



Review

Rod and cone photoreceptors: Molecular basis of the difference in their physiology

Satoru Kawamura*, Shuji Tachibanaki

Graduate School of Frontier Biosciences and Department of Biology, Graduate School of Science, Osaka University, Yamada-Oka 1-3, Suita, Osaka 565-0871, Japan

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ABSTRACT

Vertebrate retinal photoreceptors consist of two types of cells, the rods and cones. Rods are highly light-sensitive but their flash response time course is slow, so that they can detect a single photon in the dark but are not good at detecting an object moving quickly. Cones are less light-sensitive and their flash response time course is fast, so that cones mediate daylight vision and are more suitable to detect a moving object than rods. The phototransduction mechanism was virtually known by the mid 80s, and detailed mechanisms of the generation of a light response are now understood in a highly quantitative manner at the molecular level. However, most of these studies were performed in rods, but not in cones. Therefore, the mechanisms of low light-sensitivity or fast flash response time course in cones have not been known. The major reason for this slow progress in the study of cone phototransduction was due to the inability of getting a large quantity of purified cones to study them biochemically. We succeeded in its purification using carp retina, and have shown that each step responsible for generation of a light response is less effective in cones and that the reactions responsible for termination of a light response are faster in cones. Based on these findings, we speculated a possible mechanism of evolution of rods that diverged from cones.

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1. Introduction

In the vertebrate retina, there are two types of photoreceptors, the rods and cones (Fig. 1A). The rods and cones consist of two parts, outer

segment and inner segment. The outer segment is the specialized site to detect a photon signal, and the inner segment contains the nucleus and other cellular organelles necessary for cell metabolism. Rods and cones are distinctive in their morphology of the outer segment. In rods, stacks of disk membranes are surrounded by a plasma membrane, and in cones, the plasma membrane invaginates repeatedly to form a tightly stacked lamellae structure. Rods and cones are also different in their characteristics in responding to light: the

* Corresponding author. Tel.: +81 6 6879 4610; fax: +81 6 6879 4614.

E-mail address: kawamura@fbs.osaka-u.ac.jp (S. Kawamura).

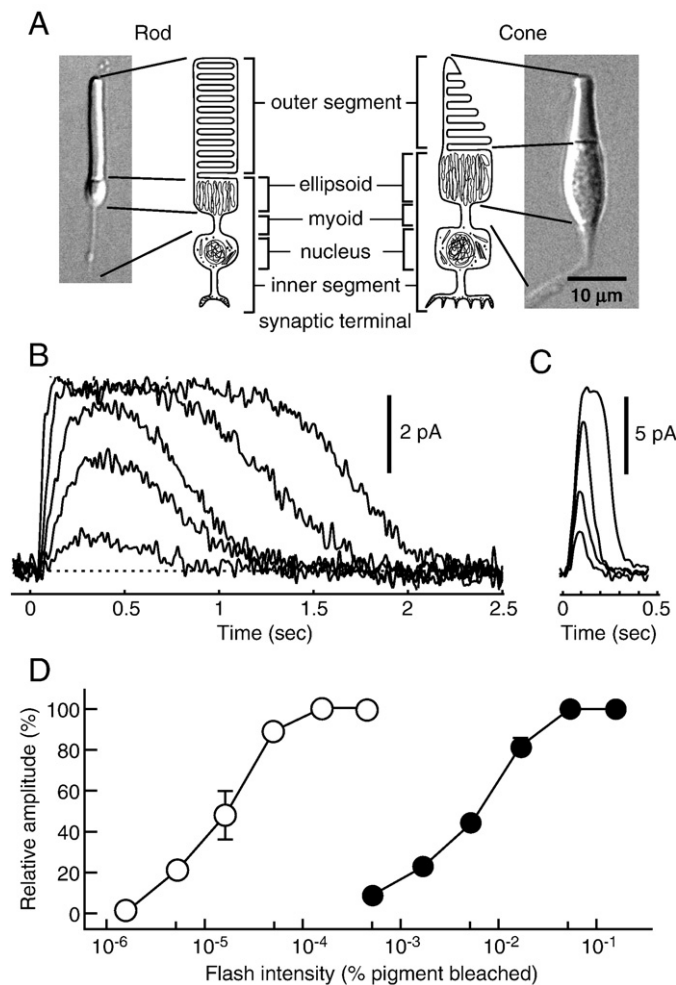


Fig. 1. Characteristics of carp rods and cones. (A) A mechanically dissociated carp rod (left) and a red-sensitive cone (right). Both consist of two parts, outer segment and inner segment. (B) A flash response family of a rod. Outer segment membrane current was recorded with a suction electrode by giving light flashes of various intensities at time 0 and they are superimposed. The light intensities used and expressed in the unit of % bleach were (from the dimmest intensity): $5.1 \times 10^{-6}\%$ (corresponding to 8 molecules of visual pigment bleached per rod; 8 R*), $1.6 \times 10^{-5}\%$ (25 R*), $5.1 \times 10^{-5}\%$ (80 R*), $1.6 \times 10^{-4}\%$ (250 R*) and $5.1 \times 10^{-4}\%$ (800 R*). (C) A flash response family of a red-sensitive cone. The light intensities used and expressed in the unit of % bleach were (from the dimmest intensity): $1.6 \times 10^{-3}\%$ (2100 R*), $5.2 \times 10^{-3}\%$ (6600 R*), $1.6 \times 10^{-2}\%$ (21,000 R*) and 0.16% (210,000 R*). (D) Light intensity–response relations of a rod (left) and a red-sensitive cone (right) shown in (B) and (C), respectively. In (B) and (C), the responses were low-pass filtered at 50 Hz.

