



Non-visual functions of opsins in Crustacea: a review

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ABSTRACT

Opsins are transmembrane proteins that have a covalent bond with a chromophore 11-cis-retinal in the intracellular region, opsins transiently bind to a G protein, which in turn is alternatively coupled to GTP or GDP. These characteristics allow opsins to function as photopigments and, after reacting with light, they launch the cascade of intracellular communication processes known as phototransduction. Commonly referred to as the starting point of the visual pathway, phototransduction as initiated by opsins, can also mediate physiological processes as varied as taxis, metabolic synchronization, and seasonal migration. This review analyzes such functions performed by opsins in crustaceans, a group with a huge diversity of species that, owing to their plasticity, have been able to invade habitats that other arthropods or terrestrial vertebrates have been unable to occupy. Our analysis emphasizes the way in which opsins take part in crustacean behavioral display under extreme habitat conditions as in the case of cave fauna), as well as in essential ontogenic events. The many functions of opsins have been scarcely investigated due to bias generated by their participation in visual processes. Attention to the non-visual activity of opsins can break new grounds towards an integrative understanding of animal physiology.

KEY WORDS: bioluminescence, cave fauna, circadian rhythms, light-induced hatching, ovary maturation, spectral sensitivity

INTRODUCTION

G protein-coupled receptors (GPCRs,) are membrane proteins capable of recognizing chemical messengers (hormones or neurotransmitters) in cells. On its cytoplasmic surface, a GPCRs is bonded to a G protein, thus called because it is coupled to the diphosphate guanosine nucleotide. Upon recognition of an extracellular messenger, the GPCR shifts its configuration and its G protein exchanges GDP for guanosine triphosphate, thus initiating an intracellular phototransduction cascade which is virtually universal among organisms (Terakita *et al.*, 2012).

Opsins are GPCRs that stand out by their ability to absorb photons (Terakita *et al.*, 2012). They can be found in the membranes of cells that capture luminous energy and translate it into several physiological responses, thus functioning as photoreceptors (Shichida & Matsuyama, 2009) (Fig. 1). Tissues that possess complex photoreceptor arrangements, such as retinas, can employ information acquired through light to portray physical characteristics of objects: shape, position in space, movement, and color, creating images as it were. Those photoreceptors make up the primary sensory neurons in the sensory transduction we call “vision.” The opsins found in the photoreceptors of the visual pathway are rhodopsin (vertebrates and invertebrates) and cone opsins (vertebrates), and hence they are grouped as visual phot-

opigments. Some other photoreceptors detect light for various functions such as phototaxis or the synchronization of circadian rhythms (Peirson *et al.*, 2009; Nilsson, 2013; Kingston & Cronin, 2015). These photoreceptors perform functions unrelated to image conformation and they may be found both within the retina as well as in any other tissue, so we call them and the opsins they contain, “non-visual opsins and photoreceptors.”

Despite being detected in a wide variety of species, studies on crustacean opsins have focused on analyzing their diversity, the structure of their codifying genes or their light-absorption spectrum (Porter *et al.*, 2007; Kashiya *et al.*, 2010; Rajkumar *et al.*, 2010; Belikov *et al.* 2014; Donner *et al.*, 2016). Studies on the possible roles of opsins in crustaceans are nevertheless scarce. It is therefore our goal outline some of the functions of these photopigments in crustaceans.

