

New light on the diversity of photoreception types in sea cucumbers

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Vision is a primordial sense in animal evolution, and it has been mainly studied in species that developed complex eyes such as chordates and arthropods. Except for the starfish eyespots, echinoderms do not have complex visual organs, but many species exhibit a great photosensitivity mediated by some opsin types (photoreceptor proteins also found in other bilaterian groups). Recent studies on sea urchins, sea stars, and brittle stars, have revealed the presence of a large opsin diversity located in various body parts such as tube feet, spines, and the nervous system (Ullrich-Lüter et al., 2011; Delroisse et al., 2014). Some species have even demonstrated low-resolution extraocular spatial vision (e.g., Sumner-Rooney et al., 2020). However, photoreception in sea cucumbers was largely unexplored, with only sporadic data available, such as observations of species moving away from a light source or retracting their oral tentacles under strong light exposure. To fill this knowledge gap, we conducted a comprehensive investigation of sea cucumber photoreception using a multidisciplinary approach. Firstly, we analyzed genomes and transcriptomes of multiple holothuroid species, revealing the presence of six ancestral opsin types in this group. Secondly, we highlighted the expression of rhabdomeric opsins, commonly found in protostome eyes, in oral tentacles and tube feet of *Holothuria forskali*, a European species belonging to the Holothuriida order. Our investigation also focused on the Apodida order, a group of sea cucumbers with snake-shaped bodies lacking tube feet. Previous authors have proposed the presence of visual-like structures at the base of the tentacles and/or in association with the oral nerve ring in different species (e.g., Ludwig, 1889; Yamamoto & Yoshida, 1978). Our study revealed the expression of ciliary opsins, typically found in vertebrate eyes, in the neuroepithelial structures forming eyespots at the base of tentacles in the tropical species *Euapta godeffroyi*. We also detected the expression of ciliary opsins in the sensory cupules of *Oestergrenia digitata*, a burrowing European species. Until now, the functions of these cupules located on the inner surface of tentacles had remained unexplored. Finally, ethological tests conducted on both Holothuriida and Apodida species revealed that *H. forskali* and *E. godeffroyi* moved away from a light source, while *Synapta maculata* (another Apodida species) exhibited a movement toward it, specifically in response to blue and green lights. These findings provide new insights into the evolution and the diversity of photoreception mechanisms in sea cucumbers.

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