



Contents lists available at ScienceDirect

General and Comparative Endocrinology

journal homepage: www.elsevier.com/locate/ygcen

Review article

Seasonal changes in color perception

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ARTICLE INFO

Article history:

Received 30 October 2017

Accepted 26 December 2017

Available online xxxxx

ABSTRACT

In temperate zones, organisms experience dynamic fluctuations in environment including changes in color. To cope with such seasonal changes in the environment, organisms adapt their physiology and behavior. Although color perception has been believed to be fixed throughout life, there is increasing evidence for the alteration in opsin gene expression induced by environmental stimuli in a number of animals. Very recently, dynamic seasonal plasticity in color perception has been reported in the seasonally breeding medaka fish. Interestingly, seasonal changes in human color perception have also been reported. Therefore, plasticity of color perception, induced by environmental stimuli, might be a common phenomenon across various species.

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1. Introduction

Organisms living outside of tropical zones experience dynamic fluctuations in environmental parameters, such as day length, temperature, and rainfall. These changes in turn, lead to dramatic differences in local vegetation, including changes in color. To better adapt to these seasonal changes in the environment, animals change their physiology and behavior, including those involved in reproduction, migration, molting and hibernation. Recent comparative studies uncovered the signal transduction pathways that regulate seasonal reproduction in mammals, birds and fish (Ikegami and Yoshimura 2016; Ikegami et al., 2014; Nakane and Yoshimura 2014; Nakane et al., 2010, 2013, 2014; Nakao et al., 2008; Ono et al., 2008; Yoshimura et al., 2003).

Animals have evolved body coloration and ornamentation to attract mates (Gray and McKinnon 2007). Some species exhibit unique body colors specifically during the breeding season, a phenomenon known as nuptial coloration. These dynamic changes in body color and appearance emphasize the importance of vision in seasonal breeding. The vertebrate retina contains rod and cone photoreceptors involved in image-formation. Rods function at low light intensities and mediate scotopic vision, whereas cones function in daylight and mediate photopic vision, which provides

the basis for color vision (for review, see Bowmaker and Hunt 2006). Rod and cone photoreceptors contain photopigments consisting of a protein moiety (opsin) and a chromophore (retinal; a derivative of vitamin A). In early vertebrates, four successive gene duplications produced five opsin gene lineages encoding proteins involved in image formation (for review, see Trezise and Collin 2005). Four of these lineages encode photopigments for cone photoreceptors: SWS1 (ultraviolet), SWS2 (blue/violet), RH2 (green), and LWS (red). The fifth lineage encodes photopigment RH1 (rhodopsin) for rod photoreceptors. In addition to these classical image-forming visual pigments, non-image-forming visual pigments (e.g., OPN4, OPN5) participates in entrainment of the circadian clock, pupillary reflex, and seasonal reproduction (Hattar et al., 2002; Panda et al., 2002; Nakane et al., 2010).

2. Seasonal changes in human color perception

Although humans are generally considered to be non-seasonal animals, seasonal changes in color perception have been reported in humans (Jordan and Mollon 1993; Welbourne et al., 2015). Humans perceive four “unique hues”: blue, green, yellow, and red. A unique hue is defined as a color that is pure and does not contain mixtures of other colors. A recent study in humans examined seasonal changes in unique hues and demonstrated that the wavelength settings for “unique yellow” are significantly shifted to shorter wavelengths in summer than those in winter. Interestingly, a separate study revealed that patients with seasonal affective disorder (SAD; also known as winter depression) show electroretinogram (ERG) changes in winter, with lower rod and

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cone sensitivity than that in healthy subjects (Lavoie et al., 2009; Rosenthal et al., 1984). The altered retinal sensitivity in SAD patients becomes normal following light therapy or in summer. These studies further highlight the importance of the retina in seasonality, potentially even in humans. However, the molecular basis of these seasonal changes remains unknown.

3. Effects of environmental changes on opsin gene expression in various animals

Recently, changes in opsin gene expression caused by various environmental stimuli have been reported in a number of species. Exposure to UV light induces SWS1 opsin expression in newt (Martin et al., 2016). Water depth affects expression of cone opsins in salmon, damselfish, and stickleback (Cheng and Flamarique, 2004; Stieb et al., 2016; Veen et al., 2017). The spectrum and angle of environmental light influence the level of opsins in cichlid (Dalton et al., 2015). Expression of SWS2B is different between wild-caught and lab-reared cichlids (Hofmann et al., 2010). Expression of cone opsins is different between guppies reared in clear and turbid water (Ehlman et al., 2015). Photoperiod affects the expression of LWS opsin in stickleback and OPN4-related genes in zebrafish (Matos-Cruz et al., 2011; Shao et al., 2014). Plasticity in opsin expression levels due to changing environmental conditions has also been reported in *Drosophila* and butterfly (Everett et al., 2012; Vasiliauskas et al., 2011). Although these gene expression changes appear to cause alterations in the spectral sensitivity of vision, their physiological and ecological significance remain unclear.