waveform of a flash light response is different (Fig. 1B and C), and the light-sensitivity is different (Fig. 1D). (These flash responses were newly recorded to compare the electrophysiological study and the biochemical study in this review.) These differences of responses in rods and cones determine the characteristics of our vision, because basic characteristics of our vision are determined by these initial light detectors. Rods are very sensitive to light (Fig. 1D), and respond to a single photon. Because of this high light-sensitivity, rods mediate twilight vision. The time course of a rod flash light response is slow (Fig. 1B). Notably, the recovery of a response delays significantly after termination of a light stimulus, and because of this characteristic, in the twilight, it is not easy to detect an object moving quickly. Cones are less sensitive to light (Fig. 1D) and mediate daylight vision. Cones respond to on and off of a light stimulus without significant delays (Fig. 1C). For this reason, we can follow an object moving quickly with our eyes during daylight.

The differences in the light response characteristics between rods and cones have been known for many years. The first intracellular

recordings of vertebrate light responses were made in early 60s (Tomita, 1970). The finding that vertebrate photoreceptors hyperpolarize on light stimulation was a great surprise to neurobiologists because it was an exceptional case that a neuron shows a hyperpolarization, not a depolarization, on stimulation. The molecular mechanism of light detection in rods, the rod phototransduction mechanism, has been studied extensively from around early 70s, and it was well understood by the mid 80s (Burns and Arshavsky, 2005; Lamb and Pugh, 2006; Fu and Yau, 2007). The key players in rod phototransduction were known, and measurements of efficiencies of the reactions in the phototransduction cascade (see below) were made, so that the very high sensitivity of a rod is now understood quantitatively at a molecular level. However, the phototransduction mechanism in cones has not been studied in detail (Tachibanaki et al., 2007). This is because studies of the phototransduction mechanism were possible in rods but not in cones. Rods can be obtained from the retina of animals such as bovine or frog in a quantity large enough to study them biochemically, but cones are not easy to purify in such a quantity. We fortunately developed a method to purify cones using the carp retina and have been studying the phototransduction mechanisms in cones in a quantitative way to understand the underlying differences between rod phototransduction and cone phototransduction (Tachibanaki et al., 2001; 2005). We recently wrote a short review and summarized our recent studies (Tachibanaki et al., 2007). Here in this present review, in addition to summarize our recent progress of the study in cone phototransduction, we will compare biochemical and electrophysiological measurements both made in our laboratory using rods and cones purified from the same animal species (carp). Furthermore, based on this comparison, we will provide an evolutionary view of the divergence of rods that are known to be evolved from cones.

2. Molecular basis underlying the light response in rods

The molecular mechanism of the generation and the recovery of a light response are well understood in rods. In this chapter, this mechanism is briefly overviewed, and for details, see other reviews published recently (Burns and Arshavsky, 2005; Lamb and Pugh, 2006; Fu and Yau, 2007).

2.1. Phototransduction in rods: a general overview

In rods, a photon is absorbed by the visual pigment, rhodopsin. Rhodopsin is composed of a chromophore, 11-*cis* retinal and a protein moiety, opsin. The chromophore is covalently linked to the ϵ -amino group of the lysine residue of opsin, and is embedded in the protein moiety (Palczewski et al., 2000). A photon isomerizes 11-*cis* retinal to all-*trans* retinal, which eventually induces a conformational change in the protein moiety. Rhodopsin absorbs green light most effectively, and for this, rhodopsin looks red when it is observed in the dark-adapted state. After the conformation of rhodopsin changes, rhodopsin does not absorb light at the visible region of the spectrum and bleaches. There are several bleaching intermediates in this process (Shichida and Imai, 1998), and one of them, metarhodopsin II, is believed to be the effective intermediate that triggers the subsequent phototransduction cascade to generate a hyperpolarizing light response (Fig. 2).

Metarhodopsin II, designated as R* hereafter, catalytically activates a GTP-binding protein, transducin, by replacing bound GDP with cytosolic GTP (Fung and Stryer, 1980). Activated transducin activates an enzyme, cGMP phosphodiesterase (PDE) that hydrolyzes cGMP. The visual pigment, transducin and PDE are all localized on the disk membrane. One molecule of R* activates >50 molecules of transducin per second (Leskov et al., 2000), and one molecule of activated transducin activates one molecule of PDE that hydrolyzes >1000 molecules of cGMP per second (Yee and Liebman, 1978). As a

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