Analysis of Optical Model and Mechanism of Polarization Identification for Mantis Shrimps Eyes

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Keywords: mantis shrimp eyes, index ellipsoid, linear polarized light, circular polarized light

Abstract. Mantis shrimp eyes possess apposition compound eyes, complex visual systems, and unique ability of polarization identification. Within row 5 and row 6 in the mid-band of mantis shrimp eyes, the arrangement of microvilli in retina cells (R1-8) provides possibility of polarization identification. This paper analyses the structure of rhabdome in the mantis shrimp ommatidia. According to the birefringence of microvilli layer of R8 cells, the alternate microvilli layers of R1-7 was simulated by calculating method of index ellipsoid and the layers can be simplified to a cuboid-shaped uniaxial crystal which optical axis is parallel to the direction of rhabdome. Then, we introduce a kind of simplified model of the polarization system for mantis shrimps eyes. Meanwhile, based on the absorption of microvilli, we analyses the way mantis shrimp identify linear polarized light and circular polarized light.

Introduction

Mantis shrimp eyes possess complex structure, and the compound eyes are consisted of thousands of ommatidium [1]. On the surface of the mantis shrimp eyes, the ommatidia can be divided into three morphologically discrete regions, a mid-band and two laterally placed hemispheres (ventral and dorsal). (Fig. 1 and 2)

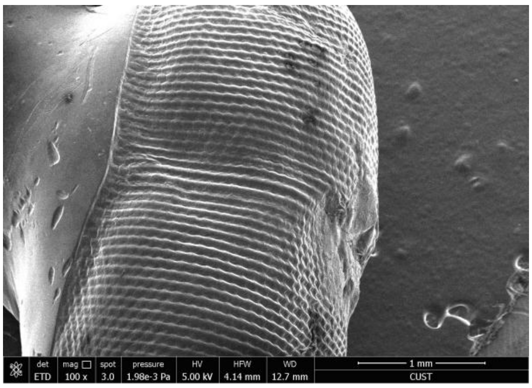

Fig. 1 A mantis shrimp eye is shown by transmission electron microscope.

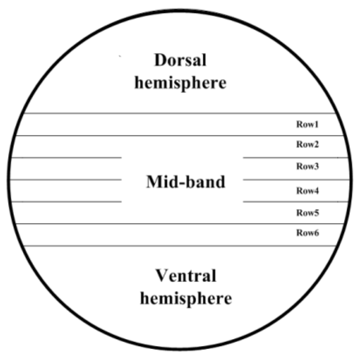

Fig. 2 sketch map of mantis shrimp eye. The mid-band is between dorsal hemisphere and ventral hemisphere, and is divided to six rows. The dorsal hemisphere is beside row 1 and the ventral hemisphere is beside row 6.

Structure of rhabdome in mantis shrimp eyes

The retina cells form two rhabdome, a distally positioned R8 cell constracts a short R8 rhabdome, and under the R8 rhabdome, ring of seven R1-7 cells makes a longer fused rhabdome.(Fig. 3) The middle of these rhabdome is consisted of microvilli layers by special arrangement, which could be taken as photoconductive material to transfer light.[2-3]

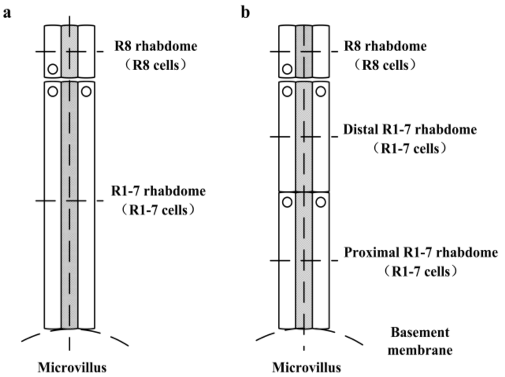

Fig. 3 sketch map of rhabdome. Rhabdome in Row5, Row6 and hemisphere are similar, like **a**; rhabdome in Row1-4 in the mid-band are similar, the R1-7 rhabdome is divided into 2 tiers, like **b**.

