields. No wonder mantis shrimps are constantly moving their eyes --- they have “tunnel vision”.

Ommatidia in Midband Rows 1-4

These ommatidia are much larger and more complex than those in the hemispheres. One major difference is in the structure of the rhabdoms. Instead of the R1-7 cells being arranged in a ring, they consist of two tiers of cells grouped around a central axis, with the planes of microvilli in the top tier being perpendicular to the planes in the bottom tier. In rows 1, 3, and 4 these perpendicular planes probably destroy sensitivity to linear polarization, but there is recent evidence that row 2 does have sensitivity to linear polarization [4]. This could be related to the curious fact that the tiers in rows 1, 3, and 4 consist of 4 cells above 3 three cells, but in row 2 this is reversed.

In all rows, the different tiers have different spectral sensitivities to visible light, with the upper tier always sensitive to shorter wave lengths. The rhabdoms in rows 2 and 3 are unique in having coloured filters at the boundaries between the tiers and between the top tier and the overlying R8 cell. Each row is sensitive to a specific colour: row 1 = violet, row 2 = yellow, row 3 =red, row 4 = blue. The colour sensitivities of the various tiers and filters are very narrow. The 8 tiers and 4 filters comprise an elegant 12-channel spectrum sampler that spans the range 300-720 nm, with spectral bandwidths of around 40 nm. These are among the sharpest spectral sensitivities in the animal kingdom. The bottom tier in row 3 has the longest wavelength sensitivity of any known visual system.

It is suspected that the various R8 cells in these rows have different sensitivities to ultraviolet light. In fact, stomatopods possess more UV photoreceptor types than any other animal.

Ommatidia in Midband Rows 5 and 6

The ommatidia in these rows are not tiered like those in rows 1-4. Instead, they are similar in structure to those in the hemispheres, but are much larger and have very different R8 cells.

Behavioural studies [4] have demonstrated that stomatopods have linear polarization vision, but they did not indicate which region of the eye is responsible for it. Recent electrophysiological evidence [5] indicates that midband rows 5 and 6 may be responsible. The anatomies of these ommatidia certainly support this contention:

- the large R8 cells have very well-ordered **unidirectional** microvilli
- the R1-R7 cells have very evenly-sized microvilli arranged in neat, thin, orthogonal layers of similar thickness

- the planes of microvilli in the R8 cell are oriented at an angle of 45° to **each** of the two sets of planes in R1-R7
- the R1-R7 cells send information from alternating microvillar layers to two discrete signal receivers

All of these attributes point to the existence of linear polarization sensitivity instead of its destruction. But there's more. **The ommatidia in row 6 are rotated by 90 degrees about the long axis relative to the ommatidia in row 5.** It is well known that morphological differences in well-ordered photoreceptors showing a 90° rotation between different photoreceptor populations suggests polarization sensitivity [6].

Perhaps the most interesting feature of the row 5 and 6 ommatidia is their sensitivity to **circularly polarized light (CPL)** [7]. A circularly polarized light wave consists of two linearly polarized components, with the planes of polarization of their electric vectors perpendicular to each other, and with one of the components out of phase with the other by 90° . The resultant electric vector rotates uniformly in a circle that is perpendicular to the light wave's direction of propagation. CPL is created when unpolarized light passes through a **birefringent** material having just the right thickness. Such a material has the special property that it transmits one linearly-polarized component at one speed while transmitting the perpendicularly-polarized component at a slower speed. If, after traversing and exiting the material, the two components happen to be a quarter wavelength (90°) out of phase, they will recombine to produce a circularly polarized wave. Optical engineers actually create devices that work in this way to produce circularly polarized light. They are known as quarter-wave retarders. If a CPL wave created by a quarter-wave retarder is passed through another quarter-wave retarder, it emerges as a linearly polarized wave.

What is startling is that **the R8 cells in row 5 and 6 ommatidia are approximately quarter-wave retarders for light in the visible spectrum.** Given the microvillar structure of the R1-R7 cells, this indicates that one purpose of the R8 cell is to convert CPL into linearly polarized light, which will then be processed by the R1-R7 cells. Because of the 45° orientations of the R8 and R1-R7 microvillar planes, the R1-R7 cells are able to distinguish between clockwise-rotating and counterclockwise-rotating electric vectors, i.e. between **right circular polarization** and **left circular polarization**.

The existence of CPL sensitivity has been corroborated by electrophysiological and behavioral evidence [7]. However, the reason for its existence has not yet been established. It is known that in turbid media or living tissue, scattered light can become circularly polarized, and the ability to distinguish between right and left circular polarization could be useful for enhancing the contrast between objects and their background. [Humans use CPL filters for photography and for object-detection in turbid waters]. This capability may also be used for complex intraspecific social interactions. For example, at least three species of stomatopods are known to reflect CPL from the cuticles of males but not females. Since the cuticles are on parts of the body that are often used for behavioral displays, the CPL reflections could be mating signals.

A great deal of progress has been made in the past 20 years with respect to understanding the structure and functionality of the stomatopod eye, but there are still many unanswered questions. Which region

of the retina is responsible for the observed polarization sensitivity: the hemispheres, rows 5 and 6, or a combination? Why are the ommatidia in the hemispheres skewed to view the same small strip of space? Is there communication between the colour and polarizations systems? What is the biological significance of all this complexity?

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