4. Seasonal changes in phototransduction pathway in medaka eye

The seasonally breeding Japanese medaka fish (*Oryzias latipes*) is an excellent model for studying the mechanisms underlying seasonal adaptation in animals (Awaji and Hanyu 1989). When medaka fishes are transferred from short day and cool temperature (SC) or winter conditions (10 h light: 14 h darkness, 8 °C) to long

day and warm temperature (LW) or summer conditions (14 h light: 10 h darkness, 26 °C), their gonads develop significantly. The temporal pattern of gene expression in the medaka eye associated with changes in photoperiod and temperature was examined by microarrays (Shimmura et al., 2017). This analysis identified 824 summer-induced and 727 -suppressed genes. These include various opsin genes and genes involved in downstream phototransduction pathways (Fig. 1). For example, seven opsin genes (*SWS1*, *RH2-A*, *RH2-B*, *LWS*, *RH1*, *OPN4L* and *OPN5L*) were up-regulated by summer stimulus (Fig. 2). Rhodopsin and cone opsins couple with the G-protein transducin (rods: *GNAT1*, *GNB1* and *GNGT1*; cones: *GNAT2*, *GNB3* and *GNGT2*), with an observed up-regulation of these genes due to summer stimulus. Because activation of transducin by rhodopsin and cone opsins is the first amplification step in the phototransduction cascade (Fu and Yau 2007), summer-induced transducin genes appeared to increase the light sensitivity under summer conditions. Light converts 11-*cis* retinal to all-*trans* retinal. All-*trans* retinal must be converted back to 11-*cis* retinal for photoreceptors to function, and retinol dehydrogenase 8 (*RDH8*) is primarily responsible for this activity (Parker and Crouch 2010). It is reasonable to assume that the expression of *RDH8* was also induced by summer stimulus when various opsin genes were up-regulated.

5. Functional significance of seasonal visual plasticity

Medaka fishes are active and swim throughout the tank during summer, whereas during winter they are less active and restrict themselves to the bottom of the tank. Their response to light stimulus also differs according to the conditions (Shimmura et al., 2017). Both positive and negative phototaxis have been reported in fishes (Brockerhoff et al., 1995). For example, zebrafish larvae swim toward a weak light stimulus (i.e., positive phototaxis), but avoid strong light signals (i.e., negative phototaxis). When the tank was exposed to white light, summer medaka fishes exhibited negative phototaxis, while winter medaka fishes swam randomly. This suggests that medaka fishes are less sensitive to light stimulus under winter conditions, compared to summer conditions.

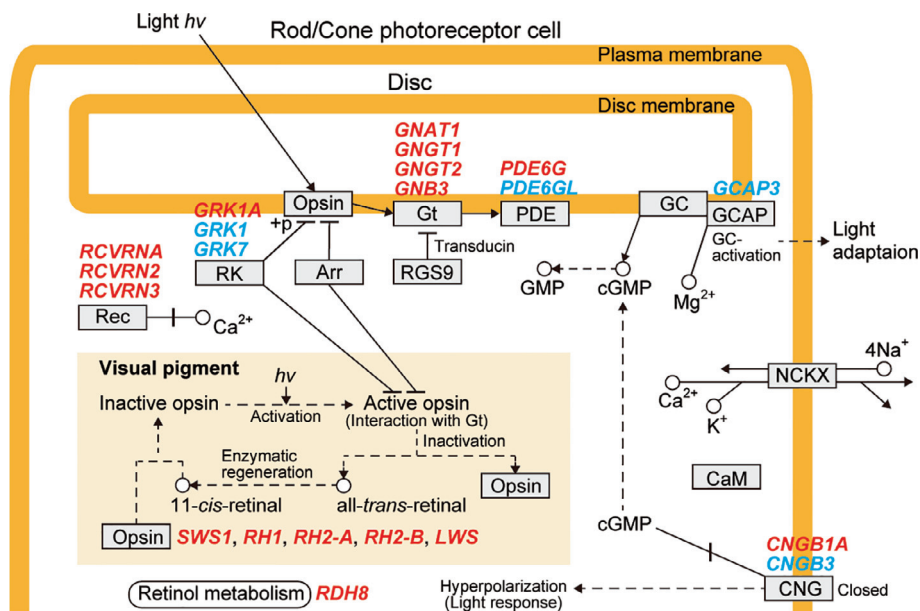


Fig. 1. Seasonal changes in the expression of genes encoding photopigments and their downstream phototransduction pathways. Gene symbols in red and blue indicate up- and down-regulated genes by summer condition, respectively. Adapted from the KEGG (Kyoto Encyclopedia of Genes and Genomes) phototransduction pathway. Modified from Shimmura et al. (2017).

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