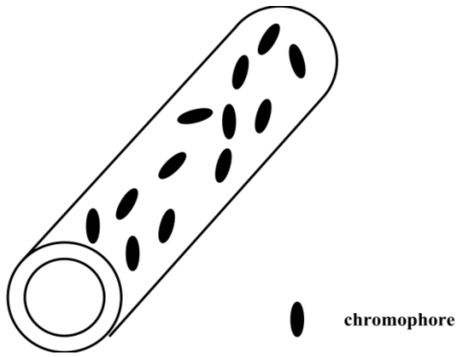

Fig. 4 sketch map of microvillus. The microvillus is like a long tube, covered with a photopigment-bearing membrane. There is lots of chromophore on the photopigment-bearing membrane.

Microvilli

Mantis shrimps belong to invertebrate, figure 4 shows that the microvilli of invertebrate is like a long tube, covered with a photopigment-bearing membrane. There is lots of chromophore on the photopigment-bearing membrane. (Fig. 4) Chromophore has the ability of absorbing the particular direction and wavelength of polarization and stimulating the photopigment. Meanwhile, a 2:1 preponderance of chromophore groups can absorb the polarization which parallel to the orientation of microvillus[4]. This means that microvilli can absorb the particular wavelength linear polarization which parallel to the orientation of microvilli.

Ommatidia of Row 5 and Row 6 of mantis shrimp eyes

The structure of ommatidia of row 5 is similar with row 6 in mid-band of mantis shrimp, because of unique arrangement of microvilli, mantis shrimp eyes possess the ability of polarization identification. On the cross section of rhabdome which consisted of R8 cells, R8 rhabdome have an unusually oval shape microvilli layer and contain very well ordered, unidirectional microvilli and the orientation of microvilli is along to the minor axis of the oval. This R8 microvilli layer possesses the property of birefringence. According to the research, in the range of 400nm to 700nm, R8 microvilli layers play a role as quarter-wave plate, and the fast axis of quarter-wave plate is parallel to the orientation of microvilli. Under the R8 rhabdome, there is a longer rhabdome which made up of R1-7 cells. The rhabdome have particularly well structured diamond shapes with very evenly sized microvilli arranged in orthogonal layers of similar thickness that are both neat and relatively thin (Fig. 5). This kind of orthogonal layers is consisted of two groups of cells--R1,4,5 and R2,3,6,7. The orientation of microvilli of R1,4,5 microvilli layer is at -45° to the orientation of microvilli of R8 microvilli layer, and the orientation of microvilli of R2,3,6,7 microvilli layer is at +45° to the orientation of microvilli of R8 microvilli layer. The difference of row 5 and row6 is that row 6 ommatidia are rotated 90° relative to those of row 5. The microvilli of row 6 R8s are vertical relative to the outside world (when the mid-band is horizontal) and those of row 5 horizontal[2-3].

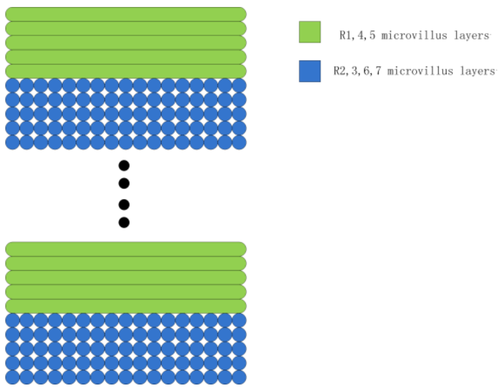

Fig. 5 sketch map of longitudinal section of R2,3,6,7 and R1,4,5 microvilli layers. The green part shows R1,4,5 microvillus layers and the blue part shows R2,3,6,7 microvillus layers.

Optical Model of Mantis Shrimp Eyes

In the rhabdome of mantis shrimp eyes, the layers consisted of R1-8 cells be taken as photoconductive material to transfer light. According to the analysis of normal incidence pass through the ommatidia of Row 5 and Row6, we simplified the microvilli layers and set up the optical model. The rhabdome of ommatidia of Row 5 is taken as sample, because the structures of Row 5 and Row 6 are same. R8 microvilli layer possesses the features of birefringence and plays a role as quarter-wave plate[5]. The fast axis of quarter-wave plate is parallel to the orientation of microvilli. Based on this feature, we discuss the property of R1,4,5 microvilli layers and R2,3,6,7 microvilli layers.

