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Review

Cone visual pigments ☆

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ABSTRACT

Cone visual pigments are visual opsins that are present in vertebrate cone photoreceptor cells and act as photoreceptor molecules responsible for photopic vision. Like the rod visual pigment rhodopsin, which is responsible for scotopic vision, cone visual pigments contain the chromophore 11-*cis*-retinal, which undergoes cis–trans isomerization resulting in the induction of conformational changes of the protein moiety to form a G protein-activating state. There are multiple types of cone visual pigments with different absorption maxima, which are the molecular basis of color discrimination in animals. Cone visual pigments form a phylogenetic sister group with non-visual opsin groups such as pinopsin, VA opsin, parapinopsin and parietopsin groups. Cone visual pigments diverged into four groups with different absorption maxima, and the rhodopsin group diverged from one of the four groups of cone visual pigments. The photochemical behavior of cone visual pigments is similar to that of pinopsin but considerably different from those of other non-visual opsins. G protein activation efficiency of cone visual pigments is also comparable to that of pinopsin but higher than that of the other non-visual opsins. Recent measurements with sufficient time-resolution demonstrated that G protein activation efficiency of cone visual pigments is lower than that of rhodopsin, which is one of the molecular bases for the lower amplification of cones compared to rods. In this review, the uniqueness of cone visual pigments is shown by comparison of their molecular properties with those of non-visual opsins and rhodopsin. This article is part of a Special Issue entitled: Retinal Proteins — You can teach an old dog new tricks.

1. Introduction

In the retinas of most vertebrates, there are two types of photoreceptor cells, rods and cones (Fig. 1). Rods are responsible for scotopic vision, the vision working under dim light conditions where cones are not functional, whereas photopic vision, the vision working under daylight conditions is mediated by cones. In agreement with this visual duplicity, rods are more sensitive than cones and can generate a response from even a single photon. Although less sensitive than rods, cones respond and regenerate more rapidly than rods and exhibit considerably greater adaptive ability than rods. Rods contain a single rod visual pigment (rhodopsin), whereas cones use several types of cone visual pigments with different absorption maxima. Integration of the photon signals from cones having cone visual pigments with different absorption maxima enables animals to discriminate the color of materials.

Investigation of visual pigments at the molecular level started in the 1950s using the bovine rhodopsin as a representative visual pigment, and several fundamental properties of rhodopsin were elucidated in the 1950s to 1960s. Physico-chemical and biochemical studies of rhodopsin have been widely performed to elucidate the detailed molecular mechanism of light absorption and G protein activation by rhodopsin since Prof. George Wald won the Nobel Prize in 1967 [1]. Investigation of the cone visual pigments also started in the 1950s, and multiple types of cones with different spectral sensitivities were identified in primates and fishes by microspectroscopy [2,3] and electrophysiology [4]. However, molecular-level investigations were hampered due to the difficulties of isolation of cone visual pigments from retinas. In the 1980s, our group began to isolate and separate chicken cone visual pigments by using more than ten thousand chicken eyes and succeeded in obtaining absorption spectra of four kinds of cone visual pigments and characterizing their bleaching processes after absorption of a photon [5–7]. We also prepared monoclonal antibodies against chicken red (iodopsin) [8] and determined the amino acid sequences of four kinds of cone visual pigments by cDNA cloning [9,10].

Textbooks at the time we started investigating cone visual pigments stated that photopic and scotopic vision were diversified before the acquisition of color vision (e.g. [11]). That is, it was inferred that rod and cone visual pigments diversified first and then multiple types of cone visual pigments with different absorption maxima were diversified. Therefore, we expected that we might discover new molecular mechanisms, which had not been obtained from the studies of rhodopsin, in a study of cone visual pigments. However, our subsequent cDNA cloning experiments and phylogenetic analysis clearly showed that ancestral vertebrate visual pigments first diverged into four kinds of cone visual pigments, and that rhodopsin diverged from one of the cone visual pigment groups later [10] (Fig. 2). Furthermore, subsequent investigations on the so-called non-visual opsins such as pinopsin [12], parapinopsin

