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Growth and light/dark adaptation in *Lysiosquillina maculata* (Stomatopoda, Crustacea)

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Abstract

Stomatopod eyes are divided by 2 or 6 rows of ommatidia in dorsal and ventral halves. While the midband ommatidia subserve color vision those in the 2 halves analyze shapes, distances and motion of objects, due to skewing of ommatidia and the resulting patterns of overlap of visual fields. Each ommatidium is composed of the corneal facet, 2 corneagenous cells, a crystalline cone, constituting the dioptric apparatus and the sensory apparatus of 8 retinular cells surrounding a fused rhabdome. The rhabdome transduces light into electric energy, which is transferred to the retinular cells who transmit information to the nervous system.
Morphological changes in light/dark adaptation are due to contractions and relaxations of the myofibrils in the 6 primary (veils, surrounding the cones) and 6 secondary cells (accessory pigment cells, surrounding the retinular cells).
Postlarval eyes grow from the inner cornea-stalk junction substituting the larval eye. The adult eyes grow by increasing sizes of all components of the ommatidia, but also at the inner cornea-stalk junction a special, well ordered tissue adds few new corneagenous and primary pigment cells, while cones and retinular cells grow from inside the eye. During the molt, the corneagenous cells add the new larger and thicker cornea facets; and in the area between the growing cornea and the stalk a particular growth tissue is present.
The corneagenous cells contain large amounts of glycosaminoglycan molecules, which may provide chitin for the new cornea for the molt. The corneagenous cells may also have an optical function and moreover constitute an hydraulic cushion to protect the apex of the cone during light-dark adaptation.

Introduction

Stomatopods live at all ocean depths from bright light tropical surface waters, to the mesopelagic and bathypelagic zones (Schiff *et al*, 1997) and in all climates.
Each eye explores the environment indipendently from the other until a prey enters the visual field of one of the eyes. Then eyes are fixed in a characteristic position. Eyes are divided by a midband (mb) in two hemispheres. While the mb subserves color and polarization vision (Cronin *et al*, 2002) the two hemispheres of each single eye analize sizes, motion, shapes and distances of prey (Schiff *et al*, 1989, Schiff *et al*, 1997). Near to the mb ommatidia are skewed towards the mb such that visual fields overlap with those of the other half of the eye and with those of the mb ommatidia (Schiff *et al*, 2002). The patterns of superposition of visual fields depend on the region and size of the eye and on sizes, location and motion of the object. For an object passing in front of a column of ommatidia (across the mb) maxima of stimulation, due to parallel ommatidia, occur at the center of each hemisphere (fig. 1). A configuration of ommatidia is stimulated at each instant and excitation transferred to the nervous system via the lamina ganglionaris. From the lamina parallel channels transmit information according to the different tasks to be accomplished (Schiff *et al*, 1993).
Light/dark adaptation involves mechanical changes of the dioptric apparatus and the retina as described by us for *Squilla mantis* (Dore *et al*, 2005).
Crustacean eyes continue to grow through lifetime (Keskinen et al., 2002) increasing sizes of eyes and ommatidia and adding new cornea and ommatidia.
Materials and methods: as described in Schiff *et al.* (2002) and Dore *et al.* (2005).

Results

The ommatidia.

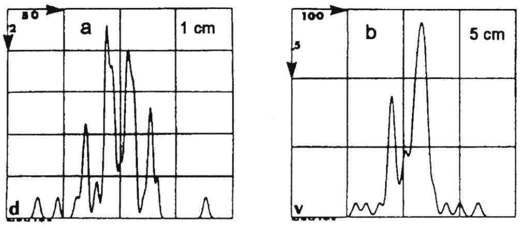

Fig. 1 - Outputs from the ommatidia when a luminous point moves in front of a sequence of ommatidia across the mb at a speed of 10 cm/sec. Ordinate = number of ommatidia in whose visual field the point is at the instant given on the abscissa. The pattern of simultaneously stimulated ommatidia is similar for a point at distance 1 cm for a small eye (a) and at 5 cm for a large eye (b), thus adapting the prey hitting distance to the lengths of the raptorial appendages.

Sizes of ommatidia and their components depend on the size (age) of the animal, the region of the eye and on light/dark adaptation. Each ommatidium is composed by the corneal facet, 2 corneagenous cells and the crystalline cone constituting the dioptric apparatus which is connected to the sensory apparatus of 7+1 retinular cells surrounding a fused rhabdome. The rhabdome transduces light into electric energy, which is transferred to the retinular cells which transmit information to the nervous system. Towards the interior of the eye the two wedges of the corneagenous cells surround the distal cone. The crystalline cone, composed by four cells, is attached with a thin part to the center of the corneal facet. Towards proximal the cone widens and contains an enforced four part ring. The four parts are situated around the widest part of the cone. At each of the six corners of the corneal facet a bundle of myofibrils is attached to the cornea. These fibrils are immersed in a thin veil which is attached to the cornea and the corneagenous cells, surrounding the corneagenous cells and the cones. From the cornea towards the retina the veils restrict and six bundles of myofibrils surround each cone (fig. 2). Each bundle though belongs to three