The microvilli of R1-7 cells are similar with R8s, and the structure of the R1,4,5 microvilli layers and R2,3,6,7 microvilli layers are same as the R8 microvilli layers. According to the properties of R8 microvilli layers, we infer that R1,4,5 microvilli layers and R2,3,6,7 microvilli layers have the same property of birefringence, and the fast axis of R1,4,5 and R2,3,6,7 microvilli layers are parallel to respective microvilli. We take the R1,4,5 and R2,3,6,7 microvilli layers as two same phase retarders, but the fast axis of them are perpendicular to each other. Because R1,4,5 and R2,3,6,7 microvilli layers appear in pairs, we take one pair of R1,4,5 and R2,3,6,7 microvilli layers to discuss for simplifying the optical model, and then expand the sample to n pairs of R1,4,5 and R2,3,6,7 microvilli layers.

Setting up the optical model (Fig. 6), take the orientation of R1,4,5 microvilli as x axis, the orientation of R2,3,6,7 as y axis, and the orientation of rhabdome as z axis,

According to the optical axis, the equation of the index ellipsoid of R1,4,5 microvilli layer is :

$$\frac{x^2}{n_e^2}+\frac{y^2}{n_o^2}+\frac{z_{R1,4,5}^2}{n_o^2}=1 \quad (1)$$

The equation of the principal section perpendicular to optical axis is:

$$\frac{x^2}{n_e^2}+\frac{y^2}{n_o^2}=1 \quad (2)$$

And the equation of the index ellipsoid of R2,3,6,7 microvilli layer is:

$$\frac{x^2}{n_o^2}+\frac{y^2}{n_e^2}+\frac{z_{R2,3,6,7}^2}{n_o^2}=1 \quad (3)$$

The equation of the principal section perpendicular to optical axis is:

$$\frac{x^2}{n_e^2}+\frac{y^2}{n_o^2}=1 \tag{4}$$

The angle between the orientation of wave normal and the optical axis is θ. The serif of the plane, which is perpendicular to the wave normal through the center of the ellipsoid, must be an ellipse. The minor axis and the long axis of this ellipse are the D vector of the two waves in the wave normal, and the length of each semi-axis equal to the refractive index of each direction of vibration[6]. With assumption of the incident direction is normal, the θ is 90°, based on Eq.1 and Eq.3, we can know that the principal section of the R1,4,5 and R2,3,6,7 microvilli are the equation (2) and (4). Then, we can get $n_{exl}=n_{eyr}=n_o$ and $n_{eyl}=n_{exr}=n_o$. Here, the n_{exl} and n_{eyl} represent the refractive index of x and y part of linear polarized light which pass through the x-o-z plane and y-o-z plane of the R1,4,5 microvilli layers. Then, the n_{exr} and n_{eyr} represent the refractive index of x and y part of linear polarization light which pass through the x-o-z plane and y-o-z plane of the R2,3,6,7 microvilli layers.

Polarized light can be divided into two linear polarizations which perpendicular to each other. Here, we can divide the polarization light into two linear polarizations, one is parallel to the direction of x axis, and the other one is parallel to the direction of y axis. Then, we can get phase change that x component of polarization and the y component of polarization pass through a pair of R1,4,5 and R2,3,6,7 microvilli layers.

The phase change of x component of polarization is:

$$\delta_x=\frac{2\pi}{\lambda}(n_{exl}+n_{exr})d=\frac{2\pi}{\lambda}(n_e+n_o)d \tag{5}$$

The phase change of y component of polarization is:

$$\delta_y=\frac{2\pi}{\lambda}(n_{eyl}+n_{eyr})d=\frac{2\pi}{\lambda}(n_o+n_e)d \tag{6}$$

