



Non-directional Photoreceptors in the Pluteus of *Strongylocentrotus purpuratus*

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In comparison to complex visual systems, non-directional photoreception—the most primitive form of biological photodetection—has been poorly investigated, although it is essential to many biological processes such as circadian and seasonal rhythms. Here we describe the spatiotemporal expression pattern of the major molecular actors mediating light reception—opsins—localized in the *Strongylocentrotus purpuratus* larva. In contrast to other zooplanktonic larvae, the echinopluteus lacks photoreceptor cells with observable shading pigments involved in directional visual tasks. Nonetheless, the echinopluteus expresses two distinct classes of opsins: a Go-opsin and a rhabdomic opsin. The Go-opsin, *Sp-opsin3.2*, is detectable at early (3 days post fertilization) and four armed pluteus stages (4 days post fertilization) in two cells that flank the apical organ. To rule out the presence of shading pigments involved in directional photoreception, we used electron microscopy to explore the expression domain of Go-opsin *Sp-opsin3.2* positive cells. The rhabdomic opsin *Sp-Opsin4* expression is detectable in clusters of cells located around the primary podia at the five-fold ectoderm pentagonal disc stage (day 18–21) and thereafter, thus indicating that *Sp-Opsin4* may not be involved in the photoreception mechanism of the larva, but only of the juvenile. We discuss the putative function of the relevant cells in their neural context, and propose a model for understanding simple photodetection in marine larvae.

Keywords: eye evolution, Go-opsin, invertebrate larvae, r-opsin, sea urchin, zooplankton

INTRODUCTION

While the vast majority of studies on animal photoreception have so far focused on directional photoreceptors—systems comprising at least one cell with a photosensitive opsin together with shading pigments that enable it to discriminate the directionality of light—, less is known about non-directional photoreception, the simplest and earliest evolving type of photoreception. Non-directional photoreceptors, which can be difficult to detect due to a lack of visible screening pigments, allow the monitoring of absolute light intensities of the environment. Consequently, they are widely used as an input to the circadian clock system and also for a wide variety of other tasks. For instance, non-directional photoreceptors can be used as a depth gauge, as a warning for harmful levels of UV radiation, for shadow detection, or be involved in the regulation of feeding, movement and reproduction rhythms (Bennett, 1979; Paul and Gwynn-Jones, 2003; Leech et al., 2005; Nilsson, 2009, 2013).