Crustaceans occupy a wide range of habitats and light environments, where they have developed a wide variety of visual and photodetection systems. Naupliar eyes, compound eyes, intracerebral ocelli, and caudal photoreceptors are part of this diversity of photodetectors (Meyer, 2001). While groups such as the stomatopods have some of the most complex visual systems in the animal kingdom, possessing a great diversity of photopigments (Porter *et al.*, 2013), some cave crustaceans suffer

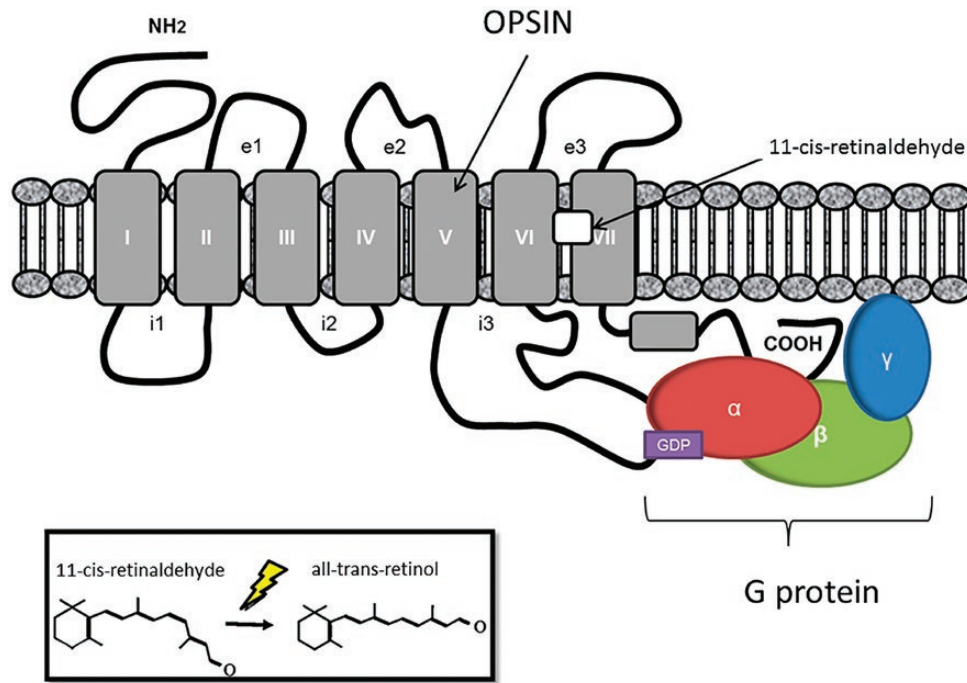


Figure 1. Prototype diagram for opsins. Photopigments are composed of an isomer of a retinaldehyde chromophore (vitamin A) bonded to an opsin protein. Opsins consist of seven α -helix transmembrane domains (TI-TVII) linked by three cytoplasmic loops (i1, i2, i3) and three extracellular loops (e1, e2, e3) as well as an eighth α -helix within the cytoplasm. The first step in phototransduction is the absorption of a photon by 11-cis retinaldehyde, which triggers an all-trans isomerization (inset). The configuration shift in the chromophore allows intracellular opsins to interact with G proteins and leads into a phototransduction cascade by exchange of GDP by GTP (not shown). Scheme based on Porter *et al.*, 2007, Peirson *et al.*, 2009, and Lledó-Riquelme *et al.*, 2010.

from a reduction or loss of their eyes, developing more than visual systems, i.e., non-visual sensory functions most useful in the dark (Mejía-Ortiz & Hartnoll, 2006). Such diversity makes crustaceans an attractive group to study visual and photodetection systems.

ROLE OF OPSINS IN CIRCADIAN RHYTHMS

Most of organisms are exposed to the geothermic cycle of day and night, the circadian rhythms that are synchronized to the levels of light in the environment. This entrainment of the circadian rhythms to the day and night cycle by environmental light is known as photosynchronization (Sullivan *et al.*, 2009). Photosynchronization avoids the shifting of the circadian rhythms that otherwise delay their start in the absence of any environmental clue and progressively occur at different day times. Likewise, photosynchronization is achieved by both visual and non-visual photoreceptors and opsins. A description of the types of photoreceptors is essential in the description of the photosynchronization of a species. Crustaceans, distributed in such wide variety of habitats, comprise one of the groups more amenable to analyze and compare the role of the photoreceptors mediating photosynchronization.