The Eq.5 and Eq.6 show that the phase difference of x component and y component of polarization passing through a pair of R1,4,5 and R2,3,6,7 microvilli layers is:

$$\delta=\delta_y-\delta_x=0 \tag{7}$$

Based on the equation, There is no phase difference between phase of the x component and y component of polarization when the incidence is normal. Meanwhile, the principal section of R1,4,5 and the principal section of R2,3,6,7 can be approximated to a circle, the equation is:

$$\frac{x^2}{(n_o+n_e)^2}+\frac{y^2}{(n_o+n_e)^2}=1 \tag{8}$$

Further, we can approximate the R1,4,5 and R2,3,6,7 microvilli layers to one, and the equation of the index ellipsoid is :

$$\frac{x^2}{(n_o+n_e)^2}+\frac{y^2}{(n_o+n_e)^2}+\frac{z^2}{4n_o}=1 \tag{9}$$

Then, a pair of R1,4,5 and R2,3,6,7 microvilli layers can be simplified to a uniaxial crystal, the shape of the crystal is cuboid and the optical axis is parallel to the orientation of rhabdome. We can superpose n pairs of R1,4,5 and R2,3,6,7 microvilli layers, and the orientation of the optical axis of these pairs are same, and perpendicular to the x-o-y plane, so we can the whole microvilli of R1-7 cells as a uniaxial crystal, and the optical axis is same with the orientation of rhabdome.

Finally, we can get the simplified optical model of the rhabdome of the ommatidium within the Row 5 and Row 6. The model is like that a cuboid uniaxial crystal under a quarter-wave plate (Fig.7).

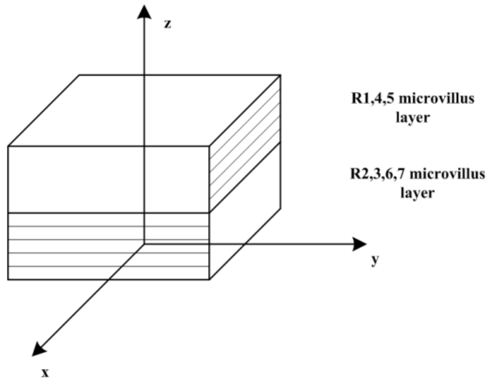

Fig. 6 one pair of R1,4,5 and R2,3,6,7 microvillus layers in the coordinate system we set up.

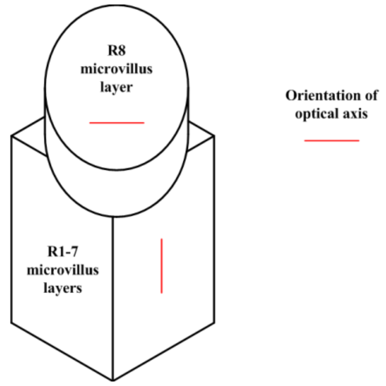

Fig. 7 the optical model of the R1-8 microvillus layers. R8 microvillus layer is like a quarter-wave plate and the R1-7 microvillus layer is like a cuboid uniaxial crystal.

Analysis of Mechanism of Polarization Identification of Mantis Shrimps Eyes

We consider that polarization identification of mantis shrimp eyes depends on absorption of chromophore on the microvilli of retinal cells.

Recognition of linear polarization

When animals recognize the polarization, there is an angle between polarization and their eyes. In mantis shrimp eyes, the identification of linear polarization depends on R8 cells, and the range of wavelength is from 300nm-400nm in ultraviolet[7-8]. As fig, we can get the component of polarization along the orientation of microvilli, and the angle of microvilli of the R8 cells of Row 5 and linear polarization is θ, and the orientation of Row5 microvilli and the orientation of Row6 microvilli perpendicular to each other, so the angle of the R8 cells of Row6 and linear polarization is $90° - \theta$ (Fig.7), let I_0 as the intensity of linear polarization, I_5 as the intensity of absorption at the orientation of the microvilli of row 5 R8 cells, and I_6 as the intensity of absorption at the orientation of the microvilli of row 6 R8 cells, based on Malus law, we can get the equations:

$$I_5 = I_0 \cos^2 \theta, I_6 = I_0 \cos^2 (90° - \theta) \quad (10)$$

Let I_5 subtracts I_6, we can get the equation:

$$I_5 - I_6 = I_0 \cos 2\theta \quad (11)$$

When $\theta = k\pi$, the value is maximal value, and now, linear polarization are parallel to the mid-band (the orientation of mid-band are parallel to the microvilli of R8 cells of row5 and perpendicular to Row 6, and $I_5 = I_0$ and $I_6 = 0$, according to Beer law:

$$I = I_0 \exp(-\beta Cz) = E \cdot E^* \exp(-\beta Cz) \quad (12)$$

Because of the same structure of ommatidium of Row 5 and Row6, we consider that their microvilli possess same absorbance C. Therefore, the intensity of absorption of Row 5 R8 microvilli is the maximum, but the microvilli of R8s of row 6 absorb nothing. When $\theta = \frac{\pi}{2} + k\pi$, the value of intensity is minimum, linear polarization perpendicular to mid-band, and $I_6 = I_0$ and $I_5 = 0$. To sum up, we infer that mantis shrimp can recognize linear polarized light which are parallel to mid-band or perpendicular to mid-band.

Recognition of circular polarized light

Identification of circular polarized light is related with the orientation of microvilli of R1,4,5, R2,3,6,7 and R8 microvilli layers. Because the size and shape of microvilli of R1-7 cells are similar, we think that they possess the same absorbance. According to the introducing of the structure of Row 5 and Row 6 in the second part, we get the relationship of the orientation of microvilli of R1,4,5, R2,3,6,7 and R8 microvilli layers (Fig. 8).

We have known that R8 microvilli layer possesses the features of birefringence and plays a role as quarter-wave plate. The fast axis of quarter-wave plate is parallel to the orientation of microvilli. After passing through R8 microvilli layers, the left hand circular polarized light becomes linear polarized light, and the angle of the orientation of linear polarized light and the orientation of microvilli of R8 cells is -45°, and now, the microvilli of R1,4,5 microvilli layers fully absorbs this linear polarized light, and the microvilli of R2,3,6,7 doesn't absorb any polarization, we infer that the mantis shrimp recognizes the left hand polarized . However, when the incident light is right hand circular polarized light, after passing through the R8 microvilli layers, the right hand circular polarized light becomes linear polarized light, and the angle of the orientation of linear polarized light and the orientation of microvilli of R8 cells is +45°, and now, the microvilli of R2,3,6,7 microvilli layers fully absorbs this linear polarized light, and the microvilli of R1,4,5 doesn't absorb any polarization, we infer that the mantis shrimp recognizes the right hand polarized.

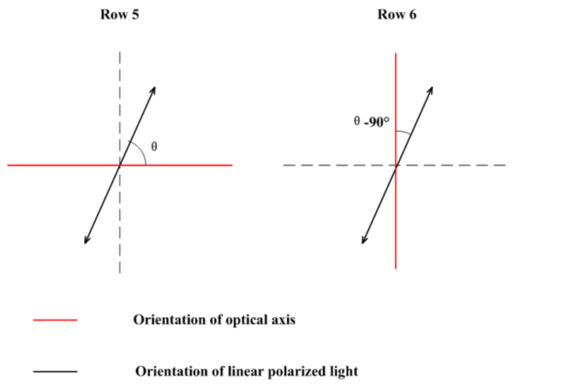

Fig. 8 the relationship of Row 5 and Row 6 and the orientation of microvillus and linear polarized light

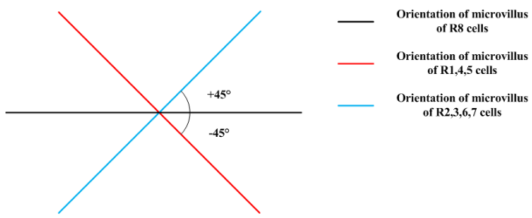

Fig. 9 the angle relationship of the orientations of microvillus of R8 layers, R1,4,5 layers and R2,3,6,7 layers

Summary

This paper used the index ellipsoid to discuss with the layers of microvilli of R1-8 cells, and set up the optical model of the structure of layers of microvillus of R1-8. The layers are simulated by a quarter-wave plate above a cuboid-shaped uniaxial crystal which optical axis is parallel to the direction of rhabdome. Meanwhile, the orientation of microvillus of the layers, absorption of chromophore, structure of microvillus layers and process of identifying circle polarized light and linear polarized light. Polarized light passing through the rhabdome may be related with the shape of cross section of microvillus layers, the length of rhabdome. The optical model in this paper based on that the microvillus layers of R1-7 cells has the same properties with the microvillus layers of R8 cells, so we need more experiment to research.

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