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Study of sea cucumber photoreception

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It has been known that echinoderms, despite lacking complex eye structures, exhibit photosensitivity mediated by opsins, photoreceptor proteins also found in other bilaterians. Recent studies on sea urchins, sea stars, and brittle stars, have revealed opsins in various body parts such as tube feet, spines, and the nervous system (Ullrich-Lüter *et al.*, 2011; Delroisse *et al.*, 2014). The eyespot located at the sea star arm tips has also been studied extensively. Some species have even demonstrated low-resolution extraocular spatial vision (e.g., Sumner-Rooney *et al.*, 2020). However, photoreception in sea cucumbers has remained 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 (Panninothuria) 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 *Oostergrenia 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.(P.) forskali* and *E. godeffroyi* moved away from a light source, while *Synapta maculata* exhibited a movement toward it, specifically in response to blue and green lights. These findings provide new insights into the mechanisms and evolution of photoreception in sea cucumbers.

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