The daily vertical migrations up and down the water column of many planktonic crustaceans also show one of the most striking examples of circadian rhythms. Individuals commonly migrate to the surface at dusk and go down to deep water before dawn in order to evade predators (Zaret & Suffern, 1976; Briereley, 2014). Light is thought to be the main external stimulus that

synchronizes this behavior in zooplankton (Forward, 1976), since the migration cycles correspond to those of light and darkness (Haney, 1988; Ringelberg, 1995).

The Antarctic krill *Euphausia superba* Dana, 1850 is a euphausiid crustacean in which opsin expression related to the photosynchronization of circadian rhythms has been studied. These crustaceans are distributed along the Southern Ocean, where ecosystems exhibit extreme variations in day length, light intensity, and light spectrum (Meyer *et al.*, 2010). De Pittà *et al.* (2013) analyzed the krill's transcriptome to identify the components of its circadian system that allow its adaptation to the peculiar variations in ambient lighting encountered. Findings suggest that individuals periodically express several genes during the day. Among these, an opsin with two isoforms, dubbed EsRh1a and EsRh1b, was identified as part of the photosynchronization process of the circadian system, specifically the behavioral synchronization and several physiological processes that address severe seasonal changes such as varying availability of food (De Pittà *et al.*, 2013).

Six additional opsins were identified by Biscontin *et al.* (2016). Four were middle-wavelength sensitive (EsRh2, EsRh3, EsRh4, and EsRh5), one (EsRh6) was long-wavelength sensitive, and another, designated EsPeropsin, was a non-visual opsin part of the peropsin group. All opsins were expressed in compound eyes and cerebral ganglia, but EsRh2 and EsPeropsin were found in the abdomen as well (Biscontin *et al.*, 2016). Furthermore, EsRh3 and Peropsin genes showed daily oscillations in their expression, which could be relevant for the synchronization of the physiological, metabolic, and behavioral processes

that the Antarctic krill displays in the presence of daily radiation changes and spectral composition of light throughout the seasons (Biscontin *et al.*, 2016).

Bathypelagic shrimps of the family Oplophoridae also make diel vertical migrations of hundreds of meters. Some species that can emit bioluminescence probably use opsins to regulate it. DeLeo & Bracken-Grissom (2020) suggested that bioluminescent organs could indirectly assist in vertical migrations of hundreds of meters. The oplophorid shrimp *Systellaspis debilis* (A. Milne-Edwards, 1881) has two opsins, MWS2 and LWS2, that are expressed in the photophores throughout the body and, although the difference is not significant, it seems that the former has a higher expression during the day when the individuals are in deeper water (Grinnell *et al.*, 1988). During migrations, shrimp orient their bodies vertically as they move up or down the water column (Grinnell *et al.*, 1988), and since the photophores orient along the entire the body, dorsally, laterally, and ventrally, light sensitivity could help maintain proper orientation during long migrations.

It is noteworthy that in *S. debilis* the expression of these opsins was localized in extraocular body areas, such as in the cerebroid ganglion and abdominal segments, which points to the fact that opsin phototransduction extends to sensory processes besides vision (Grinnell *et al.*, 1988). Overall, data suggest that besides circadian rhythms, opsins can intervene both in the krill's general physiology and its synchronization of behavioral activities that depend on environmental light levels (environmental lighting). Alternatively, it is tempting to think that opsins could be involved in cell communication processes not related to sensory transduction (see below).

OPSINS IN REPRODUCTION-RELATED PROCESSES

Several studies in vertebrate physiology have revealed the rising interest in the existence of non-visual phototransduction by different opsins and how these processes take part in photosynchronization and photomodulation. Unlike the histological and functional pervasiveness that has been described for vertebrate opsins (see reviews by Peirson *et al.* (2009) and Foster *et al.* (2020)), there is a paucity of studies about the role of opsins in crustacean physiology (aside those on vision) even though data on the expression of these photopigments in several anatomical regions have been published.

