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# Evolutionary Optics: How Mantis Shrimps Enhance Photoreception and Signaling Effectiveness

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**Abstract:** Mantis shrimps (stomatopod crustaceans) have evolved numerous adaptations in their photoreceptors and in body structures used to produce visual signals. Novel optical structures exist at microscales and nanoscales, often operating by previously unknown optical mechanisms. © 2021 The Author(s)

## 1. Main Text

### 1.1. Introduction

Humans have used nanostructural and photonic approaches to manipulate the appearances of objects or enhance the performance of technology for perhaps a century. Living things, on the other hand, have been at it for millenia. When vision first appeared more than 500 million years ago, its arrival created intense selective pressure for predators, prey, and competitors to evolve new solutions for survival. Among these were the first structural colors and other features that relied on sub-wavelength structures [1]. Here, I will introduce several sub-wavelength devices that are used by mantis shrimps, scientifically classed as stomatopod crustaceans. Specifically, I will discuss ordered microvillar arrays that form phase-delay structures, aligned molecular polarizers, shape-anisotropic vesicular polarizers, and 3-dimensional photonic crystals acting as wavelength-specific reflectors.

### 1.2. Aligned Microvillar Arrays

Mantis shrimps inhabit water where color can be an unreliable source of information. They depend on polarized light for many tasks, including communication, visually detecting it using photoreceptors with parallel sets of microvilli that are naturally dichroic to visible or ultraviolet light. However, mantis shrimps uniquely also sense the handedness of circularly polarized light [2]. They use microvilli to construct a quarter-wave retarder (Fig. 1a), converting incoming circularly polarized light to linearly polarized light, which then passes on to typical linear-polarization receptors [2,3]. The retarder functions because the lipid bilayer forming the margin of each microvillus is lipid-based, while the cytoplasm surrounding and inside the microvillus is aqueous. Each microvillus is about 40 nm in diameter, and thus subwavelength, and the entire receptor consists of a parallel stack of microvilli about 150  $\mu$ m in length (Fig. 1a). Microvilli are inherently birefringent, and the array produces form birefringence [3]; the two retardances are opposite in sign and wavelength-dependence. Over the length of the structure, these cancel and provide 90° retardance that is essentially independent of wavelength – a quarter-wave achromatic retarder built entirely of sort biological material [2,3].

### 1.3. Molecular Polarizers

Microvilli can also form linear polarizers (Fig. 1b). The keto-carotenoid astaxanthin (the red-colored molecule in Fig. 1b) consists of a dichroic, linear hydrophobic chain of conjugated double bonds that terminates in hydrophilic carbon rings. The length of the chain just spans the separation of lipid bilayers, with each carbon ring placed in the hydrophilic glycerol binding the membrane's phospholipids and the conjugated chain crossing the hydrophobic fatty-acid tails [4]. The overall arrangement makes all the chains parallel, so the entire membrane becomes dichroic for light passing through obliquely [5] and can be used as a linear polarizer for visual signaling.

### 1.4. Shape-Anisotropic Polarizers

Besides dichroic polarizers, some species of mantis shrimps have evolved a previously undescribed method of reflecting linearly polarized light (Fig. 1c). They use structures consisting of typically six to eight parallel layers, each layer made up of rows of oblong membrane vesicles about 550 nm x 250 nm x 150 nm in size [6]. The sizes

and separations of the vesicles are not fully ordered, but the array possesses short-range order, so the structure can be analyzed using a Bragg scattering model for an “amorphous photonic solid”. The results of such an analysis closely duplicate empirical measurements of the polarized-light reflection from body parts containing this structure, with good reflection of horizontally polarized light (perpendicular to the long axes of the vesicles) in the range 400 to 600 nm and weak reflection of vertically polarized light across the entire visible-light spectrum [6].

### 1.5. Three-Dimensional Photonic Crystals

There are numerous other interesting sub-wavelength features in mantis shrimps, but a final - quite spectacular - structure discussed here is a three-dimensional array within photoreceptors of some mantis shrimp larvae, each about  $11 \times 5 \mu\text{m}$  in size, containing electron-dense spherical vesicles  $\sim 150$  nm in diameter (Fig. 3d). These are highly ordered at similar scales on all three axes. Their presence is revealed inside the eye by a bright green-yellow eyeshine for on-axis illumination of single compound eye units. Bragg analysis coupled with finite-distance time-domain numerical analysis predicted reflectance spectra like those measured from eyeshine. We believe that this is the first fully-ordered three-dimensional photonic crystal seen in a crustacean eye.

### 1.6. Summary and Conclusions

The mantis shrimps exhibit a diversity of sub-wavelength structural features interacting with light for color and polarization control. Insects (and even plants) also have many novel mechanisms of light control, both for spectral and polarizational functions. No doubt, research on hard-shelled invertebrates still has much to reveal.

## 2. Figure

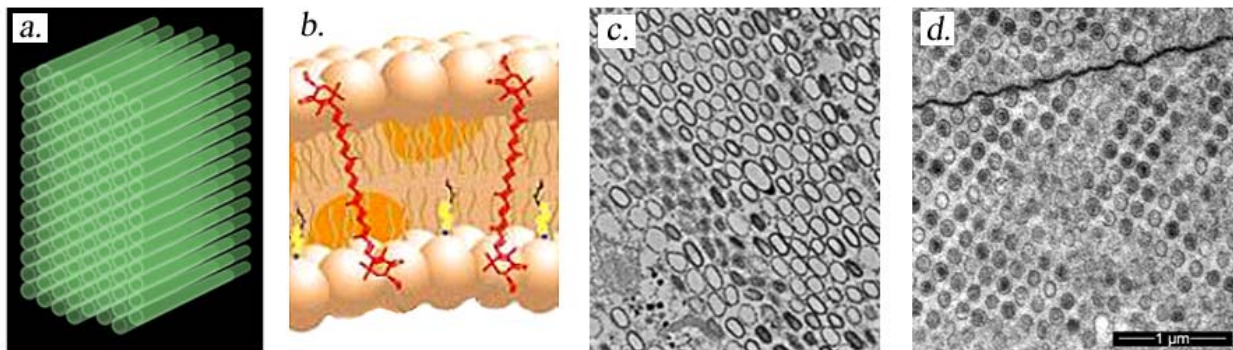


Fig 1. Sub-wavelength structures found in mantis shrimps. See text for explanation.

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