

New lights on ocellar and extraocular photoreception in sea cucumbers (Holothuroidea, Echinodermata)

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Abstract:

Echinoderms are an intriguing group of deuterostome invertebrates to study the evolution of light perception in metazoans, as they have been known to be sensitive to light despite lacking complex eye structures. Previous studies on sea urchins, sea stars, and brittle stars have identified photoreceptors in various body parts, such as tube feet, spines, and the nervous system. Some studies also lead to the discovery of low-resolution spatial (but eye-less) vision in some species! The light perception abilities of holothurians (aka sea cucumbers), however, have been largely understudied, with some punctual results from ethological studies (e.g., some species fly away from a light source while other species retract their oral tentacles under strong light exposure). To investigate photoreception in sea cucumbers, we used a multidisciplinary approach that focuses on opsins, which are prototypical photoreceptor proteins in bilaterians. Our analysis of genomes and transcriptomes from multiple holothurian species reveals six ancestral opsin types. The expression of rhabdomeric opsin-based extraocular photoreceptors was specifically detected in oral tentacles, radial nerves, and tube feet in the European species *Holothuria forskali*, suggesting a well-developed extraocular photoreception in these animals. Our investigation also focused on the clade of Apodida, a group of sea cucumbers with elongated bodies and lacking tube feet, which some researchers have suggested have visual structures at the root of their tentacles. Our study demonstrated the expression of a ciliary opsin in the photo-sensory neuroepithelial structures of the tropical species *Euapta godeffroyi*, which form eyespots at the base of each tentacle. A similar expression of opsins in the baso-tentacular nerves was observed in the small European burrowing species *Oosteregrina digitata*. Additionally, we detected opsins in the sensory cupules on the inner face of tentacles, which have unknown sensory functions. Finally, our ethological tests on three holothurian species showed that they moved away from (*Holothuria forskali* and *Euapta godeffroyi*) or toward (*Synapta maculata*) a light source, specifically for shorter wavelengths corresponding to blue and green light. Turning the spotlights on these amazing sea cucumbers and more broadly on all echinoderms is important to better understand the mechanisms and evolution of extraocular photoreception in the deuterostome lineage.