For instance, even though the visual photoreceptors group within the eyes and cerebral ganglia (Meyer, 2001), these organs are also responsible for the release of hormones that regulate gonadal maturation, including gonad-inhibiting hormone, which stops vitellogenesis (Treerattrakool *et al.*, 2008, 2014; Qiao *et al.*, 2015), thus it is tempting to speculate whether opsins located in eyes and cerebral ganglia would regulate those processes through non-visual phototransduction. A study on the eastern freshwater shrimp *Macrobrachium nipponense* (De Haan, 1849), an economic-relevant species, was performed based on these precedents. These crustaceans have long-wavelength-sensitive opsin (Mn-Lw) in their eyes, ovaries, abdominal ganglia, muscles, heart, and hepatopancreas. Females exhibit short cycles in ovary maturation as well as accelerated larval and embryonic

development during the mating season. Analysis on Mn-Lw expression suggests that during this period the highest expression levels occur in both eyes and ovaries, while gonadal expression is reduced during non-mating seasons. A specific opsin expression pattern was also found during ovarian development: opsin-gene expression increased during ovarian maturation and decreased again after ovulation. Lastly, a decrease of level of vitellogenin was observed through silencing the gene expression of Mn-Lw, which suggests that Mn-Lw function keeps the level of vitellogenin high enough to sustain ovarian development. Indeed, these data are relevant in showing how the regulatory role of opsins and their function in light detection can impact the reproductive processes in crustaceans (Li *et al.*, 2018). Even though the authors did not propose a mechanism for the association between opsins and vitellogenin synthesis, the fact has a potential economic impact because males grow faster and bigger than females and hence, opsin manipulation either lighting conditions offer a chance to bypass prawn cultures to higher-or even all-male ratios.

ROLE OF OPSINS IN EGG HATCHING

Light induces egg hatching in a wide variety of branchiopod crustaceans (Takahashi, 1975, 1977; Mitchell, 1990; Horiguchi *et al.*, 2009). The Asian notostracan *Triops granarius* (Lucas, 1864) is one of the species in which opsins are known to be involved in light induced-hatching. During the summer, females lay eggs in the mud, where eggs remain dried underground for the entire season; when the paddies are drained in spring, eggs float to the surface and hatch within a few days. Hatching is inhibited under darkness and induced under light even if the eggs are not dried. Under constant darkness, when the nauplius eyes are not yet differentiated, embryonic development stops at an early stage of organogenesis, 10 to 15 days after the eggs have been laid but resume development and hatching after being exposed to light (Takahashi, 1975, 1977; Horiguchi *et al.*, 2009).

Kashiyama *et al.* (2010) examined the gene expression of opsins in the eggs of *T. granarius* and detected five genes, RhA, RhB, RhC, RhD, and RhE. RhC is considered UV-light sensitive but its spectral sensitivity in relation to the rest of the opsins has not yet been determined. Opsin transcripts were detected in a stage of embryonic development prior to the formation of the nauplius eye, so they could be part of the primordium of nauplius eyes or of other organs.

Gene expression for arrestin, which regulates phototransduction processes in vertebrates and *Drosophila* by contact inhibition with cone opsin and rhodopsin respectively has also been detected (Kashiyama *et al.*, 2010; Kefalov, 2012). Based on gene expression found for rhodopsins and arrestin in *T. granarius* eggs, it was postulated that opsins are phototransduction molecules in light-fostered hatching, and evidence was provided that suggests that this process could share metabolic pathways with those described for photoreceptors participating in the visual pathway. In this regard, it becomes important to note that there has been no research so far on the sequence of intracellular events mediated by the opsins mentioned, so the non-visual role of opsins in phototransduction mechanisms in crustaceans is a potentially rewarding field for future research.