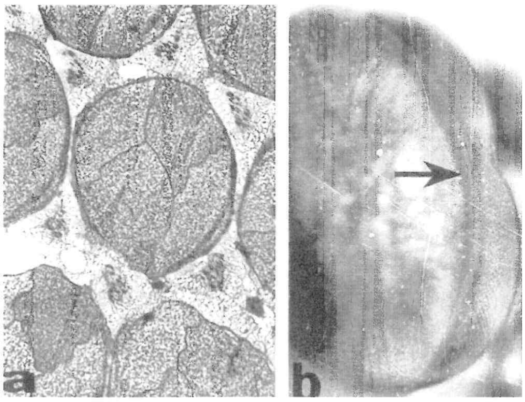

Fig. 2a - Cones, veils and myofibrils. Six bundles of myofibrils, immersed in the veils (primary pigment cells), surround each cone; b- The eye of a postlarva of Pseudosquillopsis marmorata *(stomatopoda). The adult eye (right) grows from the inner border of the larval eye (left) originating from a proliferation zone (arrow) gradually substituting the larval eye.*

ommatidia. At the distal retina these bundles form little brushes connected to the accessory pigment cells.
The six accessory pigment cells in each ommatidium are filled with a black pigment and surround the seven retinula cells in several strings which run to the basement membrane to which they are fastened by little boot shaped feet. These cells contain microtubules and myofibrils.
The fused rhabdome is surrounded by seven retinula cells. These penetrate the basement membrane as first order nerve fibers, loosing their visual pigment. Six nerve fibers end in the neurocartridges of the lamina ganglionaris, the first visual processing ganglion. The fibers from the seventh and eighth retinula cell end in the medulla externa, the second visual ganglion. At the junction between the cones and the rhabdomes the rhabdome of the four-lobed, 8th retinula cell is inserted. Retinula cells 1 to 7 contain the visual pigment granules. A thin layer covers the rhabdome separated by the perirhabdomal space from the bulk of the retinula cell. The thin layer is multiply bridged through the "empty" space to the main part of the retinula cells (Dore *et al*, 2005).

Adaptation

During dark adaptation the cones become shorter and slightly thicker. The myofibrils in the veils contract and pull the accessory pigment cells towards the cornea, such that the proximal cones are immersed in the accessory pigment cells. The retina becomes longer: cone/retina 1.5 in dark and 2.5 in light adaptation, i.e. cones in dark adaptation are twice the length of the retina and in light adaptation three times as long. As in other stomatopods the visual pigments accumulate around the rhabdome during dark adaptation. The perirhabdomal space (about 1-2 μm width) is slightly wider in dark adaptation, but the volume of the rhabdome does not seem to change in *L. maculata*. In light adapted eyes the cones are thick distally, then towards proximal slim abruptly. The mb ommatidia as well as the corneagenous cells change very little or not at all with light- or dark- adaptation. The visual field of an ommatidium can be calculated from the dimensions of its optical equipment (Snyder, 1979). The calculated visual field is approximately one degree in *L. maculata* and apparently does not change very much in light/dark adaptation.

Growth of the eyes.

In the postlarval eye the new adult eye grows over the larval eye starting at the inner border between the stalk and the cornea (fig. 3). In adult eyes a groove, the morphogenetic furrow, located at the inner margin of the eye, between the stalk and the cornea, apparently constitutes the region of growth. In oblique sections, from outside the eye towards inside, the normal cornea, showing wide layers of alternating refractive indices, is bordered by the carapax. A large, presumably new "cornea" is inserted into the stalk with thin layers of alternating refractive

Fig. 3 - Morphogenesis of corneagenous cells, veils and crystalline cones originating from a specialized proliferation tissue at the inner margin of the eye of L. maculata. *Left: proliferation tissue with hexagonal symmetries; middle: at the envelope of the tissue groups of two to four cells proliferate with treelike extensions which end on (right) growing coneagenous cells, veils and crystalline cones.*

indices decreasing still towards the inside of the eye where new layers are added. Into this a tissue is inserted, followed by the growing veils and corneagenous cells and probably new cones. This tissue has an envelope with many nuclei, while the interior is fibrous, with few nuclei, containing many granules. Towards the inside of the eye the envelope protrudes with an ordered array of many treelike extensions. Each tree starts with two to four nuclei, continues as single stems and then extends with several small branches, which end in cells which seem the precursors of the corneagenous cells and veils with their myofibrils (fig. 3).

Discussion

We think that the shortening of the cones during dark-adaptation is provoked by the contraction of the myofibrils in the veils between the cones and the simultaneous relaxation of the myofibrils in the retina. Actin and myosin have been observed around and next to the cones in other compound eyes (Baumann, 1992) and have been assumed to be able to contract (Hafner *et al*, 1992). Microtubules as well as the cone enveloping membranes instead are usually interpreted as more or less rigid structures which could help return the cones or retina to their original lengths after the myofibril contractions. In fact the microtubules in the accessory pigment cells are associated with myosin II and actin at the rhabdome margins and in the accessory pigment cells in other arthropod eyes (Baumann, 2004), thus these structures may contract during light adaptation. The cone enveloping double membranes and the cone extensions through the retina apparently contain GAG (GlucoseAminoGlycan) molecules.

The corneagenous cells stain heavily for GAGs which is composed of water-absorbing and –releasing molecules. Thus the corneagenous cells may have one or more of the following functions:

1. preparing the new cornea for the next moult contributing polysaccharides for the chitin.
2. funnel light from the borders of the visual field into the cone as suggested by their transparency and wedge shaped structure.
3. build GAG molecules transferred to the cornea and the myofibrils in the veils.
4. constitute a water absorbing and releasing hydraulic cushion involved in the morphological changes in light- and dark- adaptation.
5. as the GAG accumulate and release water they may be also involved in the detachment of the old cornea.

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