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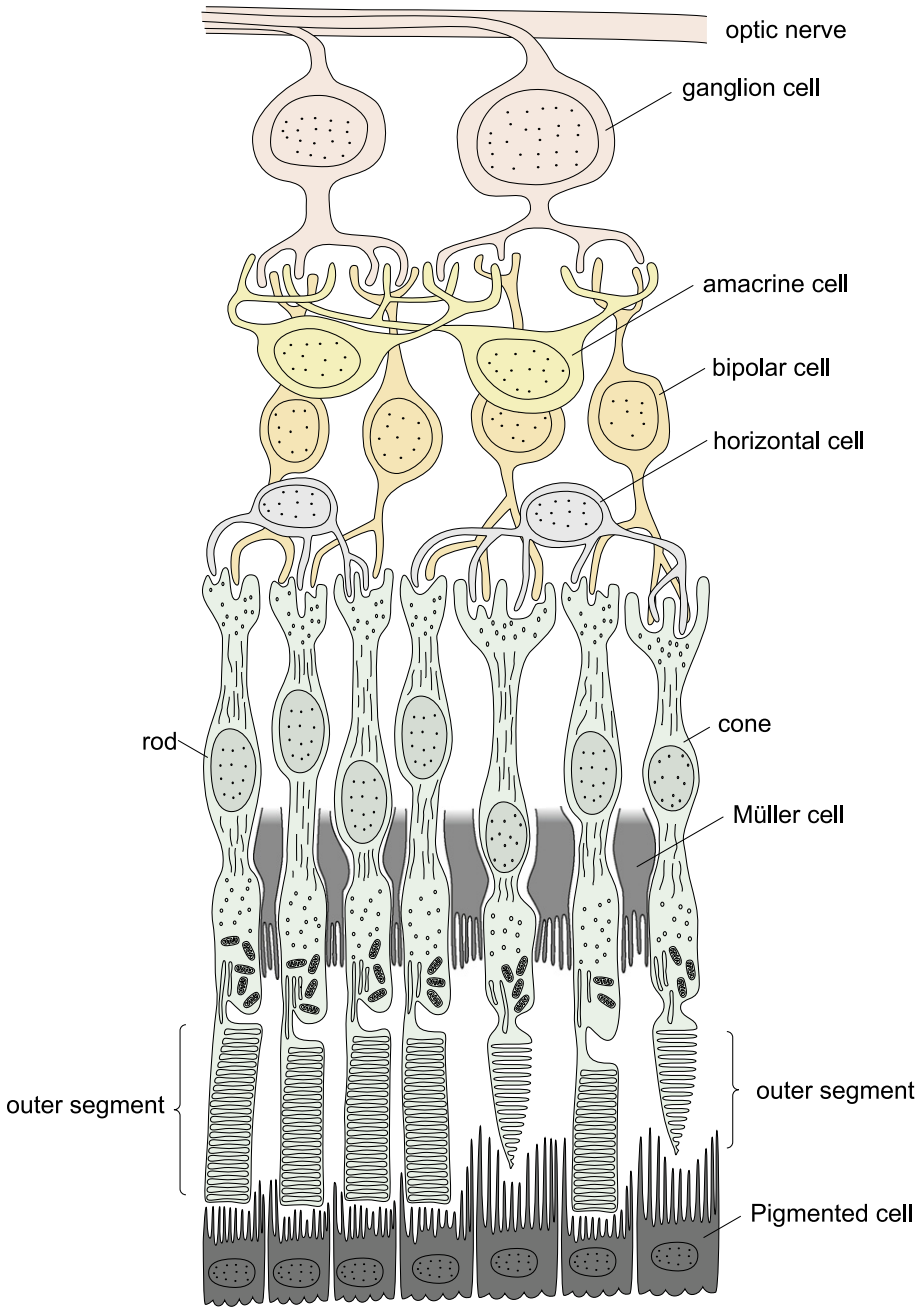

Fig. 1. Schematic drawing of vertebrate retina. In the retinas of most vertebrates, there are two types of photoreceptor cells, rods and cones.

[13], VA opsin [14] and parietopsin [15] showed that visual pigments (visual opsins) were diversified from one of the four kinds of non-visual opsins (Fig. 2). Therefore, it is important to analyze what kind of molecular properties the cone visual pigments have acquired in the course of diversification from non-visual opsins and how rhodopsin evolved from the cone visual pigments. Additionally, the diversification of multiple cone visual pigments with different absorption maxima is also an important issue to be resolved. In the present article, we summarize the molecular properties of cone visual pigments from the viewpoints described above.

2. Molecular evolution of cone visual pigments

As described above, vertebrate rod and cone visual opsins, form a phylogenetic sister group with other opsin groups such as the pinopsin, VA opsin, parapinopsin, and parietopsin groups [15]. In Fig. 2, we show these groups as having simultaneously diverged, because unambiguous determination of the phylogenetic relationship among these five groups is still difficult based on the available amino acid sequences.

In the course of our previous investigation of the functional divergence of opsins, we found that the position of the counterion was different between vertebrate visual opsins and other opsins [16,17]. Vertebrate visual opsins have a counterion at position 113, whereas many opsins have a counterion at position 181 (in the numbering system of bovine rhodopsin). We also found that the difference in the position of the counterion is correlated with the different spectroscopic and biochemical properties between these pigments. The opsins having the counterion at position 181 exhibit molecular properties of so-called "bistable" pigments in which the resting (dark) state and active state are stable at physiological temperature and are able to revert to each other