ROLE IN BIOLUMINESCENCE

Bioluminescence is an essential process for survival in aquatic environments, especially in deep water, where sunlight has a limited reach (Herring, 1983; Widder *et al.*, 1983). The basic mechanism for bioluminescence involves an enzyme (luciferase or a photoprotein) oxidating a light-emitting molecule (luciferin). This crucial phenomenon allows many marine animals to perform behavior-related functions such as communication and predator-prey interactions (Haddock *et al.*, 2010).

Oplophorid shrimps exhibit a bioluminescent mechanism by means of a blue secretion discharged through their mouths, believed to be a defense mechanism to surprise or distract predators (Herring, 1976). Some genera present a second mechanism that employs cuticular photophores, complex light-emitting organs composed of bioluminescent cells called photocytes and structures allowing the alteration of the spectrum, distribution, direction, and intensity of emitted light (Denton *et al.*, 1972, 1985; Herring 1976; Nowel *et al.*, 1998). It has been postulated that photophores work in counterillumination, emitting radiation similar to the light that flows from the surface into the deep, thus interrupting the outline of these shrimps that would otherwise be perceptible by predators approaching from below (Nowel *et al.*, 1998).

Bracken-Grissom *et al.* (2020) confirmed that the same photophores responsible for bioluminescence in the oplophorid *Janicella spinicauda* (A. Milne-Edwards, 1883) are also photosensitive, since they present two types of opsins with sensitivity to light of medium wavelengths and one more of long wavelengths (MWS1, MWS2, and LWS2). It is possible that the sensitivity to light allows adjacent photophores to detect their own emissions, and thanks to a diversity of opsins of different spectrum sensitivities, a mechanism can be formed that discriminates between the emissions of the photophores and background light, which would give photophores a very important role in bioluminescence and counter illumination.

OPSINS IN CAVE CRUSTACEANS

Cave crustaceans exhibit several adaptations that allow them to survive in environments of scarce light or with no light at all. These traits, collectively known as troglomorphy, include, among others, lengthening of ambulatory appendages, loss of body pigmentation, and reduction or absence of eyes (Christiansen, 1962; Mejía & Hartnoll, 2006).

What happens to opsin genes in species that remain in darkness? Crandall & Hillis (1997) compared rhodopsin levels in crayfishes, three pairs of species of *Procambarus* Ortmann, 1905, *Orconectes* Cope, 1872, and *Cambarus* Erichson, 1846. Each pair included one stygobite (cave) and one close epigeal (surface) species. It was expected that a meaningful difference in nucleotide substitution between cave and surface lineages would arise through a relaxation of functional constraint on opsin genes in cave organisms. Another expectation was that amino acids would switch randomly in the protein's structure regardless of functional constraint. Nevertheless, observations showed that nucleotide substitution was almost identical between cave and surface lineages regardless of habitat, which led to the conclusion that selective pressures in surface or underground environ-

ments did not affect neither synonymous nor nonsynonymous substitutions.

Some species of cave whip spiders present different degree of eye development, from total lack of eyes, reduced eyes, and fully developed eyes, independently of morphological and genetic relationships, but related to population light exposure (Baker *et al.*, 2022). It is evident that different opsins are present along the cave crustacean evolutionary history, without losing their expression capacity (Henze & Oakley, 2015; Palecanda *et al.*, 2022). This can be a clear example of epigenetic modification, where nucleotide evolutionary changes are independent of environmental selective pressures in surface or underground waters. Nevertheless, there are several habitat and biological obstacles for eco-evolutionary research of subterranean fauna (Mammola *et al.*, 2021).

A similar study was conducted with the same three genera of crayfishes listed above (*Procambarus*, *Orconectes*, and *Cambarus*), including 14 stygobite and epigeal species having different eye morphologies and pigmentation (Stern & Crandall, 2018). Due to the lack of light, genes necessary for phototransduction and visual functions might no longer be under stabilizing pressure (Wilkins, 1982), and the rate of non-synonymous mutations should increase (Yokoyama *et al.*, 1995). But the gene repertoire between cave and surface crayfishes species was very similar, although 16 of the 17 genes analyzed in cave crayfishes showed decreased expression levels relative to epigeal crayfishes.

In another example, middle-wavelength-sensitive opsins (two paralogues) were compared in three pairs of populations of the amphipod *Gammarus minus* Say, 1818, with stygobite and epigeal individuals included in each pair. Once again there was a decrease in opsin expression for cave individuals but once more there was a lack of relaxation of functional constraint in opsin genes (Carlini, 2013). A similar result was obtained by Pérez-Moreno *et al.* (2018) with the isopod *Asellus aquaticus* (Linnaeus, 1758), a recent colonizer of cave environments, and the amphipod *Niphargus hrbei* Karaman, 1932, a recent colonizer of surface environments and belonging to an almost exclusively stygobite genus. Both species present different levels of troglomorphy, but continue to express opsins and other important elements for phototransduction such as Gq proteins, arrestin, TRP ion channels, or retinal degeneration genes. The studies mentioned so far conclude that there was no relaxation of functional constraint in the lineages of cave crustaceans, which suggests that the protein is functional. Nonetheless, without light to start the phototransduction cascade, opsins would not be able to retain their original function so there is a possibility that opsins in stygobite crustaceans could have an additional function, yet to be discovered but unrelated to light absorption.

It is likely that these genes retain their structure and continue to be expressed as they are necessary for other functions in ocular tissues unrelated to phototransduction, or their function has simply been lost but their expression remains. Whether opsins would have another detection capabilities aside phototransduction is a possibility that has been shown in another arthropod. In *Drosophila*, rhodopsin actually detects aristolochic acid, a bitter-aversive molecule, performing a sort of chemotransduction activity in the adult, aside to signaling proprioception and hearing (mechanotransduction) and temperature fluctuations during

the larval stage (Leung *et al.*, 2020 and references therein). Leung & Montell (2017) proposed the perspective that opsins are poly-modal sensory receptors and crustaceans would be a rich source for prototype cases.

CONCLUSIONS

The phototransduction through opsins is responsible for bioluminescent control and light-induced hatching in crustaceans, and even though it is feasible that this would occur in another invertebrates, the use of crustaceans as model for the description of intracellular events for these phenomena opens a noteworthy research pathway that could result in the discovery of novel intracellular messengers, effector proteins and processes for the regulation of gene expression. For instance, the phototransduction pathway recently described for melanopsin in vertebrate retinal ganglion cells contains the elements described for *Drosophila* rhodopsin mediated phototransduction (reviewed in Domínguez-Solís & Pérez-León, 2015).

It is conceivable explaining the expression of opsin genes for the extravisual role of their phototransduction in abyssal zones where most of the light comes from bioluminescence. A most intriguing point is the persistence of gene expression for opsins in crustaceans that inhabit environments practically devoid of ambient lighting, such as shrimp species in caves and perhaps opsins synthesized in those environments perform some sensory transduction not triggered by light. As described above, opsins have been reported as taking part in chemotransduction, thermo-detection, and mechanotransduction (Leung & Montell, 2017) in other arthropods. Opsin research in vertebrates has opened an equally interesting pathway because their participation in thermotaxis from sperm cells to egg cells (Roy *et al.*, 2020) and in vasodilation (Sikka *et al.*, 2014). Moreover, it is feasible that some of the opsins would interact with other molecules as much in the way receptors bind ligands. We need to keep in mind that the opsins aside being photosensitive, belong to the largest group of receptors coupled to G proteins, and they might be light-activable after been discarded from an ancient ligand. It is evident that some opsins take part in processes of sensory transduction aside phototransduction, which suggests that evolution leads organisms through diverse paths besides reaching for the light.

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